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The Food of the New Zealand Common River Galaxias, *Galaxias vulgaris* Stokell (Pisces: Salmoniformes)

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Abstract

The food of the common river galaxias, *Galaxias vulgaris* Stokell, inhabiting the Glentui River, Canterbury, New Zealand, was studied between June 1970 and November 1971. Basic food consisted of Ephemeroptera: particularly the larvae of *Deleatidium* spp., *Coloburiscus humeralis* and *Nesameletus ornatus*. Secondary food consisted of Elmidae (Coleoptera), terrestrial arthropods, and the larvae of Rhyacophilidae, *Hydropsyche colonica, Olinga feredayi, Pycnocentrodes aureola* (Trichoptera), *Archichauliodes diversus* (Megaloptera), Chironomidae and Simuliidae (Diptera). Other food items were considered to be incidental. Diet varied seasonally and with size of fish. Large fish tended to eat larger food items than small fish, and there was also an increase in variety of food items with increase in fish size. Recently hatched fish fed predominantly on dipteran larvae, changing to a mainly ephemeropteran diet on moving to the adult habitat. Diet did not change significantly with age in fish sampled in the same type of habitat. Male and female diets were very similar.

Introduction

Little attention has been given to the feeding habits of the New Zealand Galaxiidae, with the exceptions of *Galaxias divergens* Stokell, *Neochanna burrowsius* (Phillipps) and the commercially important *Galaxias maculatus* (Jenyns), whose diets have been examined by Hopkins (1971), Cadwallader (1975*a*), and McDowall (1968), respectively. In addition, work on introduced salmonids has sometimes (Percival 1932; Allen 1951; Lane 1964) included information on the diet of cohabiting galaxiids. This paper presents information on the diet of the common river galaxias, *Galaxias vulgaris* Stokell, a fish which is restricted to the South Island of New Zealand and is found in most of the major river basins to the east of the Alps and in the Upper Buller River System to the west of the Alps (McDowall 1970). Stockell (1955) stated that the food of adult *G. vulgaris* consisted of 'midge larvae, mayfly larvae and caddis larvae', and Benzie (1968) suggested that *G. vulgaris* fed on 'debris and insects washed down stream'.

The Study Area

The investigation was carried out in the Glentui River, Canterbury, New Zealand. The Glentui arises at an altitude of approximately 840 m and flows into the Ashley River at a point (latitude 43°14′S., longitude 172°18′E.) 180 m above sea level. It originates in a forest of mountain beech, *Nothofagus solandri* (Hooker), and in its lower reaches flows through cultivated farmland. The sampling area consisted mainly of riffles interspersed with quiet stretches. At the time of the study, water depth varied from 20 to 30 mm in riffles to 700 m in pools formed behind obstacles such as fallen trees. The width of the river varied from 1 to 9 m, and its bed was composed of fine gravel in quiet stretches with large boulders, up to 700 mm in diameter, occurring in riffles. Fine mud was present in quiet backwaters and deep pools. Apart from isolated stands of *Myriophyllum* sp. in the quieter backwaters, the only plant cover in the river was that provided by fallen trees and other debris of terrestrial origin carried down by floods. Diatoms, notably *Gomphonema* sp., were present on most of the boulders on the river bed.

Table 1. Insects found in the Glentui River—classification according to Wise (1973)

Order	Family	Species
Ephemeroptera	Siphlonuridae	*Coloburiscus humeralis* (Walker)
		Oniscigaster wakefieldi McLachlan
		Ameletopsis perscitus (Eaton)
		Nesameletus ornatus (Eaton)
	Leptophlebiidae	*Deleatidium* spp.
		Zephlebia scita (Walker)
Plecoptera	Eustheniidae	*Stenoperla prasina* (Newman)
	Gripopterygidae	*Aucklandobius trivacuatus* (Tillyard)
		Zelandoperla decorata Tillyard
Megaloptera	Corydalidae	*Archichauliodes diversus* (Walker)
Trichoptera	Hydropsychidae	*Hydropsyche colonica* McLachlan
	Polycentropodidae	*Polyplectropus puerilis* (McLachlan)
	Philopotamidae	*Dolophilodes stenocerca* (Tillyard)
	Rhyacophilidae	*Hydrobiosis parumbripennis* McFarlane
		Psilochorema leptoharpax McFarlane
		Neurochorema confusum (McLachlan)
	Hydroptilidae	*Oxyethira* sp.
	Sericostomatidae	*Pycnocentria evecta* McLachlan
		Beraeoptera roria Mosely
		Pycnocentrodes aureola (McLachlan)
		Olinga feredayi (McLachlan)
	Helicopsychidae	*Helicopsyche* sp.
	Leptoceridae	*Triplectides obsoleta* (McLachlan)
		Hudsonema amabilis (McLachlan)
Coleoptera	Elmidae	sp.
	Helodidae	sp.
Diptera	Tipulidae	sp.
	Chironomidae	*Anatopynia* sp.
		Maoridiamesa harrisi Pagast
		Tanytarsini sp.
		Orthocladiinae sp.
	Simuliidae	*Austrosimulium multicorne* Tonnoir
		Austrosimulium ungulatum Tonnoir
	Culicidae	Dixini sp.
	Tabanidae	sp.
Hemiptera	Veliidae	*Microvelia* sp.
	Notonectidae	*Anisops* sp.

The invertebrate fauna was dominated by larval insects (Table 1). Other invertebrates found were *Gordius* sp. (Nematomorpha) and the gastropod *Potamopyrgus antipodarum* (Gray). Terrestrial arthropods together with plant debris were frequently found in the drift, and terrestrial lumbricids (Oligochaeta) were sometimes found in shallow quiet water at the river margins.

Galaxias vulgaris and the upland bully, *Gobiomorphus breviceps* (Stokell), were the most abundant fish in the river. Other fish found in the sampling area were the long-finned eel *Anguilla dieffenbachii* Gray, the short-finned eel *Anguilla australis schmidtii* Phillipps, and the brown trout *Salmo trutta* L.

After the breeding season (August and September), recently hatched *G. vulgaris* occurred in quiet backwaters and deep pools, moving into riffles, the normal adult habitat, when they were 3–4 months old.

Table 2. Maximum points allotted to *Galaxias vulgaris* stomachs of different degrees of fullness

Total length of fish (mm)	Stomach condition Half full	Full	Distended
30–60	4	8	16
61–90	6	12	24
>90	8	16	32

Materials and Methods

General Methods

Analysis of food habits of *G. vulgaris* was based on an examination of the stomach contents of 761 fish sampled at monthly intervals from June 1970 to May 1971, and a further sample of 163 fish taken in November 1971.

Recently hatched fish were taken with dip nets, but all other samples were obtained using portable electric fishing gear (Cadwallader 1975*d*). After capture, fish were anaesthetized in benzocaine and preserved in 10% formalin. Total length (TL), i.e. length from the tip of the snout to the distal end of the central rays of the emarginate caudal fin, was read to 0·1 mm using a measuring board fitted with a vernier scale (Woods 1968). Correction factors for the effect of formalin preservation on the length of *G. vulgaris* were obtained from Cadwallader (1974). Fish were sexed by examining gonads, and aged from length frequency analysis and sagittal otoliths (Cadwallader 1975*d*). Most *G. vulgaris* belonged to the age groups 0+, 1+ and 2+, a few were aged 3+ and 4+, none were aged 5+ and one was aged 6+.

The contents of each individual stomach were examined in water in a petri dish under a low-power (×6·3 to ×40) binocular microscope.

Enumeration of Stomach Contents

Both the occurrence and points methods were used to assess the composition of the stomach contents. In the occurrence method, the number of stomachs in which each food type occurred was recorded and expressed as a percentage of the total number of stomachs examined in each sample. In the points method, each food type was allotted points according to its estimated relative volume. The points allotted to each food type were summed and expressed as a percentage of the total number of points allotted to all food types in all stomachs in the sample. The allocation of points was based on a standard allocation drawn up for stomachs of fish in different length groups (Table 2). The degree of stomach fullness was estimated visually using the criteria proposed by Ball (1961).

As pointed out by Hynes (1950) and Windell (1968), the occurrence method provides no information on the quantity of each food type consumed, and does not take into account the accumulation of parts of organisms resistant to digestion. In the points method, which is essentially an approximate volumetric method, the subjective allocation of points by the investigator is the major limitation. The results obtained by the occurrence and points methods were compared by computing the product-moment correlation coefficient (Sokal and Rohlf 1969) between the percentage points

Table 3. Product-moment correlation coefficients (*r*) between the percentage points and the percentage occurrence of the same eight food types (*Archichauliodes diversus* larvae, *Coloburiscus humeralis* larvae, *Nesameletus ornatus* larvae, *Deleatidium* spp. larvae, *Hydropsyche colonica* larvae, Rhyacophilidae larvae, *Pycnocentrodes aureola* larvae, dipteran larvae, pupae and adults) in different-sized samples of *Galaxias vulgaris* stomachs

n, sample size; *A*, age group samples; *L*, total length (mm) samples; *M*, monthly samples; +, all stomachs sampled in riffles between June 1970 and May 1971

Sample	Type	n	r	95% confidence limits Lower	Upper
annual	+	701	0·9243	0·6297	0·9865
0+	A	307	0·9395	0·6946	0·9893
50–59	L	213	0·9628	0·8025	0·9935
1+	A	177	0·9692	0·8342	0·9946
80–89	L	154	0·9543	0·7577	0·9918
60–69	L	147	0·9339	0·6704	0·9882
July	M	139	0·9906	0·9488	0·9984
70–79	L	120	0·9618	0·7978	0·9933
April	M	111	0·8127	0·2526	0·9648
2+	A	109	0·8611	0·3976	0·9745
90–99	L	89	0·9670	0·8232	0·9942
May 1–2	M	69	0·8467	0·5905	0·9479
March	M	64	0·9560	0·7702	0·9922
100–109	L	59	0·9134	0·5855	0·9844
November	M	51	0·9152	0·5927	0·9848
3+	A	45	0·8871	0·4865	0·9795
August	M	44	0·7385	0·0702	0·9492
June	M	30	0·9778	0·8780	0·9661
May 29–30	M	25	0·7414	0·0766	0·9498
October	M	24	0·9843	0·9126	0·9973
>110	L	14	0·8536	0·3737	0·9730

and the percentage occurrence of the same eight food types in different-sized samples of *G. vulgaris* stomachs (Table 3). The high correlation coefficients indicate that the two methods give similar results, with similarity increasing with increasing sample size. Therefore, for large samples ($n > 120$), both methods of assessment were considered to be of equal merit in indicating the relative importance of various food types in the diet, but for small samples ($n < 120$) more reliance was placed on the points method, since it was considered to provide a better indication of the relative importance of the various food types. However, in a number of instances, small food items, such as the early instars of Diptera, were recorded by the occurrence method, but did not merit the allocation of a point and so were not recorded by the points method. Also, because of the small size of the stomachs, the occurrence method only was used to assess the diet of fish less than 30 mm in length.

Analysis of Data

Analysis was facilitated by coding the contents of each stomach onto individual computer cards and using an IBM 360/44 computer to sort the data.

The degree of similarity between pairs of samples was measured using the non-parametric Kendall rank correlation coefficient, τ, which was computed by using the formula given by Siegel (1956):

$$\tau = \frac{S}{\frac{1}{2}N(N-1)}, \tag{1}$$

where S is the observed sum of the $+1$ and -1 scores allocated by inspection of the relative position of each food type in both ranks (see Siegel 1956), and N is the number of food types in a rank. For tied observations the formula is modified to:

$$\tau = \frac{S}{\sqrt{\{\frac{1}{2}N(N-1)-T_a\}}\sqrt{\{\frac{1}{2}N(N-1)-T_b\}}}, \tag{2}$$

where $T_a = \frac{1}{2}\Sigma\, t(t-1)$, where t is the number of tied observations in each group of ties in rank A, and $T_b = \frac{1}{2}\Sigma\, t(t-1)$, where t is the number of tied observations in each group of ties in rank B. To standardize all comparisons, the same 15 food categories were used in all computations of the coefficient. The choice of categories was based on the 15 most common food types (determined by both the points and occurrence methods) found in the stomachs of all fish species in the river. The categories chosen were:

1. *Deleatidium* spp. larvae
2. *Nesameletus ornatus* larvae
3. *Coloburiscus humeralis* larvae
4. *Archichauliodes diversus* larvae
5. Plecoptera larvae
6. Rhyacophilidae larvae
7. *Hydropsyche colonica* larvae
8. *Olinga feredayi* larvae
9. *Pycnocentrodes aureola* larvae
10. Other cased Trichoptera larvae
11. Diptera larvae, pupae and adults
12. Coleoptera larvae, pupae and adults
13. *Potamopyrgus antipodarum*
14. Terrestrial Arthropoda
15. Vertebrata

The significance of τ for sample sizes greater than 10 was tested by using a normal approximation to test the null hypothesis that the true value of $\tau = 0$, using the formula given by Siegel (1956):

$$z = \frac{\tau}{\{2(2N+5)/9N(N-1)\}}. \tag{3}$$

The significance of z was determined by reference to a table of areas of the normal curve. Probability values greater than 0·05 were considered to indicate dissimilar diets, whereas lower probabilities were considered to indicate similarity. From 0·05 to 0·01 the diets were considered to be similar, and for probabilities less than 0·01, the diets were considered to be very similar.

One of the difficulties in interpreting data from stomach analyses is that variation is often greater between individuals from one sample than between the mean values of two samples, so, as suggested by Mann and Orr (1969), little importance was attached to small differences between samples, particularly if the samples were small and the within-sample variation large.

Table 4. Monthly and overall annual diets of *Galaxias vulgaris* taken in riffles from June 1970 to May 1971, assessed by the points method

Figures in body of table denote the percentage points allotted to each food item in each sample. Dash (—) indicates that the item was eaten, but did not merit the allocation of a point. All insects are larvae unless otherwise indicated. M^1 = 1, 2 May; M^2 = 29, 30 May

				1970						1971				
Month;	J	J	A	S	O	N	D	J	F	M	A	M^1	M^2	Annual
Sample size;	30	139	44	39	24	51	31	24	50	64	111	69	25	701
Allotted points;	204	691	88	61	104	282	98	121	73	248	134	131	54	2279
Archichauliodes diversus	1·5	1·9	2·3	19·7	2·9	22·3	5·1	5·8	8·2	2·8	—	2·3	1·9	5·4
Stenoperla prasina								2·5	1·4	0·4				0·2
Aucklandobius trivacuatus	1·0													<0·1
Zelandoperla decorata		0·4												0·1
Plecoptera adults						0·7								<0·1
Coloburiscus humeralis	1·0	6·5	6·8	19·7	4·8	12·4	3·1	37·2	6·8	2·8	4·5	5·3	13·0	8·1
Nesameletus ornatus	19·1	9·6	25·0	16·4	4·8	3·5				1·6	6·7	21·4	48·1	9·6
Deleatidium spp.	50·5	59·2	51·1	31·1	81·7	40·8	51·0	29·8	37·0	64·1	61·2	30·5	24·1	51·9
Oniscigaster wakefieldi	4·9													4·4
Zephlebia scita		0·3						—						<0·1
Ephemeroptera adults						0·4	—	1·7	1·4	1·6	1·5			4·4
Hydropsyche colonica	4·4	5·6	2·3		1·9	0·7	2·0	0·8		—	0·7	1·5	5·6	2·8
Polycentropodidae larvae			—			—		—	—		—	—		—
Rhyacophilidae larvae	1·0	1·6	1·1	6·6	2·9	0·7	7·1	3·3	—	4·4	6·7	25·2	5·6	4·0
Olinga feredayi		1·4	2·3			—	3·1	1·7	1·4	2·0	1·5	—		1·1
Helicopsyche sp.								—						—
Pycnocentrodes aureola	0·5	2·2	1·1	1·6	1·0	2·1	7·1	5·0	32·9	10·9	1·5	0·8	—	4·0
Pycnocentria evecta	0·5	—		—			—	0·8	—	—	—			<0·1
Hudsonema amabilis						0·4								<0·1
Beraeoptera roria		0·3		1·6		0·4			2·7	0·4		0·8		<0·1
Triplectides obsoleta		0·4												0·1
Trichoptera adults		0·1				0·4								<0·1
Tipulidae pupae			—						—		—	—		—
Tipulidae adults		0·1							—					<0·1
Chironomidae larvae	—	0·7	6·8	1·6	—	—	—	—	—	—	5·2	3·8	—	1·1
Chironomidae pupae									—[A]					—
Simuliidae larvae			—			—	1·0[B]	—	—	2·8	2·2	3·1	—	0·6
Dixidae larvae								—	2·7	—	—			<0·1
Helodidae larvae		0·1												<0·1
Elmidae larvae							19·4			5·2	0·7	1·5		1·5
Elmidae adults						2·8	—	3·3	1·4	—				0·6
Gordius sp.		0·3												<0·1
Oligochaeta	15·2	2·0												2·0
Terrestrial Arthropoda		6·7				11·0	1·0	8·3	2·7	0·8	6·7	3·8		4·2
Pisces			1·1[C]	—[C]		0·7								<0·1
Plant material		0·4		1·6		0·7			1·4		0·7		1·9	0·4

[A] Includes one chironomid adult. [B] Includes one simuliid adult. [C] Fish eggs.

Results

Overall Diet

The food of *G. vulgaris* sampled in riffles at monthly intervals from June 1970 to May 1971, together with the total diet for that period, is shown in Table 4 (points method) and Table 5 (occurrence method).

Ephemeropteran larvae, particularly *Deleatidium* spp. and to a lesser extent *Coloburiscus humeralis* and *Nesameletus ornatus*, were the most important food types in the diet. Both free-living and cased trichopteran larvae occurred frequently. Larval

Table 5. Monthly and overall annual diets of *Galaxias vulgaris* taken in riffles from June 1970 to May 1971, assessed by the occurrence method

Figures in body of table denote the percentage occurrence of each food item in each sample. All insects are larvae unless otherwise indicated. M^1 = 1, 2 May; M^2 = 29, 30 May

				1970						1971				
Month;	J	J	A	S	O	N	D	J	F	M	A	M^1	M^2	Annual
Sample size;	30	139	44	39	24	51	31	24	50	64	111	69	25	701
Archichauliodes diversus	6·7	5·8	2·3	10·3	4·2	23·5	9·7	20·8	4·0	3·1	0·9	2·9	4·0	6·3
Stenoperla prasina								4·2	2·0	1·6				0·4
Aucklandobius trivacuatus	3·3													0·1
Zelandoperla decorata		0·7												0·1
Plecoptera adults						2·0								0·1
Coloburiscus humeralis	3·3	12·9	9·1	10·3	8·3	15·7	3·2	33·3	8·0	9·4	3·6	7·2	8·0	9·6
Nesameletus ornatus	43·3	18·0	20·5	10·3	16·7	11·8				6·3	3·6	26·1	32·0	13·6
Deleatidium spp.	73·3	67·6	52·3	43·6	91·7	74·5	74·2	70·8	48·0	73·4	42·3	49·3	36·0	59·9
Oniscigaster wakefieldi	3·3													0·1
Zephlebia scita		1·4						4·2						0·4
Ephemeroptera adults						2·0	3·2	12·5	4·0	7·8	1·8			2·0
Hydropsyche colonica	10·0	16·5	4·5		4·2	2·0	3·2	8·3		1·6	2·7	1·4	8·0	5·7
Polycentropodidae larvae			2·3			2·0		4·2	2·0		1·8	2·9		1·1
Rhyacophilidae larvae	13·3	13·7	9·1	10·3	8·3	11·8	22·6	25·0	2·0	15·6	9·9	29·0	16·0	14·0
Olinga feredayi		5·8	2·3			2·0	9·7	8·3	4·0	10·9	1·8	1·4		3·9
Helicopsyche sp.								4·2						0·1
Pycnocentrodes aureola	3·3	8·6	9·1	10·3	8·3	21·6	25·8	20·8	14·0	17·2	2·7	7·2	8·0	10·7
Pycnocentria evecta	3·3	2·2		5·1			3·2	4·2	4·0	1·6	0·9			1·7
Hudsonema amabilis						2·0								0·1
Beraeoptera roria		1·4		2·6		2·0			4·0	1·6		1·4		1·1
Triplectides obsoleta		0·7												0·1
Trichoptera adults		0·7				2·0								0·3
Tipulidae pupae			2·3						2·0		1·8	1·4		0·7
Tipulidae adults		0·7							2·0					0·3
Chironomidae larvae	3·3	10·1	38·6	12·8	16·7	5·9	3·2	16·7	12·0	6·3	21·6	33·3	12·0	15·5
Chironomidae pupae									6·0[A]					0·4
Simuliidae larvae			4·5			2·0	12·9[B]	8·3	2·0	17·2	7·2	15·9	8·0	5·9
Dixidae larvae								4·2	6·0	1·6	1·8			1·0
Helodidae larvae		0·7												0·1
Elmidae larvae							51·6			9·4	1·8	4·3		3·9
Elmidae adults						21·6	3·2	33·3	14·0	1·6				4·0
Gordius sp.		0·7												0·1
Oligochaeta	3·3	2·9												0·7
Terrestrial Arthropoda		5·0				9·8	3·2	29·2	10·0	3·1	4·5	4·3		5·0
Pisces			2·3[C]	2·6[C]		2·0								0·4
Plant material		1·4		2·6		3·9			2·0		0·9		4·0	1·1

[A] Includes one chironomid adult. [B] Includes one simuliid adult. [C] Fish eggs.

Rhyacophilidae were the most common free-living caddises, although *Hydropsyche colonica* was also taken regularly. Larvae of *Pycnocentrodes aureola* and *Olinga feredayi* were the most common cased larvae, all other cased caddises occurring infrequently. Larvae of the megalopteran *Archichauliodes diversus* occurred regularly, while plecopteran larvae were found rarely.

Dipteran larvae, notably Chironomidae and Simuliidae, occurred quite regularly and were often present in large numbers. However, because of their small size they accounted for less than 2% of the diet, on a points basis. Chironomid larvae eaten included *Maoridiamesa harrisi* and species of Orthocladiinae, Tanytarsini and *Anatopynia*, while the simuliid larvae eaten included *Austrosimulium multicorne* and *Austrosimulium ungulatum*.

Coleopterans in the diet consisted almost entirely of adult and larval elmids, which occurred in approximately equal numbers and contributed substantially to the diet, particularly in summer.

Fish were also represented in the diet, the remains of one *Gobiomorphus breviceps* being taken from a stomach in November. Eggs of *Galaxias vulgaris* were found in two stomachs; five eggs in the stomach of a male in August, and one egg in the stomach of another male in September. The small number of eggs present in each stomach suggests that they were eggs which had been displaced from a nest, since larger numbers would have been expected if the fish had been feeding on an egg mass.

Table 6. Kendall rank correlation coefficients for comparisons of the diet of *Galaxias vulgaris* in winter (samples size, n = 210), spring (n = 113), summer (n = 104) and autumn (n = 239)

Figures in parentheses are values of z for testing the significance of τ. The top right portion of the table contains the results of comparisons based on the occurrence method; the bottom left portion of the table contains the results of comparisons based on the points method

	Winter	Spring	Summer	Autumn
Winter	—	0·5196 (2·7001)**	0·3862 (2·0068)*	0·6699 (3·4809)***
Spring	0·5686 (2·9547)**	—	0·5174 (2·6886)**	0·6108 (3·1740)**
Summer	0·3565 (1·8522)	0·4357 (2·2638)**	—	0·6931 (3·6015)***
Autumn	0·5686 (2·9547)**	0·4902 (2·5471)*	0·4951 (2·5725)*	—

* $0{\cdot}05 \leqslant P \leqslant 0{\cdot}01$. ** $0{\cdot}01 \leqslant P \leqslant 0{\cdot}001$. *** $P < 0{\cdot}001$.

Food of terrestrial origin included lumbricids, which were found in five stomachs, and a wide variety of arthropods, including adult Hymenoptera, Coleoptera, Lepidoptera, Orthoptera and Diptera, which were taken mainly in summer and formed a substantial part of the diet. Plant material was found in only eight stomachs and consisted of seed cases, leaves and small pieces of twig and bark, all of terrestrial origin. On a points basis, material of terrestrial origin made up 6·6% of the total diet, and a further 4·5% was provided by adult Trichoptera, Ephemeroptera and Plecoptera, all of which have aquatic larvae.

Seasonal Variation in Diet and Feeding Intensity

To investigate seasonal differences in diet, the monthly samples were divided into four groups representing winter (June, July, August), spring (September, October, November), summer (December, January, February) and autumn (March, April, May). Kendall rank correlation coefficients between pairs of these samples (Table 6) indicate that the degree of similarity in the diets is greatest between adjacent seasons. The greatest difference is that between summer and winter. This was caused mainly by an increase in the number of Elmidae and terrestrial arthropods, and to a lesser extent *Pycnocentrodes aureola* larvae, and a reduction in the number of *Nesameletus ornatus* larvae eaten during summer (Tables 4 and 5). Such seasonal variation in the diet has usually been correlated with the relative availability of the dietary items.

In the present study, no information was obtained on the relative availability of the benthic and drift fauna at different times of the year, but terrestrial arthropods were abundant only in the summer months.

The proportion of empty stomachs was highest in samples taken during autumn and winter, and lowest in samples taken in spring and summer (Fig. 1).

Relationship between Diet, Fish Size and Age

The diets of fish in 10 mm TL groups are shown in Figs 2 (points method) and 3 (occurrence method). Kendall rank correlation coefficients computed between pairs of these groups (81 analyses; 36 on points method, 45 on occurrence method) indicate that the diet of small fish (TL < 40 mm) is significantly different ($P > 0 \cdot 05$) from the diet of larger fish. The major difference between the diets of fish above and below

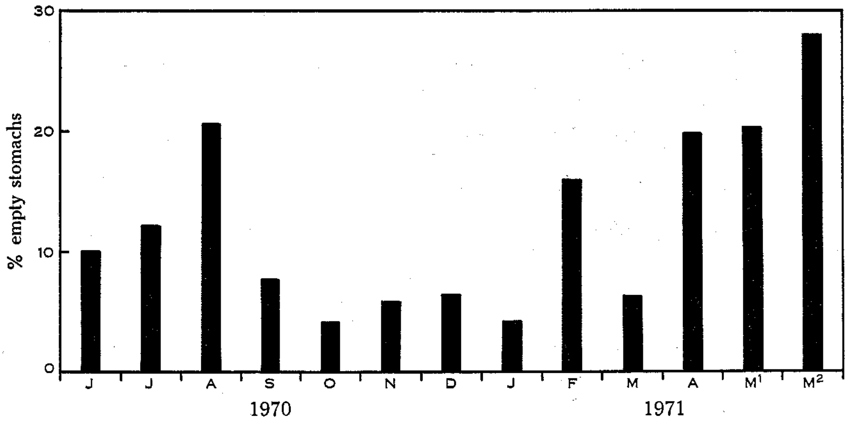

Fig. 1. Percentage occurrence of empty stomachs in samples of *Galaxias vulgaris* taken in riffles in the Glentui River from June 1970 to May 1971. (Sample sizes are as in Tables 1 and 2; M^1 = 1, 2 May; M^2 = 29, 30 May.)

40 mm TL is the occurrence of large food items such as the larvae of *Archichauliodes diversus* (which may reach up to 30 mm in length), *Coloburiscus humeralis* and *Nesameletus ornatus* in the larger fish. Also, when food items such as *Deleatidumi* spp. occurred in the diet of all TL groups, it was found that larger fish frequently took larger individuals than did smaller fish. Furthermore, there was a greater variety of food types in the diet of larger fish. Recently hatched fish fed on only six food types, Orthocladiinae larvae predominating. They also ate simuliid and tipulid larvae, and *Zephlebia scita* larvae were more important on the basis of frequency of occurrence in fish less than 30 mm TL than in any group of larger fish.

Analysis of the relationship between diet and age was confined to fish caught in riffles, and therefore exposed to the same food organisms. Diets of fish of increasing age (Fig. 4) follow the same pattern as the diets of fish of increasing size, with older (and therefore larger) fish taking larger food items than young fish. Kendall rank correlation coefficients for comparisons of the diets of different age groups indicate that diet does not change significantly with age, although the coefficients tend to decrease with increasing age gap between samples (Table 7).

Diets of Males and Females

Kendall rank correlation coefficients for comparisons of the diets of males and females in 10 mm length groups, age groups and season groups indicate that the diets of both sexes are very similar (Table 8). However, in spring, the coefficient is much lower than for the other seasons, on both the occurrence and points assessments.

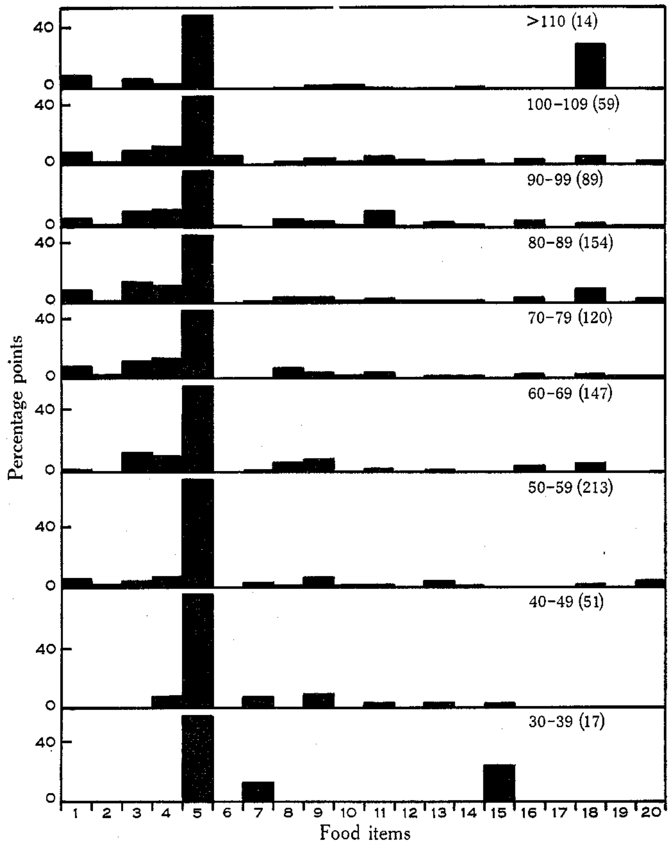

Fig. 2. Diet of *Galaxias vulgaris* in 10 mm TL groups, assessed by the points method. Food types (larvae unless othewise indicated): 1, *Archichauliodes diversus*; 2, Plecoptera; 3, *Coloburiscus humeralis*; 4, *Nesameletus ornatus*; 5, *Deleatidium* spp.; 6, other Ephemeroptera; 7, Ephemeroptera and Trichoptera adults; 8, *Hydropsyche colonica*; 9, Rhyacophilidae; 10, *Olinga feredayi;* 11, *Pycnocentrodes aureola*; 12, other cased Trichoptera; 13, Chironomidae larvae, pupae and adults; 14, Simuliidae larvae, pupae and adults; 15, other Diptera; 16, Coleoptera larvae and adults; 17, Gastropoda; 18, terrestrial Arthropoda; 19, Pisces; 20, others (mainly Lumbricidae and plant material). Values in parentheses are sample sizes.

This may be the result of differences in behaviour during the spawning period, males remaining at the nest site longer than females (Cadwallader 1973). Also, the coefficient for the diets of age 4+ males and females is relatively low, particularly on the points assessment. This may be explained, at least in part, by the difference in size of age 4+ fish, females being up to 10 mm longer than males, and by the small sample sizes in this age group.

Discussion

Nikolsky (1963) recognized three main categories of food on the basis of their importance in the diets of fish: basic food, that normally eaten by the fish and comprising most of the stomach contents; secondary food, that which is frequently

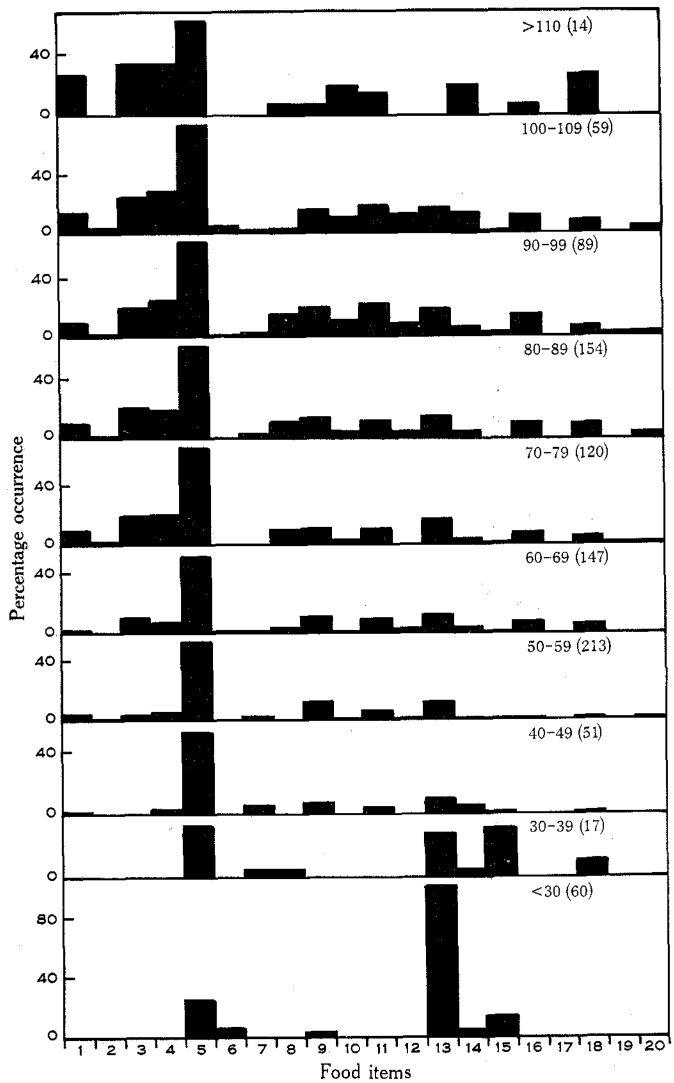

Fig. 3. Diet of *Galaxias vulgaris* in 10 mm TL groups, assessed by the occurrence method. Food types (1–20) as for Fig. 2. Figures in parentheses are sample sizes.

found in the stomach, but in smaller amounts; and incidental food, that which is found only rarely in the stomach contents. The basic food of *G. vulgaris* consisted of larvae of the ephemeropterans *Deleatidium* spp., *Coloburiscus humeralis* and *Nesameletus ornatus*, which occurred in 83·1% of the stomachs examined and comprised 69·6% of the total diet on a points basis. Secondary food, comprising 27·3%

of the total diet, consisted of Elmidae (Coleoptera), terrestrial Arthropoda, and the larvae of Rhyacophilidae, *Hydropsyche colonica*, *Olinga feredayi*, *Pycnocentrodes aureola* (Trichoptera), *Archichauliodes diversus* (Megaloptera), Chironomidae and Simuliidae (Diptera). The remaining items in the diet were regarded as incidental food.

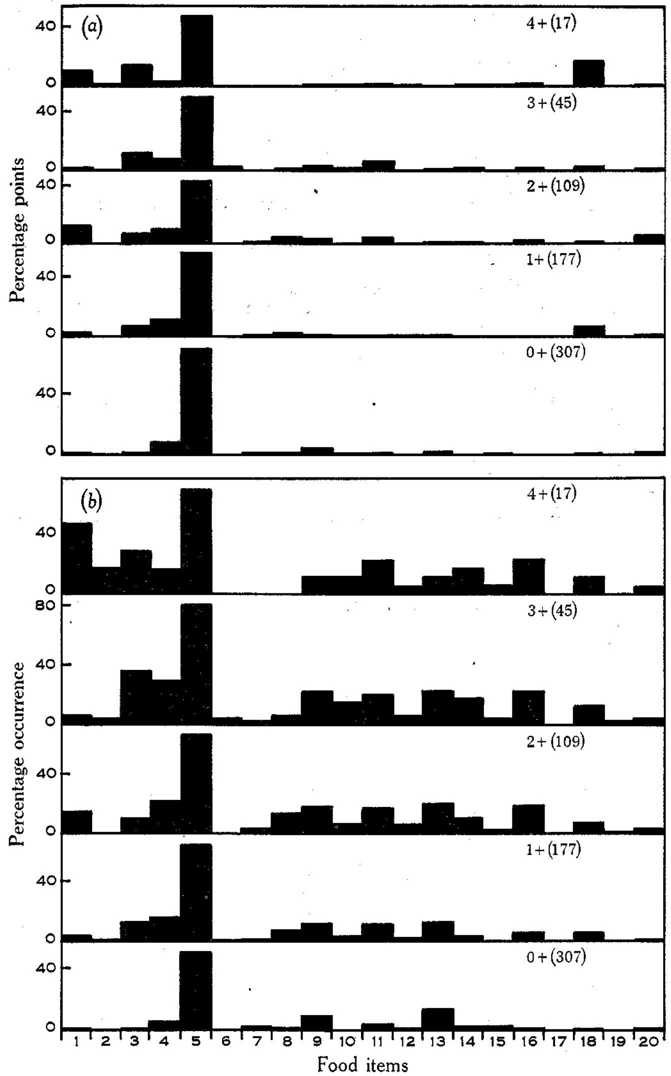

Fig. 4. Diet of *Galaxias vulgaris* in different age groups, assessed by (*a*) the points method and (*b*) the occurrence method. Included are those fish sampled in riffles from June 1970 to May 1971. Food types (1–20) as for Fig. 2. Figures in parentheses are sample sizes.

More empty stomachs were found in autumn and winter than during spring and summer. Metabolic requirements are reduced at low temperatures so that in temperate regions, assuming a constant food supply, food consumption may be expected to be less in winter than in summer. However, within the normal temperature range of a species, the rate of gastric digestion is higher at high temperatures than at low temperatures (Molnár and Tölg 1962*a*, 1962*b*; Tyler 1970; Elliott 1972), so that food is generally digested more quickly in summer than in winter. Thus, the low proportion of empty stomachs in spring and summer suggests an increase in food consumption at that time. The relatively large number of empty stomachs found in late winter (August) may be associated with spawning. At that time of the year the normal diel activity pattern is reversed, so that *G. vulgaris*, which is normally nocturnal, becomes active mainly during daylight (Cadwallader 1975*b*). Since *G. vulgaris* feeds mainly at night, when its prey is more available (Cadwallader 1975*b*, 1975*c*), it would be expected that a shift to diurnal activity would affect food consumption.

Table 7. Kendall rank correlation coefficients for comparisons of the diet of *Galaxias vulgaris* in different age groups

Figures in parentheses are values of z for testing the significance of τ. The top right portion of the table contains the results of comparisons based on the occurrence method; the bottom left portion of the table contains the results of comparisons based on the points method. Sample sizes are as shown in Fig. 4

	0+	1+	2+	3+	4+
0+	—	0·8237 (4·2800)***	0·7452 (3·8724)***	0·6269 (3·2573)**	0·4772 (2·4797)*
1+	0·6809 (3·5381)***	—	0·7500 (4·2800)***	0·8078 (4·2081)***	0·5874 (3·0523)**
2+	0·6878 (3·5736)***	0·6957 (3·1648)**	—	0·7513 (3·9039)***	0·6073 (3·1558)**
3+	0·6740 (3·5024)***	0·5854 (3·0417)**	0·5631 (2·9261)**	—	0·6971 (3·6223)***
4+	0·4376 (2·2738)*	0·5972 (3·1031)**	0·4953 (2·5735)**	0·6001 (3·1183)**	—

* $0·05 \leqslant P \leqslant 0·01$. ** $0·01 \leqslant P \leqslant 0·001$. *** $P < 0·001$.

A change in diet with increase in size as observed in *G. vulgaris*, with larger fish eating larger food items, has been widely reported: e.g. Keast (1966), Larsen (1967) and Munro (1967). The gape of a fish's mouth determines to some extent the animals on which it feeds (Thomas 1962), but, although mouth size imposes a limit on the size of food eaten, the structure and behaviour of the food organisms may determine the size of the minimum gape required to feed on certain prey (Hartman 1958). Prey selection may be important in some fish (Allen 1960; Bryan and Larkin 1972; Khan and Siddiqui 1973) and can occur actively or passively. Active selection may depend on experience, whereas passive selection depends on the 'natural habit' of the species (Maitland 1965). The 'natural habit' of *G. vulgaris* changes at the end of the juvenile phase, when fish leave the quiet stretches of the river and become riffle-dwellers. Dipteran larvae formed the basic food of recently hatched fish, with ephemeropteran and free-living trichopteran larvae being secondary foods. The change from a mainly dipteran diet to one dominated by Ephemeroptera, particularly *Deleatidium* spp., occurred when fish reached about 40 mm in length. This coincides with the length at which fish normally leave the quiet stretches of the river and move into riffles. In riffles they have access to a more diverse fauna, including the larvae of *Coloburiscus humeralis*, *Deleatidium* spp., *Archichauliodes diversus*, *Hydropsyche* *colonica*, Rhyacophilidae, *Olinga feredayi*, *Pycnocentrodes aureola* and Simuliidae, all of which are more common in the heterogeneous stony substrate of riffles than in the quieter parts of streams, where the substrate consists of smaller even-sized particles (Pendergrast and Cowley 1966; McLay 1968).

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Table 8. Kendall rank correlation coefficients (τ) for comparisons of the diet of male and female *Galaxias vulgaris* in total length groups, age groups and season groups

Comparisons are made on the results obtained by both the occurrence and points methods. Values of z are used to test the significance of τ

	Sample size		% occurrence		% points	
	Male	Female	τ	z	τ	z
Total length groups (mm)						
30–49	32	34	0·7512	3·9032***	0·8328	4·3274***
50–59	100	109	0·9160	4·7956***	0·9281	4·8225***
60–69	69	78	0·8822	4·5838***	0·8169	4·2449***
70–79	66	54	0·8266	4·2950***	0·6432	3·3433***
80–89	61	93	0·8266	4·2950***	0·7898	4·1471***
90–99	41	48	0·7500	3·8973***	0·6139	3·1899**
>100	21	52	0·7248	3·7663***	0·6921	3·5960***
Age (years)						
0+	148	154	0·8528	4·4314***	0·8654	4·4967***
1+	81	96	0·7800	4·0530***	0·7326	3·8066***
2+	47	62	0·7762	4·0333***	0·7193	3·7375***
3+	21	24	0·9796	5·0901***	0·7803	4·0547***
4+	6	11	0·7344	3·8154***	0·5569	2·8935**
Season						
Winter	106	104	0·8715	4·5276***	0·7863	4·0858***
Spring	48	65	0·6114	3·1768**	0·4977	2·8589**
Summer	47	57	0·8103	4·2103***	0·6563	3·4102**
Autumn	89	150	0·8283	4·3041***	0·6032	3·1344**

** $0·01 \leqslant P \leqslant 0·001$. *** $P < 0·001$.

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