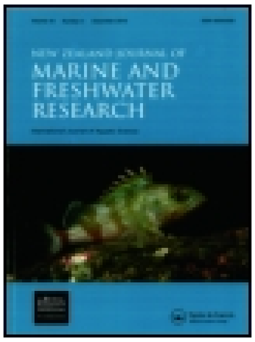

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New Zealand Journal of Marine and Freshwater Research

ISSN: 0028-8330 (Print) 1175-8805 (Online) Journal homepage: https://www.tandfonline.com/loi/tnzm20

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New Zealand Journal of Marine and Freshwater Research, 1997, Vol. 31: 147–154

0028–8330/97/3102–0147 $7.00/0

Mouth gape, food size, and diet of the common smelt *Retropinna retropinna* (Richardson) in the Waikato River system, North Island, New Zealand

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Abstract The feeding ecology of the common smelt, *Retropinna retropinna*, was determined at several locations on the Waikato River system. The mean size of the dominant prey was found to increase as smelt mouth gape increased. Smelt smaller than 40 mm total length fed mostly on zooplankton. Chironomid larvae, pupae, and adults were the dominant foods of larger fish from most sites, although mysids and amphipods were the major prey in Lake Waahi and the Waikato River estuary. Algae were the dominant food in many smelt but ingestion was probably incidental. Seasonal and annual differences in dominant foods were minor. Common smelt are generalists, capable of feeding on the majority of smaller organisms present in their different environments; however, they may grow faster and achieve a larger adult size when food of optimal size and nutritive value is present.

Keywords New Zealand; Waikato River; fish; smelt; *Retropinna retropinna*; feeding; mouth gape

M94015
Received 13 June 1994; accepted 14 February 1997

INTRODUCTION

The common smelt, *Retropinna retropinna* (Richardson), is a major component of the freshwater fish communities inhabiting the lakes, reservoirs, streams, and the estuary of the Waikato River system. The populations can be divided into three groups: lacustrine, reservoir, and diadromous populations (McDowall 1972; Northcote & Ward 1985; Ward et al. 1989). The lacustrine group may be subdivided into populations that are truly landlocked in lakes and those that inhabit lakes with direct or indirect access to the sea. Reservoir smelt populations are isolated from the other two groups, although some adults and juveniles are displaced down stream (Ward et al. 1989). In some lowland lakes, lacustrine and diadromous populations are sympatric (McDowall 1979; Northcote & Ward 1985; Hicks 1993).

Diadromous smelt spend the initial stages of their lives at sea, in the estuary, or in the lower reaches of the river. Some migrate up stream and into lowland lakes with direct access to the main river as maturing fish in spring (Northcote & Ward 1985). They feed during summer and early autumn and spawn on sand bars in the main river in late autumn and winter. In the Waikato River, diadromous smelt are abundant down stream from the Karapiro Dam. Lake and reservoir populations do not migrate but feed and reproduce in their respective habitats. Lacustrine and reservoir smelt spawn primarily in spring and early summer rather than in autumn and winter (Northcote & Ward 1985; Ward et al. 1989).

The diets of common smelt in lakes are dominated by various species of limnetic and littoral zooplankters with aquatic insect larvae, particularly chironomids, forming a significant component (Jolly 1967; Mitchell 1986; Cryer 1988; Donald 1990). Less information is available regarding the food of diadromous smelt. Reported food includes juvenile aquatic insects, and vegetable debris with crustaceans a minor component (Eldon & Greager 1983).

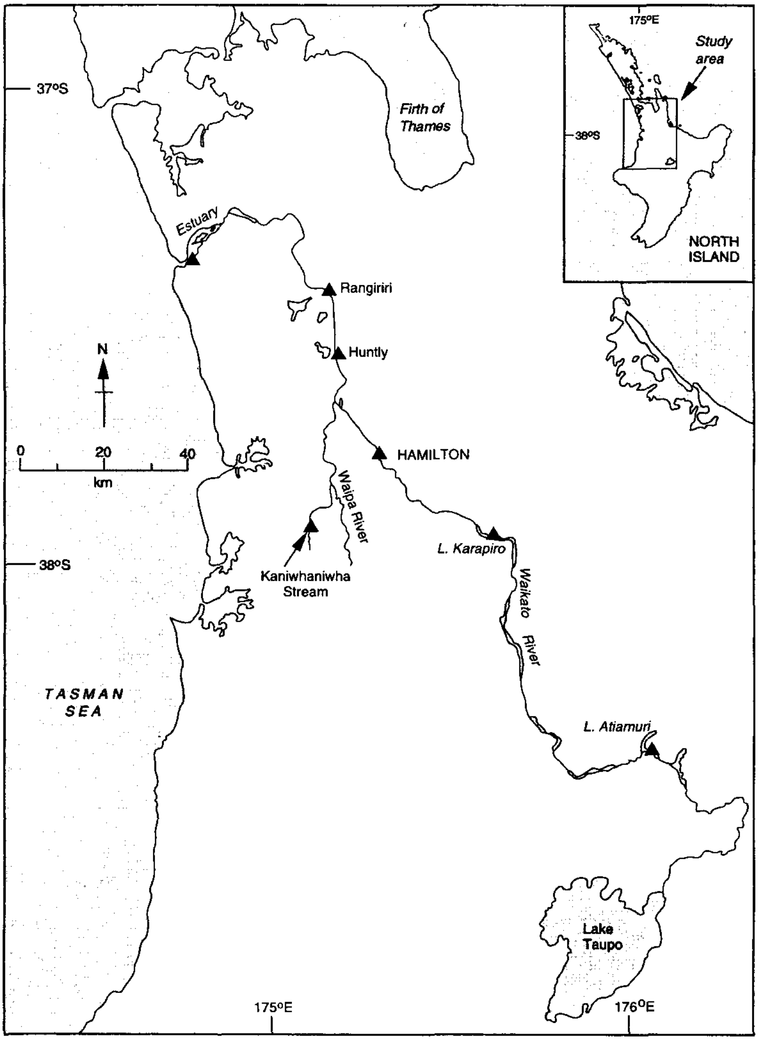

Fig. 1 The Waikato River system, North Island, New Zealand, showing sites used to capture common smelt for these diet studies.

Our principal objective is to report on the feeding ecology of some populations of common smelt in the Waikato River system. We examine the relationships between smelt body length, mouth dimensions, and prey size; describe the dominant food of smelt taken at different sites on the Waikato River system; and discuss seasonal and annual differences in the dominant prey.

METHODS

Mouth gape was measured by inserting the tip of a conical brass device, calibrated in mm, into the mouth cavity of smelt until the jaws were well separated (Ward & McCulloch 1991). The height of the cone (depth of insertion in mm) was used to estimate the diameter of the base, using the tip of the lower jaw as the reference point. The base diameter in mm at this reference point (GAP) was taken as an estimate of maximum jaw gape. The jaw mechanism of smelt, particularly juveniles, is very flexible. Consequently care was taken to minimise mouth distortion when GAP measurements were taken.

The GAP–total length regression (SAS 1988) was calculated for 152 smelt (total length, TL=26–96 mm) collected from Karapiro Reservoir and three sites (Hamilton, Huntly, and Estuary) on the lower

Waikato River (Fig. 1). This regression equation was used to estimate GAP from the lengths of 368 smelt collected from three sites in the lower Waikato River (Hamilton, Huntly, and Estuary), from the Kaniwhaniwha Stream, and from Atiamuri Reservoir. The body depth or width (whichever was the greatest)—referred to hereafter as D—of the largest prey items found in the guts of each fish in this sample was also measured, using a compound microscope fitted with a calibrated eye piece. D values could be determined for some partially digested items, for example for some fish remains. The relationship between D and estimated GAP was determine by regression analysis (SAS 1988).

Smelt diet was determined from the stomach contents of 1686 fish captured using beach seines from eight sites on the Waikato River system. (Fig. 1, Table 1). Fish were preserved in 4% formalin and subsequently the total length (in mm) of each fish was recorded. Food items were identified to genus and species level when possible, but were either reported as genera or grouped into categories (e.g., larvae, pupae, and adults for chironomids).

To evaluate the importance of prey in the diet of smelt, the item that formed the largest fraction by volume of the stomach content of a fish was determined by observation and recorded as the dominant food of that fish. The number and percentage of smelt in which each particular food item dominated was recorded for each sample. The taxon that was dominant in the greatest number of fish was defined as the major dominant food item. If two or more categories had similar dominant values they were all classified as major dominants.

Smelt sampled from Huntly (1984–85, 1987–88) were arranged according to season of capture with months assigned as follows: spring, September–November; summer, December–February; autumn, March–May; winter, June–August. Seasonal diet data were also available for both the Rangiriri and Karapiro sites. The seasonal feeding patterns found were similar to those observed at Huntly and, therefore, the data are not presented.

RESULTS

Mouth gape and food size

The regression of mouth gape (GAP) on total length (TL) was linear over the length range of the sample (Fig. 2A). The relationship was highly significant ($F = 2009$; $r^2 = 0.93$; d.f. = 1, 150; $P < 0.001$). The equation for the regression was: GAP = 0.199TL–3.102. The predicted GAP for the smallest (26 mm) and largest (96 mm) smelt was 2.08 mm and 16.04 mm, respectively.

The D values of major prey items found in smelt varied from 0.1 to 8 mm (Table 2). In contrast with the linear GAP–TL regression, the line of best fit for the mean D–predicted GAP relationship was a second-order polynomial; i.e., the relationship was exponential (Fig. 2B). The equation for the regression was $D = 0.186 + 0.059\text{GAP} + 0.003(\text{GAP})^2$ ($F = 86$; $r^2 = 0.86$; d.f. = 1, 366; $P < 0.001$). At predicted GAP dimensions from 1 to 6 mm, there was very little variation in D values, but as GAP increased the confidence intervals widened about each mean D.

Table 1 Location, dates, number of fish in samples, and total length (TL) of common smelt taken from the Waikato River system for diet studies.

Site	Date	No.	TL (mm) Min.	Mean	Max.
Huntly	15 Feb 84–10 Apr 85	513	30	66	121
Rangiriri	28 Mar 84–23 Mar 85	474	44	63	121
Huntly	22 Sep 87–14 Sep 88	463	30	64	129
Estuary	15 May 88, 8 Sep 88	27	46	62	85
Lake Waahi	24 Feb 93	49	47	66	104
Huntly	28 Nov 88	10	24	32	36
Kaniwhaniwha	31 Mar 88	29	74	94	113
Hamilton	17Sep 87	20	70	86	104
Karapiro Reservoir	19 Nov 87, 11 Jan 88, 11 Apr 88, 22 Aug 88, 12 Oct 88	78	32	58	88
Atiamuri Reservoir	18 Feb 88	23	18	27	32
Total	15 Feb 84–24 Feb 93	1686			

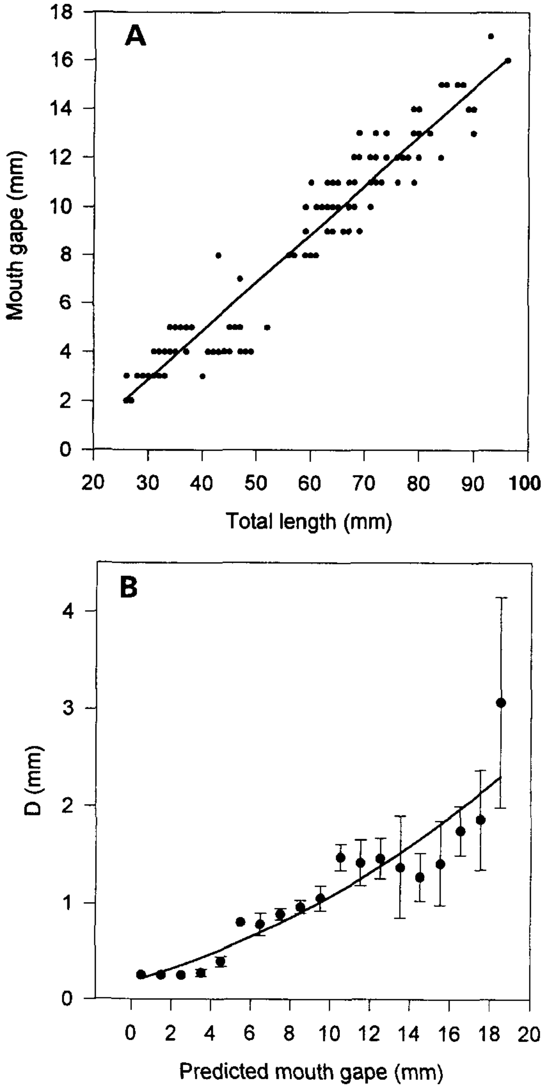

Fig. 2 Associations found in common smelt between mouth gape, length, and prey size. **A**, Relationship between mouth gape (GAP) and length; **B**, relationship between mean prey depth or width (D) and mouth gape (GAP); 95% confidence intervals are shown for mean D values.

Small copepods and cladocerans with D values from 0.1 to 0.4 mm (average 0.34 mm) were the exclusive prey of smelt 30–40 mm in length (predicted GAP 2.9–4.1 mm) captured from the Waikato River near Huntly in 1987–88. Chironomid larvae (D = 0.35–0.6 mm) were the dominant food of smelt between 40 and 50 mm in length (predicted GAP 4.1–5.3), with small crustaceans also present. Amphipods (D = 4.0 mm) were dominant only in smelt longer than 50 mm (predicted GAP 5.3). Trichopteran larvae and pupae (D = 1.0 and 1.1 mm), were occasionally dominant in the stomachs of fish in the 50–60 mm length range (predicted GAP 5.3–6.3 mm). Small chironomid larvae and small crustaceans persisted as dominant foods in many of these fish. An individual mosquito fish (*Gambusia* sp., D = 4.0 mm), was found in a smelt 77 mm long (predicted GAP 12.3 mm), and an entire shrimp (*Paratya* sp.) (D = 8.0) was recorded in an 80 mm smelt (predicted GAP 12.9 mm).

Table 2 Mean maximum body depth or width (D) of prey found in common smelt from the Waikato River system.

Category	Group	D (mm)
Copepods	Harpacticoids	0.10
	Calanoids	0.25
	Cyclopoids	0.40
Cladocerans	*Bosmina* sp.	0.25
	Ceriodaphnia sp.	0.40
Chironomids	Small larvae, e.g., Stage IV orthoclads	0.35
	Large larvae, e.g., Stage IV chironomini	0.60
	Small pupae, e.g., orthoclads	1.10
	Large pupae, e.g., chironomini	1.50
	Adults	1.20
Trichopterans	Larvae	1.00
	Pupae	1.10
Mysids		1.80
Fish	Remains	2.30
	Gambusia sp.	4.00
Amphipods		4.00
Paratya sp.		8.00

The "steps" in the relationship, i.e., similar D values over a range of predicted GAP measurements (Fig. 2B), were caused by variations in the size spectrum of prey present in the stomachs of fish sampled at the different sites. At both the Kaniwhaniwha and Hamilton sites, the dominant prey were small even though the smelt were large (Table 1). For example, although some of the largest fish (mean TL = 94 mm, predicted GAP = 15.6 mm) were taken from the Kaniwhaniwha Stream (Table 1), the largest prey in their stomachs were chironomid pupae, D = 1.5 mm (Table 2).

Diet

Unidentified adult insects (mainly chironomids) were the major dominant food in the stomach of smelt captured at Hamilton, Huntly, and Rangiriri (Table 3). The main difference between the sites was that larvae of the freshwater shrimp, *Paratya* sp., were an important dominant food among smelt taken near Rangiriri but was never dominant in fish captured at the upriver sites.

For the 1984–85 period, adult insects were major dominant prey for 39 and 64% of smelt captured at Huntly in spring and winter, respectively; however clumps of filamentous algae were the major dominant item in the guts of most smelt captured in summer and autumn (Table 4). Detritus was often dominant in smelt captured in summer and autumn whereas cladocerans were dominant in some smelt only during the spring season. Chironomid larvae were dominant in a few fish during spring.

Seasonal changes in food composition of smelt taken near Huntly in 1987–88 were similar to those obtained in 1984–85. The main difference was that chironomid larvae and cladocerans were dominant in a greater proportion of fish in 1987–88 than in 1984–85, particularly in summer.

Similar to the Hamilton, Huntly, and Rangiriri sites, the dominant foods of the smelt from the Karapiro Reservoir comprised adult insects, particularly chironomids (Table 3). However, some prey items, notably mysids and *Paratya* sp., were

Table 3 Dominant food items (% of fish examined) found in common smelt captured in the Waikato River system. Major dominant values are shown in bold.

	Lower Waikato River							
Location:	Hamilton	Huntly	Huntly	Rangiriri	Estuary	Karapiro Reservoir	Lake Waahi	Kani-whaniwha Stream
Collection date:	17 Sep 87	1984/85	1987/88	1984/85	1988	1987/88	24 Feb 93	31 Mar 88
Algae	15.0	29.8	**22.6**	12.5	0.0	0.0	0.0	0.0
Fish	0.0	0.6	1.5	0.0	0.0	0.0	2.0	0.0
Small crustaceans								
Copepods	0.0	2.0	0.0	1.3	11.1	0.0	0.0	0.0
Cladocerans	0.0	3.3	5.8	0.0	0.0	3.9	0.0	0.0
Paratya larvae	0.0	0.0	0.0	5.5	0.0	0.0	0.0	0.0
Others	0.0	0.0	4.5	0.2	14.8	0.0	0.0	0.0
Large crustaceans								
Mysids	0.0	1.0	1.9	0.0	3.7	0.0	22.5	0.0
Amphipods	0.0	0.4	1.3	0.2	**59.3**	0.0	0.0	0.0
Paratya parts	0.0	0.4	0.4	0.4	0.0	0.0	0.0	0.0
Others	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0
Aquatic insects								
Larvae								
Chironomids	**30.0**	4.5	13.2	3.8	0.0	6.4	10.2	24.2
Odonata	0.0	0.0	0.4	0.4	0.0	5.1	0.0	0.0
Trichopterans	5.0	4.3	3.7	1.3	0.0	6.4	0.0	0.0
Pupae								
Chironomids	0.0	0.0	5.6	0.0	0.0	9.0	0.0	20.7
Trichopterans	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10.3
Terrestrial insects	0.0	1.2	3.0	3.6	0.0	0.0	0.0	0.0
Chironomid adults[1]	–	–	–	–	0.0	**43.6**	0.0	**31.0**
Unid. adult insects	**30.0**	**40.2**	**22.2**	**45.6**	0.0	16.7	10.2	13.8
Spiders	0.0	0.2	1.3	0.2	0.0	0.0	0.0	0.0
Molluscs	0.0	0.0	0.0	1.3	0.0	0.0	0.0	0.0
Annelids	0.0	0.4	0.0	1.1	11.1	0.0	2.0	0.0
Detritus	5.0	9.0	3.9	13.7	0.0	1.3	4.1	0.0
Other	5.0	1.0	5.0	6.3	0.0	7.7	4.0	0.0
Empty	10.0	2.0	2.8	2.7	0.0	0.0	**44.9**	0.0
Totals %	100	100	100	100	100	100	100	100
n	20	513	463	474	27	78	49	29

[1]Chironomid adults not separated from other adult insects for Hamilton, Huntly and, Rangiriri.

absent from this upstream site. Similarly, smelt captured in the Estuary, in Lake Waahi, and in the Kaniwhaniwha Stream also had a different spectrum of prey. Amphipods (59%) were the major dominant prey in the estuary (Table 3). Insect taxa were not dominant in any of these fish. In Lake Waahi, almost 45% of the 49 smelt examined contained no food (Table 3). Mysids were dominant in 23% (11) of the sample. Chironomid larvae and unidentified adult insects were the only other significant diet item. Most smelt taken from the Kaniwhaniwha Stream fed on adult chironomids (31%), chironomid larvae (24%), and chironomid pupae (21%) (Table 3).

The 23 juvenile smelt taken (mean TL = 27 mm) from Atiamuri Reservoir had fed almost entirely on small copepods (69.6%), the only other food item found being cladocerans (13%). Four of these fish (17.4%) had empty stomachs. Similarly, the stomach content of 10 small fish (mean total length 32 mm), captured near Huntly in November 1988, were dominated by copepods (40%), cladocerans (20%), and chironomid larvae (20%). Additional confirmation of this preference of juvenile smelt for small prey is provided by the similar values found for prey found in smelt with mouth gape (predicted GAP) measurements < 4 mm and the narrow confidence intervals about these means (Fig. 2B).

Table 4 Seasonal change in dominant food items (% of fish examined) found in common smelt captured in the Waikato River at Huntly during 1984 and 1985. Major dominant values are shown in bold.

Group	Spring	Summer	Autumn	Winter
Algae	19.7	**32.8**	**42.4**	16.8
Fish	2.5	0.0	0.0	0.0
Small crustaceans				
Copepods	2.5	3.3	1.2	1.0
Cladocerans	13.9	0.0	0.0	0.0
Large crustaceans				
Mysids	0.8	0.0	0.0	4.0
Amphipods	0.0	0.8	0.0	1.0
Paratya parts	0.0	1.6	0.0	0.0
Aquatic insect larvae				
Chironomids	12.3	4.9	0.6	1.0
Trichopterans	5.7	4.9	3.5	3.0
Terrestrial insects	0.0	3.3	0.0	2.0
Unid. adult insects[1]	**38.5**	28.7	35.3	**64.4**
Spiders	0.0	0.8	0.0	0.0
Annelids	0.0	0.0	0.6	1.0
Detritus	0.8	15.6	12.9	4.0
Other	1.6	1.6	0.0	1.0
Empty	0.8	1.6	3.5	1.0
Totals %	100	100	100	100
n	121	122	170	100

[1]Includes Chironomid adults.

DISCUSSION

Smelt size and food size

Increases in the dimensions and variety of prey are often associated with increasing fish size. As reported elsewhere (Cryer 1988; Forsyth & James 1988; Donald 1990), juvenile smelt in the Waikato River system consumed only small prey, primarily small copepods and cladocerans. Similar size-related changes in diet were noted by Stephens (1984). He reported that smelt from the littoral and pelagic zones of Lake Taupo consumed somewhat different prey. In both habitats, zooplankton were an important part of the diet of small fish, but in the littoral zone larger smelt consumed chironomid larvae, smelt eggs, and juvenile bullies.

Growth in length and weight is generally accompanied by increased mouth dimensions, allowing larger prey items to be ingested (Wong & Ward 1972; Wankowski 1979). Our results were similar. As predicted GAP values increased, so did mean D values (Fig. 2B). This increase in the mean size of prey in the diet of common smelt with increasing length is probably dependent on increasing mouth gape; however, mouth gape is not the sole factor associated with prey size. With increases in both GAP values and D values, the confidence intervals about each mean D increased too, indicating that as the fish increased in length, so did the size spectrum of prey.

An increase in the size spectrum of prey with increasing mouth dimensions can only occur if feeding is not size-selective, and prey of varying sizes are available and sufficiently abundant (Schmitt & Holbrook 1984; Ward & McCulloch 1991). Consequently, the size spectrum and relative abundance of prey of various sizes may also determine diet. Smelt at some sites, for example Hamilton and the Kaniwhaniwha Stream, were capable of feeding on larger prey than were found in their stomachs, indicating that larger prey were either absent or scarce. In these instances the fish size–mouth gape relationship was probably less important in determining diet than the size spectrum of available prey.

Food size may be more important in regulating the growth rate of fish than is the amount of food consumed (Boisclair & Leggett 1989). The increasing ability of larger fish with greater mouth gapes to capture larger prey may reduce pursuit-handling times (Werner 1974) and may result in augmented net energy intake and increased growth rates (Mittelbach 1983). In Lake Parkinson, Mitchell (1986) noted that adult common smelt increased in size when bigger food items became available after weed clearance. The absence of larger food items can lead to stunting (Werner 1974), e.g., as shown by the population of small smelt in Lake Rotomanuka near Hamilton (Donald 1990). In contrast, availability of amphipods and other large prey items (e.g., shrimp) may account for the larger adult size achieved by migratory smelt in the lower Waikato system.

The diet of large Kaniwhaniwha Stream smelt, consisting of small to moderately-sized organisms (D = 0.35–1.50 mm), seems to contradict selection for larger items with increasing fish size. However, these fish are short-term residents of the stream, arriving in late summer and leaving in autumn. Their diet and the diet of smelt captured near Hamilton probably reflects a localised limitation in the availability of larger food organisms and it is likely that these fish grew to a large size outside of the sampling location.

Diet

The range and dominance of prey items eaten by smelt varied markedly between sites. The major dominant prey of smelt in Lake Waahi comprised mysids rather than a wide spectrum of food organisms. Insects, particularly chironomids, were the most important food for smelt from Karapiro Reservoir but unlike the sites further down stream, shrimps were not found (they cannot reach or develop in the reservoir). Only at Huntly and Rangiriri was there a wide selection of dominant organisms in the diet. Even there, assuming that algae were ingested incidentally to the other taxa, insects in several forms were the most important dominant food. This undefined role of algae in the diet, and our inability to identify insect remains in a large fraction of smelt examined, made it difficult to accurately determine the real contributions of the various insect taxa to smelt stomach contents.

The most apparent seasonal differences in the diet of smelt from the Huntly site is a predominance of algae over adult insects (mostly chironomids) in summer and autumn. Assuming that algae were ingested incidentally during prey capture, or only because they had more palatable food items attached to them, the seasonal differences in the occurrences of life history stages of chironomids become more apparent. Adult insects (mostly chironomids) now appear as the major dominant food item during the four seasons; chironomid larvae are most important in spring and least important in autumn and winter. Since there were no apparent differences in the diet of smelt from Huntly between 1984–85 and 1987–88, it can be concluded that chironomids are the dominant food of maturing smelt in the middle reaches of the Waikato River. Chironomids, therefore, play an important role in maintaining large populations of smelt in the Waikato River system, thereby ensuring an important food source for trout and other large predators.

The introduction of smelt has been shown to eliminate another native fish from a small lake (Rowe 1993), but the impact on larger systems may be greater. Smelt are generalists, utilising the same or similar food resources as native galaxiids and bullies (Eldon & Greager 1983; Forsyth & James 1988; Hayes & Rutledge 1991). The varied habitats which smelt occupy, ranging from marine to freshwater, lacustrine and riverine, both clear and turbid, and their varied diet in these habitats, indicate their adaptability. Because their potential reproductive rate is so high (Ward & Boubée 1996) and because their potential prey are so diverse, they are able to succeed—often to the detriment of other species.

ACKNOWLEDGMENTS

We acknowledge the support received from the Electricity Corporation of New Zealand Limited and the Department of Biological Sciences, University of Waikato. FJW in particular, is grateful for a long and rewarding association with staff of the above department. Dr Ann Chapman has always provided us with encouragement. We thank Allan Stancliff, Adrienne Mora, and David West for assistance both in the field and in the laboratory. Brendan Hicks, Adrian Meredith, Tom Northcote, and David Rowe provided useful suggestions on drafts of this paper. Funds for the research were supplied by ECNZ, by a research grant made to FJW by the University of Manitoba, by the Department of Biological Sciences, University of Waikato, and contract 1314 from the Foundation for Research, Science and Technology (New Zealand).

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