

SHORT COMMUNICATION

Diet of rainbow trout in Lake Rotoiti: an energetic perspective

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We characterised seasonal and ontogenetic changes in diet and prey energy density of rainbow trout (*Oncorhynchus mykiss*) in Lake Rotoiti, New Zealand, to better understand the prey requirements of trout in central North Island lakes. Common smelt (*Retropinna retropinna*) was the dominant prey item of rainbow trout larger than 200 mm (77.8% of diet by weight), followed by kōura (freshwater crayfish *Paranephrops planifrons*; 6.3%), common bully (*Gobiomorphus cotidianus*; 5.5%), and kōaro (*Galaxias brevipinnis*; 3.4%). Juvenile rainbow trout (<200 mm) consumed amphipods, aquatic and terrestrial insects, oligochaetes, tanaid shrimps, and smelt. Trout consumed kōaro only in autumn and winter; consumption of other species did not vary seasonally. The maximum size of smelt consumed increased with increasing trout size, but trout continued to consume small smelt even as large adults. Consumption of larger prey items (kōaro and kōura) also increased with increasing trout size. This study indicates the importance of smelt for sustaining rainbow trout populations, as predation on other species was relatively low. These findings provide a basis for bioenergetic modelling of rainbow trout populations in lakes of the central North Island of New Zealand.

Keywords: New Zealand; predator–prey relationships; energy density; *Oncorhynchus mykiss*; *Retropinna retropinna*; *Paranephrops planifrons*; *Gobiomorphus cotidianus*; *Galaxias brevipinnis*

Introduction

Rainbow trout (*Oncorhynchus mykiss*) is a popular sports fish in the North Island of New Zealand. While some lakes support self-sustaining populations, hatchery-raised yearlings are stocked into several lakes to supplement wild stocks where spawning habitat and wild recruitment are limited. The diet of rainbow trout is highly variable, and may include small fish such as common smelt (*Retropinna retropinna*), common bully (*Gobiomorphus cotidianus*), kōaro (*Galaxias brevipinnis*), kōura (freshwater crayfish *Paranephrops planifrons*), terrestrial invertebrates and gastropod molluscs (Smith 1959; Rowe 1984; McCarter 1986; Cryer 1991). However, rainbow trout in the deep lakes of the central North Island of New

Zealand consume mainly common smelt (Smith 1959; Rowe 1984; McBride 2005). Trout and smelt dynamics have been examined in Lake Taupō (Stephens 1984; Cryer 1991), but have not been as well studied in other lakes in the central North Island, including those stocked with hatchery-raised fish. Understanding the trophic relationships between predators and their prey is vital for optimising stocking of sport fish in lakes, where fish abundance is primarily controlled by fishery managers and angling pressure. To optimise growth of stocked fish, it is important to ensure that sufficient food is available (Ney 1990). A better understanding of rainbow trout diet would help fishery managers to understand the conditions necessary for supporting optimal trout growth.

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Sports fish are often top-level predators, and have the potential to influence ecosystem structure and function through top-down processes (Carpenter et al. 1985; Northcote 1988). The effect of trout predation on prey populations in lakes in the central North Island of New Zealand is largely unknown, but previous studies have shown that rainbow trout may cause decreased survival of prey, alteration of food webs, and change of prey behaviour in receiving ecosystems (reviewed by Cucherousset & Olden 2011). Quantifying trout predation on various prey species is a necessary initial step in assessing the effects of trout on prey populations.

Previous evaluations of rainbow trout diet in the Rotorua lakes have used the percentage frequency of occurrence of each prey item and have focussed on adult fish during one to three seasons (Smith 1959; Rowe 1984). Further assessment of rainbow trout diet is required in order to understand the effects of predation on prey populations and, in turn, the influences of prey supply on trout growth. Bioenergetic models are a useful tool for quantifying predator-prey relationships, and can be used to assess predator demand for prey (Chipps & Wahl 2008), to determine whether limitations in food supply are affecting growth (Baldwin et al. 2000; Murry et al. 2010), and to evaluate the effects of predation on prey populations (Cartwright et al. 1998; Vigliano et al. 2009). Bioenergetic models require an estimate of relative proportions of prey types by weight as well as energy density; this information is currently lacking for trout in New Zealand lakes. The aims of this study were to quantify the energetic contributions of prey items to the diet of rainbow trout in Lake Rotoiti, and to assess seasonal and ontogenetic changes in diet. This study has two objectives: (1) to provide information to fishery managers about the prey resources necessary for optimal rainbow trout growth; and (2) to identify which species are likely to be most affected by trout predation.

Methods

Lake Rotoiti (38.0390°S, 176.4277°E) is a warm, monomictic, mesotrophic lake in the Bay of Plenty region of New Zealand's North Island. The lake has a surface area of 34 km², and is shallow at the western end, with depth increasing to a maximum of 125 m in the eastern basin. Lake Rotoiti was chosen for this study because it contains a significant trout fishery and is likely to be representative of other important trout fisheries in the Central North Island region (e.g. lakes Tarawera and Okataina).

One hundred and eighty-two rainbow trout were caught by angling, beach seining and boat electrofishing from a range of locations in Lake Rotoiti between March 2009 and December 2010 (Table 1). Angler-caught trout were caught using mainly shallow trolling and jigging fishing methods. Beach seining and boat electrofishing were carried out in the littoral zone. Diet was determined by stomach contents analysis of hatchery-origin and wild fish (n wild = 96; n hatchery = 86). The mean fork length (FL) of sampled trout was 444 mm, with a length range of 27–646 mm. Hatchery-origin fish were identified by fin clips. Trout from the hatchery had been at liberty in the lake for varying amounts of time, but were assumed to have adapted to lake conditions. They were present in all size classes sampled except the smallest size class (<100 mm), as this is smaller than the size at which trout are released from the hatchery. All items from the mouth, oesophagus and stomach were removed, counted and identified to the highest taxonomic level possible. The blotted wet weight of each prey type from each fish was recorded. Two metrics were used to compare diets: (1) the percentage frequency of occurrence (the percentage of non-empty trout stomachs containing a particular prey item), and (2) the percentage consumption of each prey type by weight (the proportion by weight of each prey species averaged across all non-empty stomachs). If smelt were intact, the FL was measured, otherwise FL was estimated

Table 1 Summary of methods and timing of sampling for diet analysis of Lake Rotoiti rainbow trout, with sample sizes of non-empty and empty trout stomachs for a range of length classes.

Length (mm)	Season				Method			
	Spring	Summer	Autumn	Winter	Beach seine	EF	Anglers	Total
Non-empty stomachs								
< 100	7	9	0	0	16	0	0	16
100–199	1	1	1	1	2	1	1	4
200–299	0	0	1	6	0	6	1	7
300–399	1	1	3	0	0	0	5	5
400–499	7	15	14	3	0	0	39	39
500–599	17	23	22	4	0	0	66	66
600–699	2	3	6	0	0	0	11	11
Total	35	52	47	14	18	7	123	148
Empty stomachs								
< 100	0	4	0	0	4	0	0	4
100–199	0	0	0	0	0	0	0	0
200–299	0	1	0	0	0	0	1	1
300–399	1	4	0	0	0	0	5	5
400–499	4	3	7	1	0	0	15	15
500–599	3	4	2	0	0	0	9	9
600–699	0	0	0	1	0	0	1	1
Total	8	16	9	2	4	0	31	35
% empty	18.6%	23.5%	16.1%	12.5%	18.2%	0.0%	20.1%	19.1%

EF, boat electrofishing.

from a measure of standard length (SL; to the end of the caudal peduncle) and a FL:SL regression equation derived from smelt caught in Lake Rotoiti ($FL = 1.0641 \times SL - 0.3889$; $n = 40$; $R^2 = 0.9912$, J. Blair unpubl. data).

To measure the energy density of trout prey, the principal prey items of adult trout (smelt, common bully, kōaro and kōura) were caught between January 2010 and November 2010 from Lake Rotoiti using a beach seine net and electrofishing boat. Prey were measured, weighed and dried in a Contherm oven at 60 °C for approximately 24 h until a constant weight was reached. Several common bullies and smelt were included in each sample in order to obtain enough material for bomb calorimetry, but kōura and kōaro were processed individually because few specimens were captured (mean number of individuals per sampling unit: smelt, 12; common bully, nine; kōaro, one; kōura, one). The energy density of prey items was

measured using a Parr Model 1341 Plain Oxygen Bomb Calorimeter and a Parr 1108 Oxygen Bomb using standard methods (Parr Instrument Company 2008).

Differences in prey proportions of adult trout between seasons and differences between caloric content of prey items were assessed using Kruskal–Wallis analysis of variance (ANOVA) by ranks in STATISTICA, version 9.0. The relationship between trout length and the length of consumed smelt was assessed using 0.10, 0.50 and 0.90 regression quantile estimates. Equality of the regression slopes was assessed using ANOVA. Quantile regression and associated analyses were carried out using the quantreg package for R, version 2.13.2.

Results

The percentage of trout with empty stomachs varied slightly with season and was highest in

summer, at 23.5% (Table 1). Rainbow trout smaller than 200 mm FL consumed mainly invertebrates, including amphipods (*Paracalliope fluviatilis*), tanaid shrimps (*Sinelobus stanfordi*), aquatic insects and terrestrial insects (Tables 2 and 3). Aquatic insects included chironomid pupae (Chironomidae) and caddisflies (*Paroxyethira* spp.), and terrestrial insects were mostly adult flies (order Diptera) and wasps (suborder Apocrita). Both enumeration methods showed that rainbow trout shift to a mainly piscivorous diet at around 200 mm FL; smelt were the main prey of rainbow trout larger than 200 mm. Common bullies were present in the diet of most size classes of trout, with the exception of fish < 100 mm and 300–399 mm FL. Kōaro and kōura were eaten only by trout over 400 mm long. Kōura were the only invertebrates found in the stomachs of adult trout, with the exception of one fish that had eaten a gastropod mollusc (*Potamopyrgus antipodarum*) and three fish that had eaten terrestrial insects. The occurrence method gave similar results to the weight method in most cases, but for trout between 100–199 mm FL, the occurrence method overestimated the importance of smelt (75.0%) compared with the weight method (36.1%). For trout < 100 mm, the occurrence method attributed greater importance to oligochaetes, aquatic insects, and terrestrial insects than the weight method (Tables 2 and 3).

The percentage composition by weight of smelt, kōura and common bullies in the diet of trout (> 400 mm long) did not vary seasonally (Fig. 1; Kruskal–Wallis test, $n = 116$, $P > 0.05$). Kōaro were only detected in trout stomachs in autumn and winter, and the percentage composition by weight of this species was significantly different between seasons (Kruskal–Wallis test, $n = 116$, $P = 0.018$). Specifically, weights were different between summer and autumn and between spring and autumn (Kruskal–Wallis test, multiple comparisons of mean ranks). The weight of unidentified material was significantly different between summer and autumn (Kruskal–Wallis test, multiple comparisons of mean ranks).

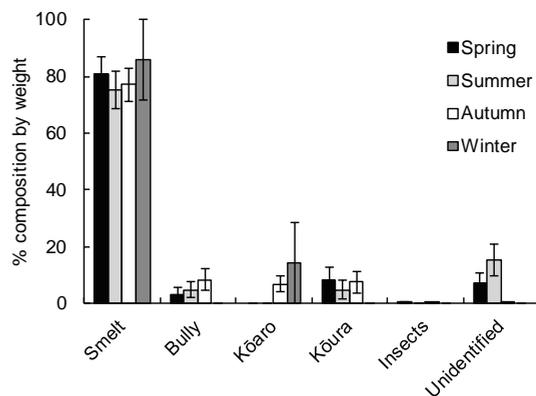
Table 2 Percentage frequency of occurrence of prey items eaten by rainbow trout of different length classes in Lake Rotoiti.

Trout length (mm)	<i>n</i> (Smith 1959)	Prey items (percentage frequency of occurrence)											
		Smelt	Kōura	Common bully	Kōaro	Amphipod	Tanaid shrimp	Aquatic insect	Terrestrial insect	Oligochaete	Mollusc	Unidentified	
<100	0	16	0.0	0.0	0.0	0.0	43.8	0.0	37.5	31.3	12.5	0.0	0.0
100–199	1	4	75.0	0.0	25.0	0.0	25.0	0.0	25.0	25.0	25.0	0.0	25.0
200–299	7	7	85.7	0.0	14.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
300–399	4	5	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
400–499	39	39	76.9	5.1	7.7	2.6	0.0	0.0	0.0	0.0	0.0	0.0	15.4
500–599	56	66	90.9	10.6	12.1	6.1	0.0	0.0	0.0	4.5	0.0	1.5	3.0
600–699	12	11	81.8	9.1	0.0	18.2	0.0	0.0	0.0	0.0	0.0	0.0	9.1
Total	119	148	76.4	7.4	8.8	4.7	5.4	0.7	3.4	6.1	2.0	0.7	6.8
Total (> 100 mm)	132	85.6	7.6	9.8	5.3	0.8	0.8	0.8	1.5	3.0	0.8	0.8	7.6
Smith (1959)	119	58.0	10.0	12.0 ^a	0.0	0.0	2.0	19.0	0.0	21.0	0.0	12.0	12.0

^aThis study did not distinguish between bullies and kōaro.

Table 3 Percentage composition by weight of prey items eaten by rainbow trout of different length classes in Lake Rotoiti (mean \pm 1 SE).

Trout length	<i>n</i>	Prey items (percentage composition by wet weight)							Unidentified		
		Smelt	Kōura	Common bully	Kōaro	Amphipod	Tanaid shrimp	Aquatic insect		Terrestrial insect	Oligochaete
<100	16	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	44.1 \pm 11.3	0.0 \pm 0.0	29.9 \pm 10.0	19.1 \pm 7.9	6.9 \pm 4.0	0.0 \pm 0.0
100–199	4	36.1 \pm 22.2	0.0 \pm 0.0	21.7 \pm 21.7	0.0 \pm 0.0	1.9 \pm 1.9	14.7 \pm 14.7	8.0 \pm 8.0	0.2 \pm 0.2	2.5 \pm 2.5	14.9 \pm 14.9
200–299	7	85.7 \pm 14.3	0.0 \pm 0.0	14.3 \pm 14.3	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0
300–399	5	100.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0
400–499	39	75.3 \pm 6.8	5.1 \pm 3.6	4.3 \pm 2.9	1.4 \pm 1.4	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	13.9 \pm 5.5
500–599	66	78.7 \pm 4.5	8.0 \pm 3.1	6.6 \pm 2.6	3.5 \pm 1.9	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.2 \pm 0.1	0.0 \pm 0.0	3.0 \pm 2.1
600–699	11	81.8 \pm 12.2	5.2 \pm 5.2	0.0 \pm 0.0	12.6 \pm 9.4	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.4 \pm 0.4
Total	148	72.3 \pm 3.5	5.5 \pm 1.8	5.5 \pm 1.7	3.0 \pm 1.2	3.2 \pm 1.3	0.4 \pm 0.4	2.3 \pm 1.1	1.4 \pm 0.8	0.6 \pm 0.4	5.7 \pm 1.8

**Figure 1** Seasonal changes in percentage composition of prey by wet weight eaten by adult rainbow trout (>400 mm) from Lake Rotoiti (mean \pm SE).

The energy density of smelt varied by almost a third between seasons and was lowest in winter (Table 4). Common bullies and smelt caught in autumn had similar energy densities, and kōaro caught in autumn had the highest energy density of all prey species. The energy density of kōura was similar to that of smelt. The mean length of smelt eaten by rainbow trout was 47.3 mm, with a range of 32.9–97.6 mm (Fig. 2). The maximum and median size of smelt eaten increased with trout size, but the minimum size of smelt did not change with trout length; the regression equations for the 0.10, 0.50, and 0.90 quantiles were $y = 37.0 + 0.00x$, $y = 34.2 + 0.03x$, and $y = 34.5 + 0.05x$, respectively, where y is smelt length (mm) and x is trout length (mm). All regressions were statistically significant ($P < 0.001$). The slopes of the 0.10, 0.50 and 0.90 regression quantiles were significantly different ($F_{(2,1303)} = 18.9$, $P < 0.001$).

Discussion

Our results indicate that smelt are the most important food source for rainbow trout in Lake Rotoiti, confirming previous estimates using stable isotopes of C and N in trout tissue (McBride 2005). Smelt now appear to be a more important food source for trout >200 mm

Table 4 Energy density of prey items of adult rainbow trout from Lake Rotoiti.

Species	Season	Mean length (mm)	Sample <i>n</i>	Mean energy density ± 1SE	
				J/g dry weight	J/g wet weight
Common bully	Autumn	43.7	4	13664 ± 370.3	3123 ± 151.1
Kōaro	Autumn	78.5	2	15299 ± 736.3	3636 ± 403.3
Kōura	Summer	113.5	2	9765 ± 53.3	2567 ± 14.0
Smelt	Autumn	38.0	4	15100 ± 261.4	2987 ± 44.8
Smelt	Spring	44.7	2	13932 ± 67.3	2605 ± 54.8
Smelt	Summer	53.7	2	13984 ± 139.8	2811 ± 14.3
Smelt	Winter	44.8	2	13485 ± 120.3	2089 ± 187.2
Smelt	Mean (all seasons)	42.5	8	14172 ± 149.6	2560 ± 95.6

compared with earlier records; rainbow trout in Lake Rotoiti have shifted from an omnivorous diet high in insects and molluscs (Smith 1959) to a mainly piscivorous diet containing few insects and molluscs (Table 3). Rainbow trout in Lake Rotoiti, which is now mesotrophic, consumed fewer insects and more common bullies and kōaro than trout in oligotrophic Lake Taupō (Cryer 1991). Nutrient inputs caused Lake Rotoiti to become more eutrophic between 1955 and the present (Vincent et al. 1984; Scholes 2009), which may have caused increases in production and smelt availability.

Subadult and small adult rainbow trout (200–400 mm) tended to eat mainly smelt, and large adult rainbow trout (>400 mm) con-

sumed a wider variety of prey items including kōura and fish other than smelt, consistent with other studies of rainbow trout in central North Island lakes (Smith 1959; Rowe 1984; Cryer 1991). In our study, differences in diet composition were not statistically significant between size classes because of low sample sizes. Patterns of prey consumption with size seem to be consistent between studies, despite the fact that Rowe (1984) and Smith (1959) sampled trout in summer and winter, respectively, and Cryer (1991) sampled trout year-round. The relationship between length of trout and length of ingested smelt (maximum size of prey increases with predator length) is consistent with that seen in predator–prey relationships where prey size is limited by the gape size of the predator (Boubée & Ward 1997; Persson et al. 1996; Nilsson & Bronmark 2000). Larger, benthic species such as kōaro and kōura were only eaten by trout larger than 400 mm, suggesting a change in feeding strategy to incorporate more benthic feeding around this length.

We found little evidence of seasonal variation in the diet of rainbow trout in Lake Rotoiti, similar to rainbow trout in Lake Taupō (Cryer 1991). In contrast, rainbow trout in Lake Rotomā displayed a seasonal dietary shift from more epibenthic prey (common bully and kōura) in summer, to more pelagic prey (smelt) in winter (Rowe 1984). However, we did find seasonal differences in the percentage of

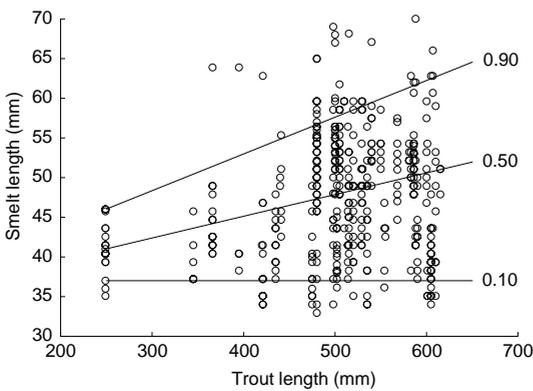


Figure 2 Relationship between smelt and trout lengths (FL), with 0.10, 0.50 and 0.90 regression quantile estimates (solid lines; *n* = 435).

empty stomachs. The proportion of empty stomachs generally increases with temperature in fish (Vinson & Angradi 2010), but the cause of increased stomach emptiness in summer in Lake Rotoiti is not known; unmeasured factors such as prey availability may have influenced the occurrence of empty stomachs. We found no evidence of prey switching in Lake Rotoiti during winter when smelt energy density was lowest, suggesting that variation in energy density was not great enough to cause a change in the prey species eaten by trout. However, the amount of prey eaten may change; this is a potential question to be addressed by bioenergetic modelling.

Though we have documented predation on kōaro and kōura by rainbow trout, the effects of trout predation on kōaro and kōura populations are not known. Impacts of introduced salmonid species on native galaxiid populations in lakes are not well understood (McIntosh et al. 2010) though historical evidence suggests that landlocked kōaro populations declined after the introduction of trout into some New Zealand lakes, including those in the Central North Island (McDowall 2006). However, competition with smelt may have also contributed to the decline of kōaro in central North Island lakes (Rowe 1993). Bioenergetic modelling has shown that rainbow trout exert significant predation pressure on native galaxiids in oligotrophic lakes in Argentina (Vigliano et al. 2009), and a similar approach should be implemented to quantify the effect of trout predation on native species in New Zealand lakes.

The accuracy of consumption estimates calculated using bioenergetic models depends on the quality of the input data. Values for prey energy density may be estimated or borrowed from other species and locations, but these practices may cause errors in consumption estimates (Ney 1993). It is therefore clear that energy density should be measured directly, in the relevant ecosystem if possible (Hartman & Brandt 1995). Seasonal changes in prey energy density should be assessed accurately because

they may be significant (Bryan et al. 1996; Rand et al. 1994), and can affect bioenergetic model outputs (Hartman & Brandt 1995). It is also important to measure seasonal changes in diet, because model outputs may be sensitive to variation in diet composition (Lyons & Magnuson 1987). The data measured in this study will provide a basis for bioenergetic modelling of rainbow trout populations in lakes of the central North Island of New Zealand. Possible further refinements of the data include characterising the variation in energy density of smelt with size, and the predation upon different size classes of smelt by trout of different sizes. Stratified sampling of rainbow trout by habitat (e.g. pelagic vs benthic) may also help to define feeding patterns.

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