Factors controlling common smelt abundance and rainbow trout growth in the Rotorua Lakes, New Zealand

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Abstract

Recreational fisheries are of considerable ecological, economic and cultural importance worldwide, and understanding the factors that influence them is an important goal of fishery managers. The two most important factors influencing the growth of fish are habitat quality and food supply. This study was undertaken to gain a better understanding of how these two factors influence rainbow trout growth in the Rotorua Lakes, central North Island, New Zealand, by surveying prey dynamics, quantifying rainbow trout diet, and assessing the effects of environmental factors and population density on trout growth.

Rainbow trout populations in lakes of New Zealand's central North Island mainly prey upon common smelt (*Retropinna retropinna*), a small, widespread, pelagic species. Routine monitoring of smelt populations would assist in trout fishery management decisions, especially for optimisation of stocking rates and timing. To recommend an effective capture technique for smelt, we tested purse seining, beach seining, drop netting, and boat electrofishing in Lake Rotoiti. Boat electrofishing in the littoral zone at night allowed us to collect more adult smelt than all other methods, and long boat electrofishing transects across the lake were the most effective method for capturing a wide size range of smelt specimens, including larvae. Most methods also caught other species as bycatch. In terms of the number of smelt caught, the most effective method was (1) boat electrofishing at night, followed by (2) scoop nets at night (i.e. boat electrofishing with the current turned off), then (3) beach seining during the day. The first two sampling methods are suggested as the best methods for collecting data on seasonal dynamics, growth, and reproduction of smelt. For enumeration of the total smelt population, these methods should be carried out in the littoral and pelagic zones and combined with a method such as hydroacoustics that can enumerate smelt in the deeper waters of the pelagic zone.

Population dynamics of common smelt in lakes are not well understood. To determine the factors influencing smelt populations in Lake Rotoiti, we examined seasonal changes in habitat and resource use by measuring spatial and seasonal changes in smelt abundance, body condition, and diet. We also characterised seasonal and spatial changes in smelt reproductive state and benthic egg abundance. Smelt abundance in the littoral zone and surface waters of the pelagic zone was highest in autumn, coinciding with peaks in smelt body condition, gonadosomatic index, and benthic egg abundance. Smelt larvae were only found in the pelagic zone, and were more abundant in spring than in summer and autumn. Body condition of smelt varied throughout the year, and was lowest in winter, a period of low abundance of littoral invertebrates and zooplankton. Smelt caught in the littoral zone during the day consumed a range of benthic and pelagic invertebrates and smelt eggs, while at night, smelt caught in the littoral and pelagic zones consumed zooplankton, smelt eggs and larval common bully (*Gobiomorphus cotidianus*). The amount of food in the stomach relative to smelt mass was higher in the littoral zone than in the pelagic zone, suggesting that food resources in the littoral zone exceed those in the pelagic zone. Predation on zooplankton was highest in winter and spring, and smelt eggs formed a large proportion of smelt diet in autumn and winter. Stomach contents and stable isotope analyses showed that smelt undergo an ontogenetic change in diet, from mainly zooplankton as juveniles to mainly benthic invertebrates as adults. The information obtained in this study is necessary for managing smelt and their predator—rainbow trout—in lakes.

To better understand the prey requirements of trout in central North Island lakes, we characterised seasonal and ontogenetic changes in diet and prey energy density of rainbow trout in Lake Rotoiti. Common smelt was the dominant prey item of rainbow trout larger than 200 mm (77.8% of diet by mass), followed by koura (freshwater crayfish *Paranephrops planifrons*; 6.3%), common bully (5.5%), and koaro (*Galaxias brevipinnis*; 3.4%). Juvenile rainbow trout (<200 mm) consumed amphipods, aquatic and terrestrial insects, oligochaetes, tanaid shrimps, and smelt. Trout consumed koaro 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 (koaro and koura) 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 bioenergetics modelling of rainbow trout populations in lakes of the central North Island of New Zealand.

Though the factors influencing the growth of salmonids in cool-temperate and boreal climates are well understood, we lack an understanding of the influences on salmonid growth in warm-temperate areas, especially in lakes. To determine the combined effects of environmental factors, including habitat, on rainbow trout growth, we investigated the growth patterns of rainbow trout (*Oncorhynchus mykiss*) in nine warm-temperate New Zealand lakes of contrasting morphometry, mixing regime, and trophic state. Mark-recapture data (some collected by anglers) from hatchery trout releases during eight consecutive years were used to calculate growth parameters and body condition factor. Fish growth rates and condition factors were highest in deep (≥20 m mean depth) lakes of moderate trophic state. Overall, growth rate increased with increasing lake size and volume of favourable habitat (i.e. dissolved oxygen >6.0 mg L^{-1} and temperature <21°C), but decreased with increasing turbidity, chlorophyll *a*, and nitrogen concentrations. A classification and regression tree (CART) analysis found that variables describing habitat volume were the most important determinants of trout growth rate, and correlates of trophic state (chl *a*, conductivity) were important secondary determinants of trout growth rate. These results suggest that lake morphometry and trophic state are important attributes structuring overall habitat quality and thus influencing growth of rainbow trout in lakes in warm-temperate climates. The effects of future ecosystem degradation and climate warming on trout growth are likely to be most severe in shallow, eutrophic lakes.

To investigate the carrying capacity and factors affecting growth of rainbow trout in Lake Rotoiti, we employed a bioenergetics model to assess the influence of past stocking rates, timing of releases, and prey abundance on growth and prey consumption. We hypothesised that stocking rates and prey abundance would affect growth and prey consumption by influencing per-capita prey availability, and that the environmental conditions encountered by fish at the time of stocking would affect growth and consumption. Prey consumption of stocked rainbow trout was calculated with the Wisconsin bioenergetics model. We calculated growth trajectories based on data from trout that were stocked into the lake in spring and autumn from 1995 to 2009 and then re-captured by anglers. Diet, prey energy density, body mass lost due to spawning, and lake temperature were measured locally. There was no difference in tag return rate between fish released in spring and autumn. Though trout released in autumn were smaller initially, they grew at a faster rate than trout released in spring. The ratio of observed to predicted change in biomass at the maximum consumption rate by individual trout in the first year of lake residence was negatively correlated with the number of yearlings released in a cohort, suggesting that stocking rates (347–

809 fish ha^{-1} $year^{-1}$) caused density-dependent effects on growth. Common smelt accounted for 85% of total prey consumption. However, no significant relationship was found between prey consumption by individual trout and adult smelt abundance, suggesting that more detailed investigations of smelt abundance are required to predict trout growth rates. Because there is little risk of non-human predation of stocked fish in Lake Rotoiti, and winter temperatures are mild (11–14°C), stocking smaller trout (~160 mm fork length) in autumn is likely to produce larger fish than stocking larger fish (~200 mm fork length) in spring. Possible reasons for this difference include higher prey abundance in the littoral zone in autumn and more suitable temperature and dissolved oxygen habitat in autumn-winter. These results suggest that optimal stocking strategies in warm-temperate systems may differ to those in cooler temperate regions.

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List of Abbreviations

a	y-axis intercept of mass-length regression equation
a'	modified y-axis intercept of mass-length regression equation
α	significance level of statistical test
ANOVA	analysis of variance
b	slope of mass-length regression equation
CART	classification and regression trees
chl a	cholorophyll a
CI	confidence intervals
CTD	conductivity-temperature-depth
df	degrees of freedom
dL / dt	fish growth rate (i.e. change of length with time)
DO	dissolved oxygen
EF	electrofishing
FL	fork length
HSD	Tukey's honestly significant difference
K	growth coefficient (the rate at which fish approach L_∞; parameter of von Bertalanffy growth model)
K-W test	Kruskal-Wallis test
L	length
L	littoral zone (Chapter 2) large smelt (> 50 mm, Chapter 3)
L_∞	theoretical maximum length (parameter of von Bertalanffy growth model)
LD	littoral zone, day
LN	littoral zone, night
L_t	length at time t (parameter of von Bertalanffy growth model)
M	medium smelt (40–50 mm, Chapter 3) monomictic (Chapter 5)
M-W U test	Mann-Whitney U test
n	sample size
P	P-value (significance) of statistical test
P	pelagic zone (Chapters 2 & 3) polymictic (Chapter 5)

pC_{max}	the proportion of theoretical maximum daily ration required for an “average” individual fish to produce the observed growth
PD	pelagic zone, day
PN	pelagic zone, night
r	Pearson correlation coefficient
S	small smelt (<40 mm)
SE	standard error
SL	standard length, measured to the end of the caudal peduncle
SS	sum of squares
T	temperature
t_0	x-axis intercept of von Bertalanffy growth model (yr)
T1–6	Transects 1–6
TDS	total dissolved solids
TLI	Trophic Level Index
TN	total nitrogen
TP	total phosphorus
W	mass
z	lake depth
Z	instantaneous rate of total mortality

Preface

The main body of this thesis is made up of five research chapters presented as individual papers, some of which have been submitted or accepted for publication in peer-reviewed publications. For this reason, there are some repetitions and slight differences in style among chapters. To conform with the preferred style of particular journals and to make my writing clearer I have often used the active tense and the personal pronoun "we" according to the general convention for articles with multiple contributors. The following data was provided by other organisations: capture records for rainbow trout were provided by Eastern Region Fish & Game, and lake water quality data was provided by the Bay of Plenty Regional Council. All other content in this thesis, unless a citation is given, is based on my own ideas and work. This work was undertaken while under the supervision of Assoc. Prof. Brendan Hicks (University of Waikato), Assoc. Prof. Nicholas Ling (University of Waikato), Robert Pitkethley (Eastern Region Fish & Game), and Dr. Ilia Ostrovsky (Israel Oceanographic & Limnological Research).

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Chapter 6 has been submitted to Freshwater Biology as "Do stocking practices influence rainbow trout (*Oncorhynchus mykiss*) growth and consumption in a New Zealand lake? A bioenergetic assessment" by J. Blair, B. Hicks, R. Pitkethley, N. Ling, I. Ostrovsky, and D. Rowe.

1 General introduction

1.1 Introduced fish, recreational fishing, and rainbow trout in New Zealand lakes

Fish are introduced into freshwater systems around the world for many reasons, including to conserve or reintroduce species, mitigate loss of stocks, to create new fisheries, and to enhance the commercial or recreational catch (Cowx 1994). In developed countries, the reason for introduction is often to provide recreational fishing opportunities (Welcomme and Bartlet 1998). Freshwater recreational fisheries provide significant ecological, social and economic benefits (Arlinghaus et al. 2002, Welcomme et al. 2010) and cultural ecosystem services (Beaumont et al. 2007, Cowx and Portocarrero Aya 2011). Angling for introduced salmonids such as rainbow trout *Oncorhynchus mykiss* is a popular pastime in New Zealand, and freshwater recreational fisheries are a valuable component of the tourism industry. Rainbow trout were introduced into several lakes and waterways around New Zealand from the late 19th century (Burstall 1980) and now form landlocked populations around the central North Island and in some South Island rivers and lakes (McDowall 2000). The lakes of the central North Island attract the most recreational fishing effort compared to lakes in other regions (Unwin 2009). Natural populations are sustained in lakes Rotorua, Taupo and Waikaremoana by spawning in the surrounding tributaries, but other lakes lack sufficient spawning area to support abundant wild populations. These lakes are supplementary stocked with hatchery-reared trout yearlings by the Eastern Region Fish & Game Council (Fish & Game; Table 1.1). Fish & Game's breeding programme, based at Ngongotaha in Rotorua, stocks yearling trout into 16 lakes in the area (Table 1.1). The aim of this breeding programme is to supplement limited wild trout stocks and enhance angler opportunities.

Table 1.1. Mean numbers of trout stocked into lakes in the Rotorua region between 1990–1999 and 2000–2009. Sources: Lake area: Scholes and Bloxham (2007), trout stocking rates: Fish & Game New Zealand (unpubl. data).

			Mean number of trout stocked per year	
Lake	Lake area (km^2)	Maximum depth (m)	1990–1999	2000–2009
Okareka	3.3	30	13600	6000
Okaro	0.33	18	415	735
Okataina	10.8	65	3368	3950
Rerewhakaaitu	5.9	15	7590	7400
Rotoehu	8.1	14	4675	4764
Rotoiti	34.6	94	13310	24250
Rotoma	11.2	83	4804	4925
Rotorua	80.8	26	1000	1000
Tarawera	41.7	88	13153	18250
Tikitapu	1.5	28	165	0

In the Rotorua area in the central North Island of New Zealand, appropriate trout stocking densities for each lake have been found through trial and error. Early attempts to improve fisheries by stocking increased numbers of hatchery-raised fingerlings resulted in a decline in trout size in several lakes in the Rotorua region (Fish 1963, Fish et al. 1968). Trout stocking rates in Lake Okareka were gradually increased between 1984 and 1997 to assess the effects of trout density on trout condition at capture, but a downward trend in length and mass of trout captured resulted in the discontinuation of the trial in 1996 (Garrick 2000). No other investigations of trout stocking density have been carried out in New Zealand lakes, and the carrying capacity of the lakes to support increased trout stocking is not known.

The distribution of rainbow trout within deep lakes in New Zealand is highly varied and is likely driven by temperature and food availability. In Lake Taupo, rainbow trout were found in higher densities in the inshore zone than in offshore regions, especially in spring, when their main prey, common smelt *Retropinna retropinna*, were spawning in the littoral zone (Cryer 1991). Rainbow trout in Lake Taupo were found to swim in the upper 20 m of the water column during the day, maintaining a body temperature of 15–16ºC (M. Dedual, Department of Conservation, pers. comm.). Similarly, in lakes Rotoiti and Rotoma (maximum depths 94 and 83 m), larger trout were found between 10 and 40 m, around the thermocline, though small trout were detected in the surface waters during autumn, when prey were abundant (Rowe and Chisnall 1995). Low dissolved oxygen concentrations in the bottom waters of Lake Rotoiti constrained habitat during summer, forcing trout into shallower waters (Rowe and Chisnall 1995). In Lake Coleridge in the South Island (maximum depth 200 m), some rainbow trout occupied the littoral zone year-round, while others occupied limnetic habitats during summer and early autumn, and moved into littoral areas in winter and spring (James and Kelso 1995). Diel changes in habitat are also possible; rainbow trout in Lake Otamangakau were observed to occupy deep water during the day, and move into surface and littoral areas at night (Dedual et al. 2000).

In shallower lakes, warm water temperatures may constrain trout distribution. Rainbow trout in the shallower lake Rotorua (maximum depth 26 m) are evenly distributed throughout the lake when water temperatures are less than 18ºC, but aggregate around the mouths of cold spring-fed inlet streams in the north-western area of the lake when the water exceeds this temperature (Boubée et al. 2006). The amount of time spent either in or near the streams may vary from a few days to several months (Boubée et al. 2006). Because rainbow trout are adapted to cold temperatures, warm temperatures in lakes of New Zealand's North Island may constrain growth, but the effects of warm temperatures in this area have not yet been examined.

The diet of rainbow trout in New Zealand is highly varied and may include small fish, terrestrial and aquatic invertebrates and the koura (freshwater crayfish), *Paranephrops planifrons.* Diet varies with ontogeny, season and lake trophic status, but the common smelt, *Retropinna retropinna*, is often the main food source for rainbow trout in central North Island lakes. In these lakes, smaller adult trout tend to consume mainly smelt, whereas larger adult trout tend to consume a wider range of prey including smelt, koura, invertebrates, and other fish (Cryer 1991, Rowe 1984, Smith 1959). A seasonal shift in diet has been observed in Lake Rotoma rainbow trout; in summer, more epibenthic prey was found in trout stomachs, whereas more pelagic prey were found in trout stomachs in summer (Rowe 1984). Additionally, stocked trout ate more pelagic prey (smelt) than wild trout, which ate more benthic prey such as common bully *Gobiomorphus cotidianus* (Rowe 1984). Trout diet also changes with lake trophic status; trout living in deep oligotrophic lakes in the central North Island eat proportionally more smelt than trout living in shallow, eutrophic lakes, where benthic feeding on common bullies is more common (McBride 2005, Rowe 1984). In comparison, rainbow trout in Lake Benmore in the South Island were found to prey mainly upon gastropod molluscs (McCarter 1986). 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 the diet of adult fish during 1 to 3 seasons (Rowe 1984, Smith 1959). 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.

1.2 Predator-prey relationships and bioenergetics modelling

Food supply is one of the most common factors influencing fish growth (Ney 1990). The relationships between prey production and predator production are complex because predator-prey relationships are mediated by several factors. For predatory fish in freshwater systems, food supply is influenced by prey density (Brandt et al. 2011), prey quality or size (Boisclair and Leggett 1989, Juncos et al. 2011, Pazzia et al. 2002), and prey encounter rate, which depends on prey density and environmental conditions (Beauchamp et al. 1999, Brandt et al. 1992, Mason et al. 1995). Insufficient food supply can lead to reduction in growth (Jobling 1994, Levin et al. 1997), decreased reproduction (Townshend and Wootton 1984, Wootton 1973) and changes in energy deposition (Miglavs and Jobling 1989). Therefore, the carrying capacity of receiving systems to support the growth of predatory fish should be considered when managing stocked sports fisheries.

Given that fish growth is influenced by many interacting factors, bioenergetics models are powerful tools for quantifying predator-prey relationships in space, time, ontogeny, and linking trophic relationships to key environmental variables (e.g. temperature). The widely-used Wisconsin bioenergetics model (Hanson et al. 1997) uses mass-balance equations to estimate the proportion of the maximum theoretical consumption rate required to produce the observed growth of fish, given the costs of activity, egestion, excretion, and specific dynamic action (the energy expended to assimilate food). The model is based on the following equation:

$$C = (R + A + S) + (F + U) + (\Delta B + G) \tag{1.1}$$

where C is consumption, R is respiration, A is active metabolism, S is specific dynamic action, F is egestion, U is excretion, ΔB is somatic growth and G is gonad production. The model can be used to find either (1) the amount of consumption required to produce the observed amount of growth, or (2) the amount of growth produced when fish are fed at a known rate. Required inputs include temperature experience, diet, growth, predator and prey energy density, and physiological parameters related to respiration, consumption, egestion, and excretion. Consumption estimates can then be scaled up to the population level if required. The Wisconsin bioenergetics model been used in a wide range of situations, including assessing the effects of temperature and prey availability, modeling contaminant bioaccumulation, modeling the effects of species introductions, and comparing predator consumption with prey production, often with the goal of optimizing fishery management practices such as stocking rates or angler catch allowances (reviewed by Ney 1990, 1993). Recent applications include assessing the energetic benefits of diel vertical migration (Busch et al. 2011, Mehner et al. 2011), predicting the bioaccumulation of contaminants after management actions or climate change (Lepak et al. 2012, Ng and Gray 2011), estimating rates of carbon turnover in fish muscle (Weidel et al. 2011), and predicting the effects of temperature (Moody et al. 2011) and food web structure on growth (Juncos et al. 2011, Wuellner et al. 2010). The broad range of possible applications of the model make it a useful tool for assessing predator-prey relationships.

1.3 Common smelt ecology

The common smelt *Retropinna retropinna* is a small, pelagic freshwater fish native to New Zealand, and is the principal prey of rainbow trout in lakes of the central North Island of New Zealand (Cryer 1991, Rowe 1984, Smith 1959). It is widespread and abundant in low-elevation rivers, estuaries and lakes, and may exist in diadromous or landlocked populations (McDowall 1990, Ward et al. 2005). Landlocked populations of smelt have been established by introductions to lakes lacking access to the sea, especially in the Rotorua and Taupo regions (Ward et al. 2005), and landlocked populations also exist in reservoirs created by hydroelectric dams on the Waikato River (Booker 2000).

Diadromous and lacustrine smelt display many differences in morphology and life history (McDowall 1990, Ward et al. 2005). Lacustrine populations in Waikato lakes, lacustrine populations in the volcanic plateau, and diadromous populations in the Waikato River are genetically distinct, either due to geographic separation, or life history differences where diadromous and lacustrine forms live in sympatry (Mitchell et al. 1993, Northcote and Chapman 1999). Smelt were probably introduced into Lake Rotorua (and therefore also into Lake Rotoiti via the Ohau Channel) prior to 1900 by Maori (Strickland 1993), and populations were also supplemented in the early 1900s to provide food for rainbow trout (Burstall 1980). Access to the sea is blocked by the Okere Falls on the Kaituna River, preventing dispersal into the lake by natural means.

Factors controlling the abundance of smelt in lakes are not well understood, but abundance appears to be regulated by their relative intolerance of conditions associated with increased eutrophication, such as increased turbidity. For example, lacustrine smelt disappeared from Lake Waahi following an increase in turbidity and loss of macrophytes (Hayes et al. 1992, Ward et al. 1987). Abundance of larval smelt is highest in lakes with high water clarity, possibly because sedimentation in more turbid lakes leads to higher smelt egg mortality (Rowe and Taumoepeau 2004). In Lake Taupo, little spawning occurred in areas where a high amount of organic detritus had built up (Stephens 1984). A reduction in feeding may also affect the ability of smelt to survive in turbid lakes; in laboratory trials, juvenile smelt showed a trend of decreasing feeding rates with increasing water turbidity (Rowe and Dean 1998). A better understanding of the factors controlling smelt abundance would help us to better predict the effects of ecosystem change on this species.

A high degree of variability has been reported in the life history parameters of smelt; for example, spawning seasons are typically variable and may last several months (Ward et al. 2005). Diadromous smelt spawn in autumn-winter in shallow parts of rivers and tributary streams (Ward et al. 1989), and lacustrine smelt spawn in spring and summer on sandy beaches or stream mouths, in water 0.5–2.5 m deep (Stephens 1984), though winter spawning is also possible (Ward et al. 2005), and smelt in the Ohau Channel have been observed to spawn year-round (Rowe et al. 2006). Stephens (1984) found that 90–95% of spawning in Lake Taupo occurred in the lake, though stream spawning accounted for 50–60% of spawning activity in the western bays of Lake Taupo, where beach habitat was limited. Spawning occurs at age 1 in most smelt (Ward and Boubée 1996), and female smelt may recover 6–8 weeks after their first spawning and spawn for a second time (Stephens 1984).

Lacustrine smelt populations often display temporal variation in habitat use. In lakes Ellesmere, Waihola, and Taupo, smelt catches in the littoral zone were highest in summer (Cryer 1991, Glova and Sagar 2000, Kattel and Closs 2007, Stephens 1984). In Lake Rotoiti, smelt occupied distinct layers in the water column during the day, and ascended to the surface at dusk (Rowe 1993). Smelt aged 0–1 years (15–43 mm F. L.) were found between depths of 2–10 m, whereas adult smelt (51–73 mm F. L.) were found at depths of 30–50 m (Rowe 1993). In lakes Taupo (Cryer 1991) and Rotoiti (Rowe et al. 2011), biomass was highest in the deeper parts of the lakes. Ontogenetic patterns in habitat use are also evident; in Lake Taupo, larval smelt were caught exclusively in the pelagic zone, whereas juvenile and adult smelt were found in both the littoral and pelagic zones (Stephens 1984).

Common smelt are generalist, opportunistic feeders and may switch prey according to availability. The mean prey size of smelt increases with smelt length and gape size (Boubée and Ward 1997); zooplankton often make up the majority of the diet of smelt <40 mm in length, while larger smelt may consume a wider range of prey including adult terrestrial and aquatic insects, aquatic insect larvae, spiders, mysid shrimp, fish larvae, amphipods and springtails (Boubée and Ward 1997, Cryer 1991, Northcote and Chapman 1999, Stephens 1984). Predation by smelt has been shown to influence zooplankton abundance (Cryer 1988). Because smelt consume benthic and pelagic invertebrates, smelt diet is dependent on production from both benthic and pelagic sources. Therefore, characterising their diet can help determine the contributions of benthic and pelagic sources of productivity to the higher trophic levels (Vadeboncoeur et al. 2002).

1.4 The Rotorua Lakes

The Rotorua area in the Bay of Plenty region of New Zealand’s North Island contains several lakes of varying size, depth and geological origin. Catchment land use varies widely among the lakes, creating a wide range of in-lake conditions. Some lakes are highly eutrophic (lakes Rotorua, Rotoehu, and Okaro) while others, such as lakes Tarawera and Okataina, remain oligotrophic (Scholes 2009). All lakes are subject to management plans that aim to reduce external and internal nutrient inputs (Burns et al. 2009).

Lake Rotoiti is a warm, monomictic, eutrophic lake in the Rotorua area, and was chosen as the main focus in this study because of its popularity as a trout fishery and because recent management actions had the potential to affect its fish populations. Nutrient inputs have caused water quality in Lake Rotoiti to decline significantly between 1955 and the present (Scholes 2009, Vincent et al. 1984), despite improvements between 1981 and 1994 (Burns et al. 1997). Lake Rotoiti's hypolimnion becomes deoxygenated during summer stratification, leading to phosphorus release from sediments (Hamilton 2003). Water flowing from Lake Rotorua into Lake Rotoiti via the Ohau Channel constituted a significant input of nutrients and algae and was chiefly responsible for the reduction of water quality in Lake Rotoiti (Hamilton et al. 2005). To improve water quality, the Bay of Plenty Regional Council built the Ohau Channel Diversion Wall, which was completed in 2008. This wall diverts water flowing from Lake Rotorua into Lake Rotoiti through the Ohau Channel. Most of the water flowing out of Lake Rotorua now flows directly down the Kaituna River rather than into Lake Rotoiti.

It is necessary to assess the effects of diversion wall construction on fish populations, because juvenile and adult smelt regularly migrate from Lake Rotoiti into the Ohau Channel (Rowe et al. 2006). Migrations occur over many months, and timing may vary; peak numbers of migrating juvenile and adult smelt have been observed in the Ohau Channel at various times between August and March (Donald 1996, Rowe et al. 2006). Monitoring of smelt populations in Lake Rotoiti has taken place before, during and after construction of the Ohau Channel Diversion Wall to detect any effects of wall construction. Acoustic surveys showed no significant change in smelt populations between 2005 and 2010 (Rowe et al. 2011). Nevertheless, it is necessary to assess the sustainability of smelt populations to support continued stocking of rainbow trout in the context of a changing lake environment as restoration measures take effect.

1.5 Objectives

The objectives of this study were to (1) determine the dynamics of the abundance of common smelt, (2) determine the factors that control smelt abundance, (3) determine the relationship between smelt abundance and trout growth, and (4) examine the factors influencing trout growth in the study area.

1.6 Thesis overview

This thesis comprises five research chapters (Chapters 2–6) that have been separately prepared for, or submitted to, peer-reviewed journals. The first chapter gives a general introduction to the topics presented in the thesis and indicates how each chapter contributes to the overall study objectives. The final chapter gives conclusions and recommendations, and suggests areas for further research.

Chapter 2 assesses the efficacy of various sampling techniques for collecting smelt in lake environments. This study was a necessary first step for assessing the dynamics of smelt abundance (Objective 1).

In Chapter 3, the ecology of common smelt in Lake Rotoiti was examined to determine the factors influencing growth and abundance (Objectives 1 and 2). This involved an analysis of spatial and seasonal changes in smelt relative abundance, body condition, spawning condition, diet, and egg densities on beaches. Benthic invertebrates and zooplankton were surveyed to determine possible food limitation.

Chapter 4 examines the contribution of various prey types to the diet of rainbow trout of different sizes in Lake Rotoiti. This was necessary to quantify the magnitude of predation on smelt by rainbow trout and to determine the importance of smelt for trout growth (Objective 3).

Chapter 5 focusses on the influences on growth and body condition of rainbow trout among lakes that vary in morphometry, trophic state, and mixing regime. This analysis assessed the relative influence of various environmental factors on trout growth (Objective 4). The effects of food supply were considered indirectly through analysis of lake productivity and trout body condition.

In Chapter 6, the effects of rainbow trout stocking rates and timing on prey consumption were investigated using a bioenergetics model. This study assessed whether food supply (i.e. smelt populations) were adequate to support optimal growth of rainbow trout given past and current rates of trout stocking, and addressed Objectives 3 and 4.

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2 A comparison of capture methods for sampling common smelt (*Retropinna retropinna*) in lakes

2.1 Abstract

Common smelt (*Retropinna retropinna*) are the main prey of rainbow trout (*Oncorhynchus mykiss*) in central North Island lakes, and are therefore important for supporting the iconic recreational rainbow trout fisheries in this area. Routine monitoring of smelt populations would assist in trout fishery management decisions, especially for optimisation of trout stocking rates and timing. To suggest an effective sampling technique for smelt, we tested purse seining, beach seining, drop netting, and boat electrofishing in Lake Rotoiti. Because smelt form large schools that are difficult to catch with hand nets while boat electrofishing, we employed a modified boat electrofishing technique by mounting two whitebait nets behind the boat's electrodes. We tested the efficacy of boat electrofishing during the day and at night in the littoral and pelagic zones. Scoop nets were also tested (i.e. using the same apparatus as boat electrofishing, but with the current turned off). Smelt catches were highly variable among methods. Boat electrofishing in the littoral zone at night (117–487 m transects) allowed us to collect more adult smelt than all other methods, and boat electrofishing transects across the lake (666–3000 m) were most effective for sampling a wide size range of smelt specimens including larvae. Most methods also caught other species as bycatch, such as common bullies (*Gobiomorphus cotidianus*), juvenile rainbow trout, and goldfish (*Carassius auratus*). In terms of the number of smelt caught, the most effective method was boat electrofishing at night, followed by scoop nets at night, then beach seining during the day. Sampling the surface waters with boat-mounted nets is suggested as the best method for collecting data on seasonal habitat use, diet, growth, and reproduction of smelt. For enumeration of the total smelt population, surface sampling should be carried out in the littoral and pelagic zones and combined with a method that can enumerate smelt in the deep pelagic zone, such as hydroacoustics or midwater trawling.

2.2 Introduction

The common smelt (*Retropinna retropinna*) is a widespread, pelagic, schooling fish found in New Zealand’s rivers and lakes. Common smelt are important for sustaining rainbow trout fisheries because they are the main prey species of rainbow trout in central North Island lakes (Chapter 4). Knowledge of inter-annual changes in relative smelt abundance gained through routine monitoring would assist fishery managers with trout stocking and management decisions. However, monitoring of smelt populations in lakes remains a challenge due to their schooling behaviour and depth distributions. Rowe (1993) showed that in deep lakes, smelt occupy deep water (30–40 m) during the day, and ascend to the surface at night. Several methods have been used to sample smelt in lakes, including purse seine nets (Mylechreest 1990), boat-mounted push nets (Kattel and Closs 2007), weighted drop nets (Stephens 1984), Wisconsin plankton nets (Rowe et al. 2011), echo sounding (Rowe et al. 2011), and beach seine nets (Cryer 1991, Stephens 1984). Sampling methods employed in rivers include boat electrofishing (Brijs et al. 2010, Tana and Hicks 2011), beach seine nets (Booker 2000), and traps (Rowe et al. 2011). These methods have been employed in different zones of lakes or rivers and target different life stages of smelt (Table 2.1).

To assess smelt population parameters such as growth and body condition, a sampling method should be able to capture a large number of fish of a wide range of sizes. Ideally, the sampling method should be inexpensive and easy to deploy for small field teams of 2 to 3 people. The aims of this study were to trial and compare various smelt sampling techniques in Lake Rotoiti and to recommend a method that can be used for routine monitoring. Additionally, we aimed to test and evaluate boat electrofishing with scoop nets as a novel methodological approach for smelt sampling.

Table 2.1. Summary of previously published smelt catch rates in New Zealand using different methods. EF = electrofishing. L = littoral; P = pelagic.

	Smelt catch			Smelt length					
Method	Mean	Range	Units	range (mm)	Season	Day/night	Water body	Zone	Reference
Methods measured in fish m^{-2}									
Boat EF	0.015	0–0.043	fish m^{-2}	42–78 (mean = 59)	Summer	Day	Ohau Channel	L	Brijs et al. (2010)
	0.001	0–0.004	fish m^{-2}	31–60 (mean = 48)	Summer	Day	Ohau Channel	L	Tana and Hicks (2011)
Purse seine	3		fish m^{-2}	14–39	Autumn	Day	Lake Tarawera	P	Mylechreest (1990)
	0.8		fish m^{-2}	12–47	Autumn	Night	Lake Tarawera	P	Mylechreest (1990)
	0.90	0.0005–2.27	fish m^{-2}	26–50	Year-round	–	Lake Taupo	L	Cryer (1991)
Echosounding	0.9	0.0–4.8	fish m^{-2}	<45	Spring	Day	Lake Rotoiti	P	Rowe et al. (2011)
	59	9–138	fish m^{-2}	–	Year-round	–	Lake Taupo	P	Cryer (1991)
Drop net	24	5–50	fish m^{-2}	15–40	Year-round	–	Lake Taupo	P	Cryer (1991)
Beach seine	9.1	0.1–32.8	fish m^{-2}	35–51 (mean = 44)	Year-round	Day	Lake Taupo	L	Stephens (1984)
	0.3	0.0–1.1	fish m^{-2}	40–82 (mean = 49)	Year-round	Night	Lake Taupo	L	Stephens (1984)
Methods measured in fish sample^{-1}									
Plankton net	–	0.42–2.52	fish sample^{-1}	0–25	Spring, autumn	Day	Lake Rotoiti	P	Rowe et al. (2011)
Drop net	7	2–26	fish sample^{-1}	8–35 (mean = 20)	–	Day	Lake Taupo	P	Stephens (1984)
Push net		0.0–1.5	fish sample^{-1}	–	Year-round	Night	Lake Waihola	L	Kattel and Closs (2007)
		0.0–0.9	fish sample^{-1}	–	Year-round	Day	Lake Waihola	L	Kattel and Closs (2007)
Method measured in fish min^{-1}									
Traps		0–9.5	fish min^{-1}	Juveniles and adults	Year–round	Day	Ohau Channel	L	Rowe et al. (2011)

2.3 Methods

We compared the efficacy of boat electrofishing, beach seining, drop netting, and purse seining to sample smelt in the littoral and pelagic zones of Lake Rotoiti, in the North Island of New Zealand. Lake Rotoiti (38.04º S, 176.44º E; Fig. 2.1) is warm, monomictic, and mesotrophic, with a surface area of 34 km^2, and a mean depth of 31 m. The western end of the lake is shallow, with depth increasing from the western to the eastern end of the lake, where the maximum depth is 125 m. A summary of sampling methods is given in Table 2.2.

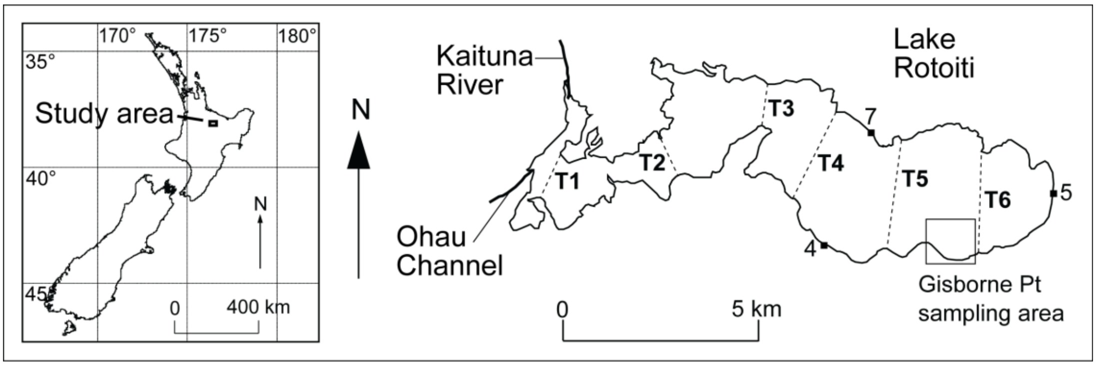

Fig. 2.1. Study area showing Lake Rotoiti and its main inlet (Ohau Channel) and outlet (Kaituna River), with sampling beaches (black squares: 4, 5 and 7), long electrofishing transects (dashed lines with bold labels: T1–T6), and Gisborne Pt. sampling area, where 10-minute transects were sampled.

Boat electrofishing surveys were carried out seasonally between February 2010 and April 2011 at Gisborne Point, in the littoral (0.9–2.8 m water depth) and pelagic (18–30 m) zones (Fig. 2.1). The electric fishing boat is 4.5 m long and equipped with a 6 kilowatt Honda-powered custom-wound generator and a 5 kilowatt gas-powered pulsator (Smith-Root, Inc., model 5.0 GPP). Pulses of direct current are emitted at 60 pulses per second, and the power output is typically between 2 and 4 amps root mean square, dependent on water conductivity (Hicks et al. 2006). Two aluminium-framed whitebait nets were mounted behind the electrodes on the electrofishing boat (Fig. 2.2). The nets were constructed from polyester hexagonal mesh, with a mesh size of 2 mm and a mouth opening area of 0.79 m^2. The effective fished depth spanned from the water surface to 2 m depth. Fish were sampled by driving the boat at 1–2 km h^{-1} along 10-minute transects with the electrofishing field turned on. Transects were roughly perpendicular to the shore. This method was tested in the littoral and pelagic zones at night and during the day in February 2010, and sampling was subsequently carried out seasonally at night. Night transects were started at least 30 minutes after sunset. Five littoral transects and 1–5 pelagic transects were fished on each occasion; pelagic sampling could not be carried out in winds >10 knots and could not be completed on all occasions due to weather conditions. Additionally, in April 2010, 5 littoral transects were fished at night with the electric current turned off (referred to as “scoop nets” hereafter).

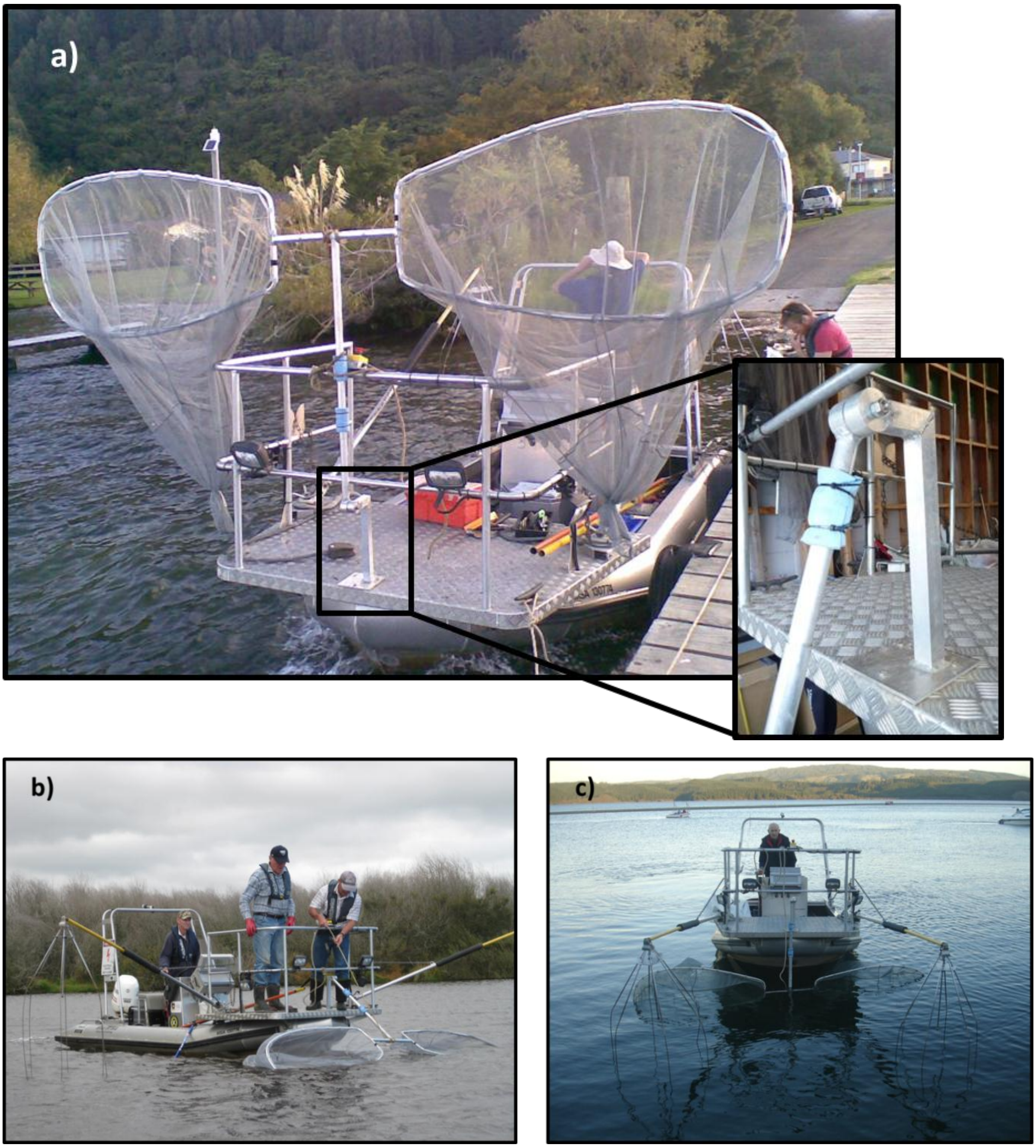

Fig. 2.2. Whitebait nets mounted on the University of Waikato’s electrofishing boat, for catching smelt in lakes: (a) the pivot system used to lower the net into the water, (b) lowering the nets into the water, and (c) the nets as used during fishing (when fishing, a person stands on the bow of the boat, lowering the nets further into the water).

Table 2.2. Sampling methods trialled in Lake Rotoiti in this study. *n* = number of samples. Sample time is the length of time taken to collect the sample; total time per sample includes processing time.

Zone, time, method	*n*	Mean area sampled (m^2) ± 1 SE	Mean volume sampled (m^3) ± 1 SE	Part of water column sampled	Range of bottom depths (m)	Maximum effective sampling depth (m)	Sample time (min)	Total time per sample (min)	Sampling effort (water volume min^{-1})
Littoral zone									
Day									
Boat EF	19	595.0 ± 58.8	1190.0 ± 117.5	Surface	0.8–2.8	2	10	15	119.0
Beach seine	186	160.0 ± 0.0	184 ± 0.0	Surface	0.9–1.2	1.15	10	10–15	18.4
Night									
Boat EF	31	673.4 ± 39.4	1346.7 ± 78.8	Surface	0.8–5.5	2	10	15	134.7
Scoop nets	5	818.7 ± 44.2	1637.4 ± 88.4	Surface	0.8–7.0	2	10	15	163.7
Pelagic zone									
Day									
Boat EF	1	834.4 ± 0.0	1668.8 ± 0.0	Surface	20.0–27.0	2	10	15	166.9
Drop net	18	0.4778 ± 0.0	16.1 ± 1.0	Whole water column	10.0–59.7		10	12	1.6
Night									
Boat EF	14	663.4 ± 52.8	1301.6 ± 105.5	Surface	20.0–35.0	2	10	15	130.2
Boat EF (L)	15	5389.6 ± 575.6	10779.3 ± 1151.2	Surface	13.1–62.0	2	50	60	215.6
Purse seine	5	25.8 ± 0.0	59.3 ± 0.0	Surface	11.5–34.0	3.5	10	15	5.9

Smelt were also sampled in the pelagic zone of Lake Rotoiti by means of long boat electrofishing transects spanning from the northern shore to the southern shore (Fig. 2.1). Fish were sampled by driving the electrofishing boat at approximately 2 km h^{-1} along transects 1–6 at night (Fig. 2.1), in September 2010 and April 2011. Transects 4–6 were also surveyed in January 2011. Only areas with bottom depths greater than 5 m depth were fished.

Beach seine sampling was carried out monthly from August 2010 to August 2011 during the day, because trials of this method in Lake Taupo showed that beach seining during the day is much more effective than at night (Table 2.1; Stephens 1984). Seine hauls were carried out at sites 4, 5, and 7 (Fig. 2.1) as these sites had ample beach habitat amenable to beach seining. A beach seine was hauled perpendicular to the shore for 30 m, then both ends of the net were brought to the shore and the fish were collected (Hahn et al. 2007). The beach seine was 1.6 m high, 6.5 m long, with a centre pocket 2.3 m long. The mesh size of the pocket was 3 mm and the mesh size of the rest of the net was 6 mm. Four seine hauls were carried out on each sampling occasion. Net hauls were carried out on separate areas of the beach (i.e. hauls did not overlap). The depth of water sampled with the beach seine ranged from 0.8–1.2 m, with an average depth of approximately 1 m.

A drop net was trialled in the pelagic zone during daylight on 17 September 2009. This net can be used in deep waters to sample the entire water column, but it becomes difficult to use in depths <5 m. The net is made up of a weighted cylinder (diameter 0.78 m) with a conical net attached to it, with a mesh size of 1.2 mm. The net terminates in a removable bucket for easy removal of the catch. The net is allowed to fall through the water column with a descent rate of approximately 1.33 m s^{-1} (Stephens 1984). Once the net hits the lake bottom or reaches the end of the rope, it is closed using a rope encircling the net and pulled to the surface using a winch. The net sampled to a depth of approximately 40 m, and was launched 18 times at varying depths at locations around the lake.

Purse seining was carried out at night on 13 January 2010. The purse seine is 18 m long, 3.5 m deep at its deepest point, and is constructed from 2 mm mesh. The seine was deployed from a small motor-powered craft and operated by deploying one end, paying out the net to create a circle, then quickly drawing in the purse line to close the net. Five samples were taken in the upper stratum of the pelagic zone (i.e. we sampled the upper 3.5 m in areas where water depth ranged between 11.5 and 34 m) between 21.40 and 22.20 h.

The area sampled by electrofishing was calculated by multiplying the length of the fishing pass (measured using GPS coordinates) by the combined horizontal length of the nets. For the drop net, the area of the net opening was used. For the purse seine, area fished was calculated as the area of a circle with a circumference equal to the length of the net (18 m).

For each sample, the total number of each species was recorded. All fish were measured to the nearest mm, except bullies. Fork lengths (FL) were measured for smelt, goldfish and trout, and total lengths (TL) measured for species without forked tails (bullies and koaro). Bullies were sorted into three size classes: <30 mm TL; 30–50 mm TL; and >50 mm TL. The total mass of each species was weighed to the nearest 0.01 g.

2.4 Results

Smelt catches and densities were highly variable among methods (Tables 2.3 and 2.4). Boat electrofishing (EF) in the littoral zone at night caught large numbers of smelt, and yielded higher catches and densities than during the day. Boat EF was more effective with the current turned on than using the scoop nets with the current turned off. During the day, beach seining in the littoral zone was more effective in catching smelt than boat EF. In the pelagic zone, the drop net was the only method that sampled throughout the water column, rather than the surface, and therefore yielded greater fish densities than the other methods (Table 2.3). Long boat EF transects sampled the greatest area and yielded the highest numbers of smelt (Tables 2.3 and 2.4). Though short EF transects in the pelagic zone caught more smelt on average than purse seining, the density of smelt caught by purse seining was higher than short boat EF transects.

Most methods deployed in the littoral zone caught significant numbers of bullies (Table 2.3). The density of bullies caught by scoop nets (i.e. boat EF with the power turned off) was lower than with the power turned on (Table 2.4). Sampling by boat EF and beach seining during the day caught a higher proportion of bullies smaller than 30 mm than sampling by boat EF at night (Table 2.5a). Of the methods tested in the pelagic zone, the drop net was the only method that caught fish other than smelt (bullies and koaro; Tables 2.3 and 2.4). This method only caught larval fish (Table 2.5b). Koaro were also caught very occasionally by beach seining and boat EF in the littoral zone at night (Tables 2.3 and 2.4). Goldfish were caught only by boat EF in the littoral zone, and juvenile rainbow trout were caught very occasionally by boat EF and beach seining in the littoral zone during the day.

The size of smelt caught varied among methods; the purse seine and drop net caught only small smelt, whereas boat EF and beach seining caught smelt of a range of sizes (Fig. 2.3). Smelt that were sampled by long EF transects in the pelagic zone were notably smaller than those sampled using other methods (Fig. 2.3; ANOVA: $F_{1,3} = 439.7$, $P < 0.0001$, Tukey's HSD test: long transects < beach seine < littoral and pelagic boat EF). Similar-sized smelt were caught in the pelagic and littoral zones by boat EF at night (Fig. 2.3). Long transects in the pelagic zone at night caught the widest size range of smelt (Fig. 2.3).

Table 2.3. Numbers of fish caught using different methods in Lake Rotoiti. Boat EF = boat electrofishing; Boat EF (L) = long boat electrofishing transects; *n* = number of samples.

		Mean area	Mean catch per sample (number of fish)									
		sampled (m^2)	Bully		Goldfish		Koaro		Smelt		Trout	
Zone, time, method	*n*	± 1 SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Littoral zone												
Day												
Boat EF	19	595.0 ± 58.8	2.40	1.0296	0	0	0	0	3.40	1.08	0	0
Beach seine	186	160.0 ± 0.0	3.84	0.69	0	0	0.013	0.010	69.04	14.50	0.06	0.03
Night												
Boat EF	31	673.4 ± 39.4	23.97	5.90	0.65	0.23	0.258	0.139	465.52	100.49	0.03	0.03
Scoop nets	5	818.7 ± 44.2	1.00	0.45	0	0	0	0	158.20	37.68	0	0
Pelagic zone												
Day												
Boat EF	1	834.4 ± 0.0	0	0	0	0	0	0	0	0	0	0
Drop net	18	0.4778 ± 0.0	1.11	0.31	0	0	0.111	0.111	3.11	1.02	0	0
Night												
Boat EF	14	663.4 ± 52.8	0.14	0.14	0	0	0	0	13.93	5.44	0	0
Boat EF (L)	15	5389.6 ± 575.6	0	0	0	0	0	0	1720.18	535.94	0	0
Purse seine	5	25.8 ± 0.0	0	0	0	0	0	0	4.80	1.71	0	0

Table 2.4. Densities of fish caught using different methods in Lake Rotoiti. Boat EF = boat electrofishing; Boat EF (L) = long boat electrofishing transects; *n* = number of samples.

Zone, time, method	*n*	Mean area sampled (m^2) ± 1 SE	Mean fish density (fish m^{-2})									
			Bully		Goldfish		Koaro		Smelt		Trout	
			Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Littoral zone												
Day												
Boat EF	19	595.0 ± 58.8	0.0297	0.0207	0.0019	0.0019	0	0	0.0035	0.0011	0.0002	0.0002
Beach seine	186	160.0 ± 0.0	0.0240	0.0043	0	0	0.00008	0.00006	0.4315	0.0906	0.0004	0.0002
Night												
Boat EF	31	673.4 ± 39.4	0.0372	0.0089	0.0011	0.0004	0.00034	0.00017	0.6390	0.1260	0	0
Scoop nets	5	818.7 ± 44.2	0.0012	0.0006	0	0	0	0	0.1886	0.0405	0	0
Pelagic zone												
Day												
Boat EF	1	834.4 ± 0.0	0	0	0	0	0	0	0	0	0	0
Drop net	18	0.4778 ± 0.0	2.3253	0.6528	0	0	0.2325	0.2325	6.5108	2.1394	0	0
Night												
Boat EF	14	663.4 ± 52.8	0	0	0	0	0	0	0.0130	0.0070	0	0
Boat EF (L)	15	5390 ± 575.6	0	0	0	0	0	0	0.3811	0.1286	0	0
Purse seine	5	25.8 ± 0.0	0	0	0	0	0	0	0.1862	0.0665	0	0

Table 2.5. Lengths of (a) bullies, and (b) goldfish, koaro, smelt and trout caught in Lake Rotoiti by beach seine and boat electrofishing (EF) in the littoral zone. Length of common bullies presented as percentages of fish caught in the length classes <30 mm, 30–50 mm, and >50 mm. The fork lengths of goldfish, smelt and trout, and the total lengths of bullies and koaro are presented. *n* = number of fish.

(a) Percentages of size classes of fish caught, by method

		Method		
Species	Length (mm)	Beach seine	Boat EF- Day	Boat EF- Night
Common bully	<30 mm	69%	56%	48%
	30–50 mm	1%	11%	8%
	>50 mm	3%	33%	45%
	Total *n*	428	139	575

(b) Lengths of fish caught, by method

		Method		
Species	Statistic	Beach seine	Boat EF- Day	Boat EF- Night
Goldfish	Mean			174.4
	SE			9.6
	Range			70–215
	Total *n*			14
Koaro	Mean	32		68.7
	SE	–		15
	Range	–		42–94
	Total *n*	1		3
Smelt	Mean	41.9	36.2	44.9
	SE	0.1	1.6	0.1
	Range	16–69	21–45	21–100
	Total *n*	5345	18	3471
Trout	Mean	75.2	148	
	SE	9.1	–	
	Range	27–105	–	
	Total *n*	11	1	

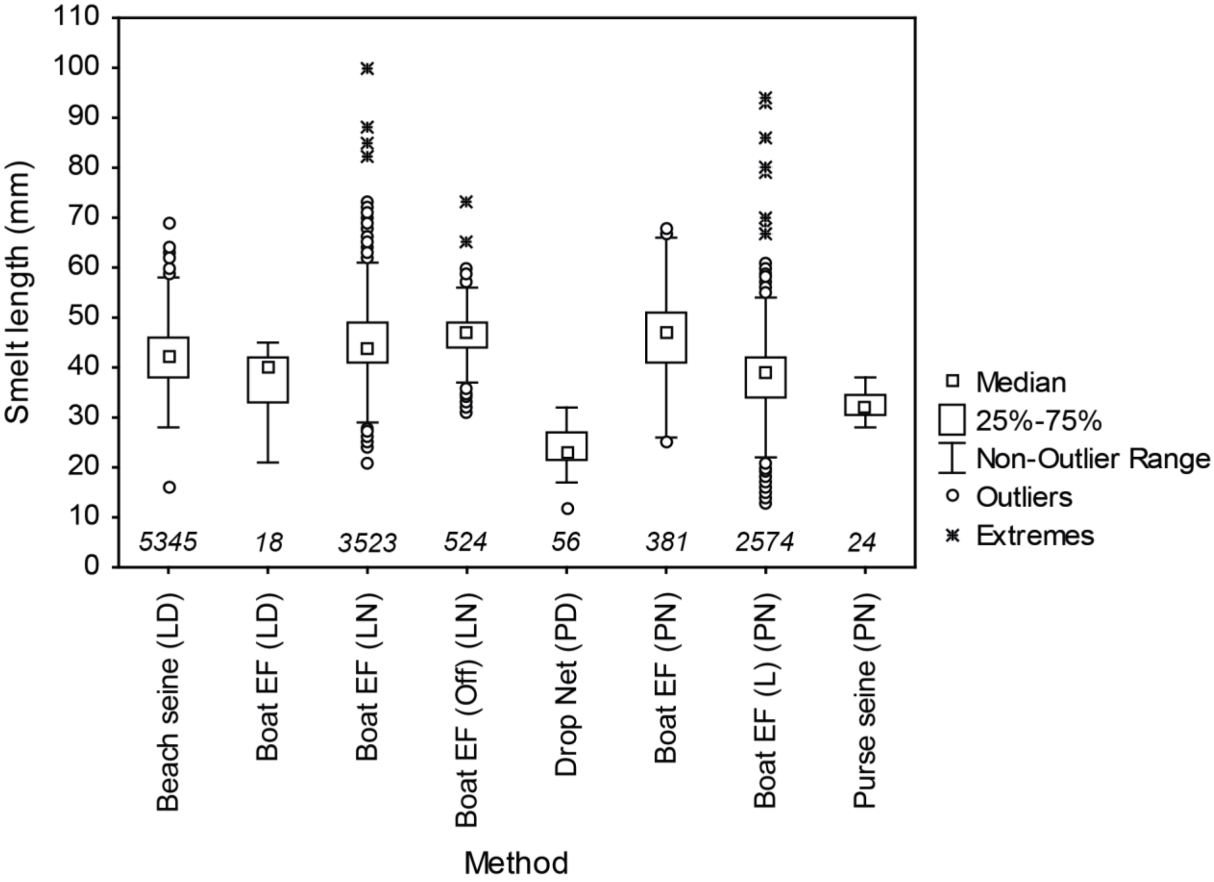

Fig. 2.3. Fork lengths of smelt caught using different methods in Lake Rotoiti, with number of smelt measured beneath boxes in *italics*. LD = littoral zone, day; LD = littoral zone, night; PD = pelagic zone, day; PN = pelagic zone, night.

2.5 Discussion

2.5.1 Advantages and disadvantages of sampling methods

Our results confirm the importance of considering diel vertical migration when selecting a method for sampling small pelagic fish in lakes. Pelagic smelt may be sampled either by hydroacoustic surveys or midwater trawling during the day, while they occupy deeper waters, or at night by boat EF when they occupy surface waters. The surface sampling undertaken in this study is a good indicator of seasonal movements of smelt in and out of the littoral zone, and could be used to provide information on habitat use, diet, body condition, and spawning timing. However, it should not be assumed that fluctuating smelt numbers in the littoral zone reflect fluctuations in the entire population, and surface sampling should not be used to provide absolute population estimates. The proportion of the population that migrates to the surface at night may vary seasonally (Mehner and Kasprzak 2011), so enumeration of the total population requires a method that is able to enumerate smelt in the deep strata of the pelagic zone, such as hydroacoustics. However, recent hydroacoustic surveys of adult smelt in Lake Rotoiti (Rowe et al. 2011) were not able to enumerate density of smelt in the littoral zone because they used a towed transducer, and could not enumerate juvenile smelt in the pelagic zone due to interference from other small fish and invertebrates. Therefore, sampling surface waters could be used concurrently with hydroacoustics to ensure that all habitats and size classes of smelt are sampled.

It is clear from our results that smelt occupy the littoral zone both during the day and at night; however, diet and stable isotope analyses suggest that smelt caught during the day in the littoral zone are separate from smelt caught at night, at least in terms of diet (see Chapter 3). From this study and previous work (Rowe 1993), it appears that two groups of smelt exist: (1) a group of smelt feeding mainly in the pelagic zone that occupies deep waters during the day and migrates to the littoral zone at night, and (2) a resident group of smelt that feeds principally in the littoral zone. In the littoral zone, smelt caught at night are more likely to represent the wider lake community (i.e. pelagic migrants) than smelt caught in the littoral zone during the day (littoral residents). Therefore, sampling in the littoral zone during the day (e.g. by beach seine), though straightforward, may not provide a representative sample, and sampling of the surface waters should be carried out at night.

The method for sampling smelt in lakes should be chosen according to the sizes of smelt required. Long boat EF transects effectively sampled a wide range of smelt, from larvae to adults. Although the mesh size of the nets (2 mm) was suitable for catching adults, some larvae may have passed through the nets. For future studies, it may be useful to use nets of a smaller mesh size, though drag and robustness could be problematic. The size of transects may need to be reduced in this case, because the 2mm mesh nets used in the present study accumulated a large amount of microalgae. Other netting methods such as purse seining and beach seining sampled a smaller size range of smelt compared to long boat EF transects and may therefore not be suitable for obtaining adequate samples of the population; this result is similar to that of

Stephens (1984). Drop netting was suitable for sampling larvae only, as adult smelt were probably able to avoid the net.

The methods tested in this study varied in terms of spatial resolution. For example, long boat EF transects (mean area ± SE = 5389.6 ± 575.6 m^2) sampled a much greater area than the 10-minute transects in the littoral zone (673.4 ± 39.4 m^2). Therefore, if the aim of future studies is to examine spatial heterogeneity of smelt populations in the littoral zone, short transects can be used; but if the aim is to obtain a representative sample of the entire lake population, longer transects spanning between lake shores are recommended.

Each method tested has advantages and disadvantages, and no fishing method is guaranteed to catch 100% of fish. Boat EF will only catch fish that are brought into the direct path of the scoop nets by the electric current; fish may escape by swimming to either side or underneath the nets. This is particularly relevant for boat EF in the pelagic zone. Therefore, surface sampling of smelt populations should ideally be combined with a method that enumerates smelt in deeper waters to gain reliable estimates of population size.

Net avoidance probably affected our samples. No smelt longer than 45 mm were caught by boat EF during the day, and beach seining during the day yielded an order of magnitude more smelt than boat EF during the day. In addition to the effects of diel migration, this variation may be partly attributable to avoidance of the EF boat by smelt during daylight. Net avoidance also probably limited the size of smelt caught by purse seining, as larger fish would have been able to swim under the net. This may be able to be remedied by using a deeper net; however, purse seining did not catch many smelt in total, meaning that sampling using this method is not recommended for analyses such as length-frequency analysis that require a large sample size that is representative of the whole population.

The aluminium whitebait nets mounted on the EF boat were generally effective in catching smelt, and the construction had some advantages and disadvantages. The advantages were that the setup was relatively lightweight and could be lowered and raised by one person, with another person driving the boat. The commercially available nets were also easy to replace when damaged. However, the whitebait nets, while light, were easily bent in currents or choppy water. For future studies, researchers implementing this method might consider constructing the nets from a sturdier material.

Here we have tested the optimal sampling methods for smelt, but the optimal methods for sampling other species are likely to be different. In the littoral zone, larger fish such as goldfish and rainbow trout were often shocked, but not caught in the nets. If sampling these species is important in future studies, the method could be modified by stationing people with pole nets on the boat to catch these escaped fish. Bullies, which live in benthic habitats, may not have been effectively sampled with boat EF, as they often do not float to the surface when shocked (J. Blair, pers. obs.). Therefore, other sampling methods such as minnow traps may be more effective than boat EF for sampling bullies in the littoral zone of lakes.

2.5.2 Comparison with other studies

Littoral smelt densities measured at night using boat EF in this study (0.64 ± 0.13 individuals m^{-2}) are comparable to those measured using other methods in New Zealand North Island lakes. However, differences in sample volume and lake conditions mean that estimates gained using different sampling gear may not be directly comparable. In Lake Taupo, estimates of smelt density in the upper 5 m of the littoral zone (i.e. the area of the lake between 3.0 and 20 m depth), calculated using purse seine catches, ranged from 0.0005 to 2.27 smelt m^{-2}. Both the mean densities of smelt measured using purse seining in the pelagic zone at night (0.19 smelt m^{-2}) and boat EF in the littoral zone at night (0.01 smelt m^{-2}) are within this range. Densities of smelt measured using offshore purse seine catches in Lake Tarawera were 0.76 fish m^{-2} at night and 3.15 fish m^{-2} during the day (Mylechreest 1990). This is higher than the densities we measured by purse seining; this may be because the net used by Mylechreest (1990) was 5 m deep, sampling more of the water column than the net used in this study.

Echo sounding surveys of the pelagic zone of Lake Rotoiti between 2005 and 2010 gave a mean smelt density of 0.7 fish m^{-2} (Rowe et al. 2011), which is similar to littoral densities measured in this study. The echo sounding surveys measured the number of smelt throughout the water column in the pelagic zone during the day; the fact that similar densities were found in the littoral zone at night, despite much smaller sample volumes, suggests that littoral habitat was important for smelt in Lake Rotoiti.

Beach seining in Lake Taupo has produced higher density estimates of smelt than were measured in this study; beach seining in Lake Taupo in depths less than 3 m produced a year-round average of approximately 9.1 smelt m^{-2} (Stephens 1984), compared to the mean of 0.43 smelt m^{-2} in Lake Rotoiti. Stephens (1984) found that beach seine hauls carried out at night were not as successful as those carried out during daylight; they caught fewer smelt, with higher variation between hauls. It might be instructive for researchers to examine whether this is also the case in Lake Rotoiti in future studies.

2.5.3 Conclusions

Results of this trial suggest that boat EF at night is the most effective sampling method for smelt in the surface waters of lakes, followed by scoop nets (i.e. boat EF with the current turned off). Overall, we recommend the use of boat-mounted nets at night for sampling smelt in lakes; whether or not an electric current is used will affect the numbers of smelt caught, but sufficient sample sizes can still be obtained without an electric current. Using boat-mounted scoop nets without the use of an electric current is also much more cost-effective, as it reduces the need for specialised boat EF equipment and accordingly trained personnel. Sampling should include both the littoral and pelagic zones to catch a wide size range of smelt.

The methods trialled in this chapter that sample only the uppermost few metres of the water column are more effective at night than during the day, because smelt migrate to the surface waters of lakes at night. However, smelt that do not migrate to the surface at night will not be sampled by surface methods. Therefore, these methods allow for the collection of useful qualitative information such as reproductive state, diet and body condition, and provide a measure of smelt habitat use, but not of lake-wide abundance. The drop net trialled in our study was effective for sampling pelagic larvae in deeper waters, but adult fish were able to avoid the net. Midwater trawling or hydroacoustics are recommended for sampling adult smelt in deeper waters and obtaining smelt population estimates that can be compared among lakes and years, though the cost of these methods may be prohibitive. Due to the limitations of hydroacoustic sampling for sampling small smelt and smelt in the littoral zone, a method that samples the surface waters could be used in conjunction with hydroacoustics to ensure that all life stages are sampled.

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3 Seasonal patterns in habitat use, reproduction and diet of smelt in Lake Rotoiti

3.1 Abstract

Common smelt (*Retropinna retropinna*) are widespread and abundant in New Zealand’s rivers and lakes, and are the main prey species that support significant rainbow trout fisheries in the lakes of the central North Island. Despite this, smelt population dynamics are not well understood. To determine the factors influencing smelt abundance in Lake Rotoiti, central North Island, we examined seasonal changes in habitat and resource use by measuring spatial and seasonal changes in relative smelt abundance, body condition, and diet. We also characterised seasonal and spatial changes in smelt reproductive state and benthic egg abundance. Smelt abundance in the littoral zone and surface waters of the pelagic zone was highest in autumn, when peaks in smelt body condition, gonadosomatic index, and benthic egg abundance occurred. Body condition of smelt was lowest in winter—a period of low abundance of littoral invertebrates and zooplankton. Smelt consumed a range of benthic and pelagic invertebrates and smelt eggs during the day, while at night they consumed zooplankton, smelt eggs and larval common bully (*Gobiomorphus cotidianus*). The amount of food in the stomach, relative to smelt mass, was higher in the littoral zone than in the pelagic zone, suggesting that food was more abundant in littoral than in pelagic habitats. Predation of zooplankton was highest in winter and spring, and smelt eggs formed a large proportion of smelt diet in autumn and winter. Stomach contents and stable isotope analyses showed that smelt undergo an ontogenetic change in diet, from mainly zooplankton as juveniles to benthic invertebrates as adults. The information obtained in this study is necessary for the management of smelt populations and their introduced predator—rainbow trout (*Oncorhynchus mykiss*)—in lakes.

3.2 Introduction

In stocked fisheries, the number of fish that can be supported is highly dependent on prey supply (Ney 1990), and changes in prey abundance and body condition can influence consumption rates and diet (Rand and Stewart 1998). However, the dynamics of prey species are studied less often than those of predators and are usually less well understood (Ney 1990). Common smelt (*Retropinna retropinna*; hereafter smelt) are a small pelagic fish native to New Zealand (Fig. 3.1). Smelt were introduced to many lakes in the central North Island of New Zealand to provide food for introduced rainbow trout (*Oncorhynchus mykiss*). Smelt are often the most important food source for rainbow trout in these lakes (Chapter 4, Cryer 1991, Rowe 1984, Smith 1959), and therefore are important for supporting the iconic and economically important rainbow trout fisheries in this area. However, information on the life history and ecology of smelt in the Rotorua lakes is lacking. Recent hydroacoustic surveys of adult smelt in Lake Rotoiti (Rowe et al. 2011) were not able to enumerate density of smelt in the littoral zone because they used a towed transducer, and cannot enumerate juvenile smelt in open water due to interference from other small fish and invertebrates. Also, seasonal variation in the abundance of smelt in different habitats (e.g. littoral vs. pelagic) has not been characterised. Knowledge of the factors influencing smelt production would assist the management of smelt populations and, as a consequence, the sustainable management of trout fisheries.

Fig. 3.1. Common smelt, *Retropinna retropinna*, from Lake Rotoiti

It is important to characterise the life history and ecological role of smelt because these vary widely among locations. For example, smelt spawning seasons may last several months (Ward et al. 2005); diadromous smelt spawn in autumn and winter in shallow parts of rivers and tributary streams (Ward et al. 1989), and lacustrine smelt spawn in spring and summer on sandy beaches or stream mouths, in water 0.5–2.5 m deep (Jolly 1967, Stephens 1984, Ward and Boubée 1996). However, winter spawning is also possible (Ward and Boubée 1996), and viable smelt eggs were found in Lake Rotorua between November and June (Jolly 1967). Ripe smelt have been observed in the Ohau Channel year-round, indicating that spawning may occur throughout the year (Rowe et al. 2006). However, it is not known whether smelt in adjacent Lake Rotoiti show a similar pattern.

The diet of smelt is also highly variable; smelt are generalist, opportunistic feeders and may switch prey according to availability. The mean prey size of smelt increases with smelt length and gape size (Boubée and Ward 1997); zooplankton often make up the majority of the diet of smelt <40 mm in length, while larger smelt may consume a wider range of prey including adult terrestrial and aquatic insects, aquatic insect larvae, spiders, mysid shrimp, fish larvae, amphipods and springtails (Boubée and Ward 1997, Cryer 1988, Northcote and Chapman 1999, Stephens 1984). Because smelt consume food from both the benthic and pelagic zones, characterising their diet can help determine the contributions of benthic and pelagic sources of productivity to the higher trophic levels (Vadeboncoeur et al. 2002).

Lake Rotoiti is home to an iconic rainbow trout fishery which relies heavily on smelt as a food source for trout (Chapter 4), and recent lake restoration measures have the potential to influence smelt production and abundance (Rowe et al. 2006). Water flowing from Lake Rotorua into Lake Rotoiti via the Ohau Channel previously constituted a significant input of nutrients and algae, reducing water quality in Lake Rotoiti (Hamilton et al. 2005). In 2008, the Ohau Channel Diversion Wall was built to improve water quality in Lake Rotoiti by diverting water flowing from Lake Rotorua directly down the Kaituna River (Fig. 3.2). This is of concern because smelt have been observed migrating between Lake Rotorua and Lake Rotoiti via the Ohau Channel, and it was thought that the diversion wall may interrupt this migration, possibly affecting smelt abundance in Lake Rotoiti (Rowe et al. 2006). The effects of changing lake productivity also need to be addressed; previous studies have shown that juvenile smelt abundance is positively correlated with Secchi depth, probably due to increased egg mortality in eutrophic lakes, suggesting that the prevention of eutrophication would benefit smelt (Rowe and Taumoepeau 2004).

In this study, to identify the factors influencing smelt abundance and reproduction, we examined spatial and seasonal changes in (1) relative abundance, habitat use, size, and body condition of smelt, (2) spawned egg abundance and smelt reproductive state, and (3) smelt diet.

3.3 Methods

3.3.1 Study site

Lake Rotoiti is located in the central North Island, New Zealand (Figs. 3.2 and 3.3). It is warm, monomictic, and mesotrophic, with a surface area of 34 km^2, and a mean depth of 31 m. The western end of the lake is shallow, with depth increasing from the western to the eastern end of the lake, where the maximum depth is 94 m.

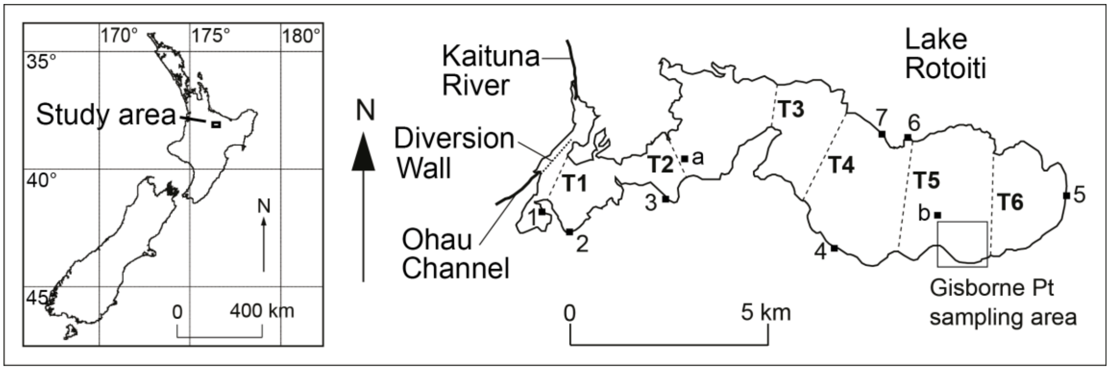

Fig. 3.2. Study area showing sampling beaches (black squares numbered 1–6), long electrofishing transects (dashed lines with labels T1–T6), Gisborne Pt. sampling area, and zooplankton sampling sites (a and b), Lake Rotoiti, New Zealand.

3.3.2 Field sampling: smelt

To assess the dynamics of smelt abundance in Lake Rotoiti, we measured littoral and pelagic smelt density seasonally using boat electrofishing (EF). Smelt migrate to the surface each night (Rowe 1984) and were therefore sampled at night in surface waters. Boat EF surveys were carried out seasonally between February 2010 and April 2011 at Gisborne Point, in the littoral (0.9–2.8 m water depth) and pelagic (16–35 m) zones (Figs. 3.2 and 3.3). The EF boat is 4.5 m long and equipped with a 6 kilowatt Honda-powered custom-wound generator and a 5 kilowatt gas-powered pulsator (Smith-Root, Inc., model 5.0 GPP). Pulses of direct current are emitted at 60 pulses per second, and the power output is typically between 2 and 4 amps root mean square, dependent on water conductivity (Hicks et al. 2006). Two aluminium-framed whitebait scoop nets were mounted behind the electrodes on the EF boat. The nets were constructed from polyester hexagonal mesh, with a mesh size of 2 mm and an ovoid mouth opening area of 0.79 m^2. This method sampled from the water's surface to a depth of approximately 2 m. Fish were sampled by driving the boat at 1–2 km h^{-1} along 10-minute transects with the EF field turned on. The area fished was calculated by multiplying the length of the fishing pass (measured using GPS coordinates) by the combined horizontal length of the nets. Transects were roughly perpendicular to the shore. As smelt undergo diel vertical migrations, we compared daytime fishing with night fishing (see Chapter 2) and sampling was subsequently carried out at night. Night transects were started at least 30 minutes after sunset.

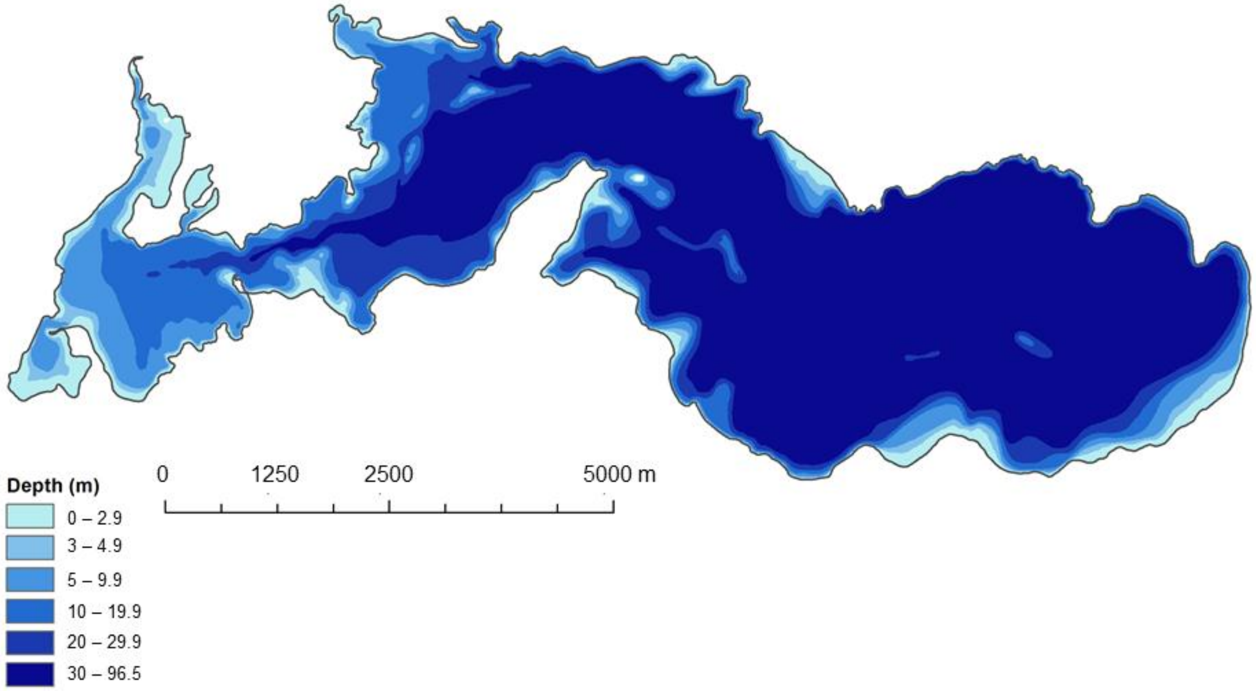

Fig. 3.3. Bathymetry of Lake Rotoiti, showing littoral and pelagic areas. Image credit: G. Stitchbury.

Five littoral transects and 1–5 pelagic transects were sampled on each sampling trip; pelagic sampling could not be carried out in winds >10 knots and could not be completed on all occasions due to adverse weather conditions.

Smelt in the pelagic zone of Lake Rotoiti were sampled by means of long EF transects spanning from the northern shore to the southern shore (Fig. 3.2). Fish were sampled by driving the EF boat at approximately 2 km h^{-1} along transects 1–6 at night (Fig. 3.2), in September 2010 and April 2011. Transects 4–6 were also surveyed in January 2011. This method also sampled from the water's surface down to a depth of approximately 2 m, but was only used in water depths greater than 5 m, to avoid the littoral zone.

To assess changes in diet and reproductive state, smelt were sampled monthly from August 2010 to August 2011 with a beach-seine net. Seine hauls were carried out at sites 4, 5, and 7 (Fig. 3.2) as these sites had ample beach habitat amenable to beach-seining. The beach seine was 1.6 m high, 6.5 m long, with a centre pocket 2.3 m long. The mesh size of the pocket was 3 mm and the mesh size of the rest of the net was 6 mm. The net was hauled perpendicular to the shore for 30 m, then both ends of the net were brought to the shore and the fish were collected (Hahn et al. 2007). Four seine hauls were carried out at each site on separate areas of the beach (i.e. hauls did not overlap). This method was deployed in water depths of 0.8–1 m at the shallower end of the net to 1–1.2 m at the deeper end; the net spanned the entire water column.

3.3.3 Fish processing

The fork length (FL) of smelt was measured to the nearest mm, and the wet mass of smelt was measured to the nearest 0.0001 g. Gonad wet mass was measured in a subsample of smelt from each sampling occasion. Ripe females were identified by assessing gonad stage under 30× magnification; ripe females were defined as those with mostly translucent eggs that run under slight pressure (Holden and Raitt 1974). Smelt gonadosomatic index (GSI) was calculated as the ratio between gonad mass and total body mass, and was used an indicator of relative reproductive state.

3.3.4 Field sampling: smelt eggs and invertebrates

Smelt eggs (typically 0.5 mm diameter) and benthic invertebrates were sampled at seven sites around the lake from September 2010 to August 2011 (Fig. 3.2). A fine-meshed D-shaped net (width of mouth = 28 cm) was used to disturb the sediment to a depth of approximately 1 cm along three 20 m transects at 0.5–1 m water depth, collecting sediment. An area of approximately 5.6 m^2 was sampled in each sample. A solution of sugar and water was used to separate eggs and invertebrates from sediments. Sites 4 and 5 were sampled fortnightly, and all other sites were sampled monthly. Sampling was discontinued at sites 1, 2, and 3 after May 2010 because no eggs had been detected between September and May. Between September and November 2011, two samples were taken per site. From December 2011 onwards, four samples were taken at each site. Sites 4 and 5 were sampled fortnightly, and all other sites were sampled monthly. Excessive weed prevented sampling at Site 2 in February and March 2011.

Samples were either kept refrigerated and processed within 24 h, or preserved in a 70% solution of isopropyl alcohol until processing. Smelt eggs and benthic invertebrates were enumerated under a dissecting microscope at 30× magnification. Invertebrates were identified to the highest taxonomic level possible.

Environmental variables were measured at sampling sites to find the conditions required for smelt spawning. Specific and ambient conductivity, dissolved oxygen, and water temperature were measured at each site in water 1 m deep, approximately 30 cm below the water surface. Approximately 500 g of sediment was collected from the upper 2 cm of sediment at 1 m depth from each sample site. Particles smaller than 1.68 mm were measured using Malvern mastersizer with Hydro 2000 G dispersal unit. For particles larger than 1.68 mm diameter, the proportion of each particle size was measured using nested sieves with 8.0 mm, 4.0 mm, 2.0 mm and 1.68 mm mesh size.

Zooplankton were sampled seasonally, in spring (October 2010), summer (January 2011), autumn (April 2011), and winter (July 2011), at two sites in Lake Rotoiti using a Schindler-Patalas plankton trap (Envco Environmental Equipment Suppliers, model 34-A10). The trap measured 292 × 292 × 413 mm in size (30 L volume) and featured a 63 µm mesh filter net and 200 mL collection bucket with 61 µm mesh stainless steel screen cloth. At each site, trap hauls were taken at the surface and at 5 m intervals to a depth of 30 m, and pooled into a single sample. Zooplankton were identified at least to family level and enumerated using a dissecting microscope at 35× magnification.

3.3.5 Diet

Diet was enumerated in a total of 347 smelt 29–86 mm FL by stomach contents analysis. Smelt were caught in autumn by (1) beach seining in the littoral zone during the day at sites 4, 5, and 7, (2) boat EF in the littoral zone at night, and (3) boat EF in the pelagic zone at night. Smelt were also caught in spring, summer, and winter by beach seining. All items from the stomachs were removed, counted and identified to the highest taxonomic level possible. The number of individuals and blotted wet mass of each prey type in individual smelt stomachs were recorded. If prey were too small to be weighed, presence was recorded. Three metrics were used to compare diets: (1) the mass of food in smelt stomachs, (2) the percentage frequency of occurrence, which is the percentage of non-empty smelt stomachs containing a particular prey taxon, and (3) the percentage composition by mass, which was calculated for the entire sample by finding the relative proportion by mass of each prey species across all nonempty smelt stomachs in the sample. The graphical method of Costello (1990) was used to compare diet among seasons and sampling techniques, i.e. percentage frequency of occurrence was plotted against percentage composition by mass.

Smelt diet was also investigated by stable isotope analysis of five smelt in each of three size classes (juveniles: <40 mm, small adults: 40–50 mm, and large adults: >50 mm), caught in (1) the littoral zone during the day by beach seining, (2) the littoral zone at night by boat EF, and (3) the pelagic zone at night by boat EF. For medium and large smelt, a sample of white muscle was obtained by dissection. Smelt <40 mm FL were processed whole after removing the head and gut to obtain sufficient sample material. Samples were dried for 48 h at 60°C, ground to a powder with a mortar and pestle, and stored in glass jars until analysis. Stable isotope ratios of C and N were analysed at the Waikato Stable Isotope Unit, Hamilton, with a Europa Scientific continuous flow 20/20 mass spectrometer with a triple ion-collector and ANCA SL inlet system. Reference samples of cane sucrose from the Australian

National University were used for $^{13}C/^{12}C$, and N_2 in air for $^{15}N/^{14}N$. Stable isotope ratios ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) are expressed as relative difference per mil (‰) delta values ($\delta^{13}C$ or $\delta^{15}N$) referenced to the international standards for carbon (Australian National University sucrose referenced to Pee Dee Belemnite) and nitrogen (atmospheric nitrogen).

3.3.6 Data analysis

Smelt densities, lengths, and diets were compared among seasons, sampling methods, and times of day using nonparametric methods because data did not meet assumptions of parametric tests, i.e. homogeneity of variances and normal distribution, in spite of data transformation. Groups were compared using Mann-Whitney *U* tests (for comparisons of two groups) or Kruskal-Wallis ANOVA by ranks (for comparisons of three or more groups).

Because smelt length varied among samples, body condition was assessed using ANCOVA, with mass as the dependent variable, length as the covariate, and life stage, sampling method, and season as categorical predictor variables (Pope and Kruse 2007). Differences in the interaction term in the model indicated that fish in different groups had different masses at given lengths (Pope and Kruse 2007). It was assumed that increased body mass at a given length indicated greater energy reserves and a generally healthier state. For the sampling method comparison, only adult smelt were compared. Seasonal comparisons also only included adult smelt and were carried out separately for sampling in the littoral zone during the day (beach seining) and at night (boat EF). Homogeneous groups were determined using Tukey's HSD. To visualise mass-length relationships between life stages, sampling methods and seasons, we calculated regressions of fork length (L; mm) vs. mass (W; g) using least-squares regression using the following formula: $\log_{10}(W) = a + b(\log_{10}(L))$. Relationships between stable isotope ratios among size classes and capture locations were assessed using factorial ANOVA, and differences between groups were assessed with Tukey's HSD. All statistical analyses were carried out with STATISTICA, version 9.

3.4 Results

3.4.1 Habitat use

The density of smelt varied among sampling method and between littoral and pelagic lake zones. Mean smelt densities were higher in the littoral zone than in the pelagic zone, regardless of method, though catches were highly variable, and this difference was not statistically significant (Table 3.1a and b; Mann-Whitney U test (M-W U): $Z = 0.905$, $P = 0.365$). In the littoral zone, sampling by boat EF resulted in higher smelt densities than beach seining (Table 3.1a; M-W U: $Z = 4.506$, $P < 0.001$). In the pelagic zone, smelt density also varied with sampling method; long boat EF transects measured higher densities than short EF transects (Table 3.1b; M-W U: $Z = 2.751$, $P = 0.006$). The long transects also caught the largest size range of smelt (37–100 mm FL). Short (10 min) boat EF transects measured an average ± SE of 680 m^2 ± 199 m^2, with a minimum area fished of 328 m^2 and a maximum of 1364 m^2 (Table 3.1a). Long pelagic transects measured an average of 5390 m^2 ± 576 m^2, with a maximum area of 8400 m^2 and a minimum of 1865 m^2 (Table 3.1b).

Samples taken in the littoral zone by beach seine during the day showed that smelt density was highest in summer (mean ± SE density: 1.71 ± 0.55 fish m^{-2}) and lowest in winter (0.25 ± 0.05 fish m^{-2}, Table 3.1a). The length of smelt sampled by beach seine varied among seasons (ANOVA: $F_{1,3} = 193.3$, $P < 0.0001$, Tukey's HSD test: summer < autumn < winter < spring). Catch rates were significantly different among seasons (Kruskal-Wallis (K-W) test: $H = 48.516$, $n = 192$, df = 3, $P < 0.001$). Smelt densities in spring, measured by beach seining, were significantly different to other seasons, probably because of high variation in catches in spring compared to other seasons (K-W test: multiple comparisons mean ranks, $P < 0.05$). However, sampling by boat EF in the littoral zone at night showed that smelt density was highest in autumn (1.30 ± 0.22 fish m^{-2}) compared to other seasons (K-W test: $H = 15.323$, $n = 30$, df = 3, $P = 0.002$). In particular, densities in spring and winter were significantly lower than those in autumn (K-W test: multiple comparisons of mean ranks, $P < 0.05$). Although smelt catches were much higher in general in the littoral zone, the density and biomass of smelt varied in a similar way over time in the littoral and pelagic zones (Fig. 3.4).

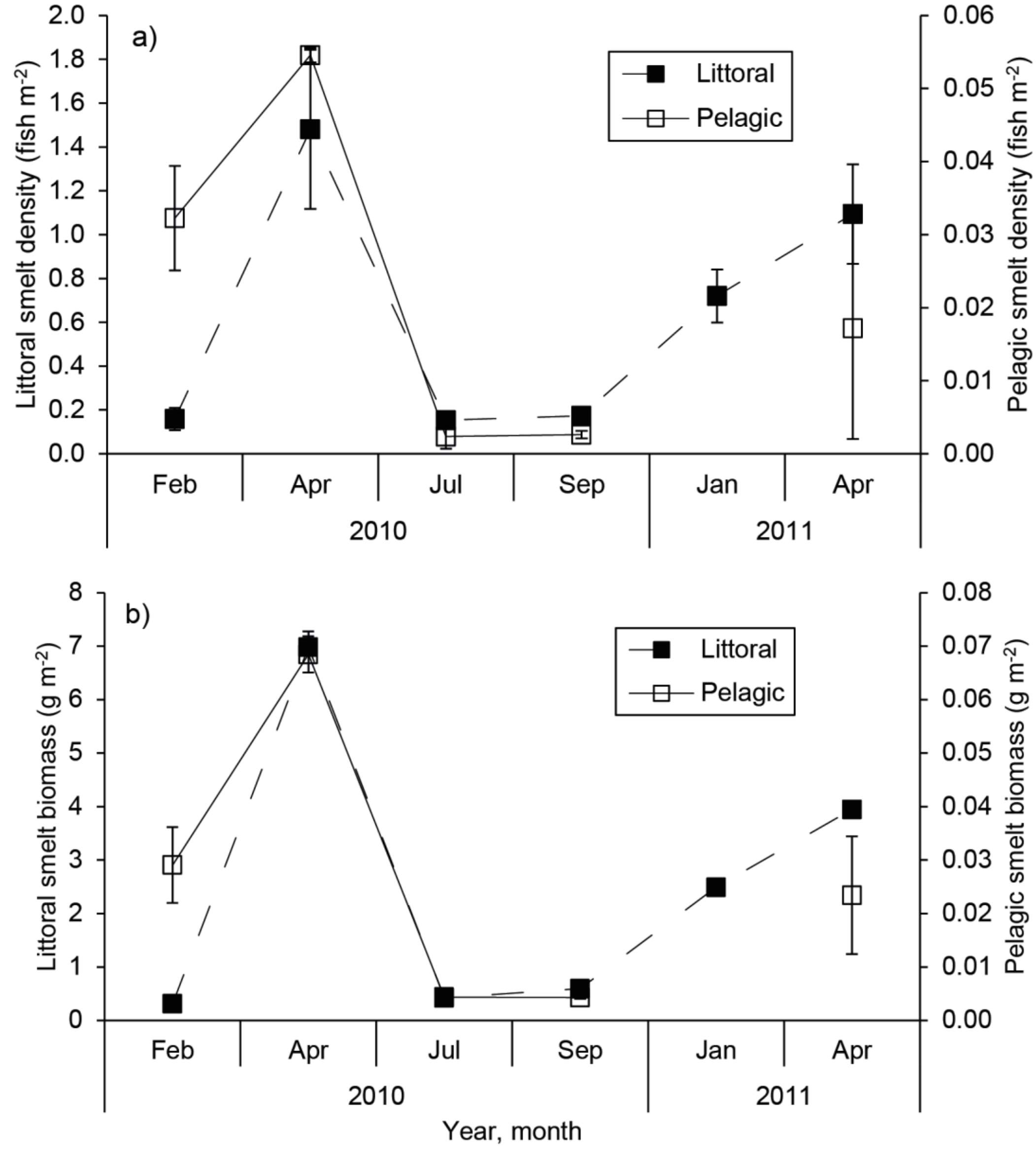

Fig. 3.4. Seasonal changes in relative (a) abundance and (b) biomass of smelt in littoral and pelagic zones, measured using 10 min boat electrofishing transects sampling water depths of 0–2 m (mean length = 240 m, mean area = 673 m^2) in Lake Rotoiti, 2010–2011. Error bars show ± 1 SE.

In the pelagic zone, the timing of peaks in smelt density also changed according to the sampling technique used. Ten-minute boat EF transects showed that smelt density was highest in summer in the pelagic zone, though this was not significantly different to other seasons (K-W test: $H = 7.223$, $n = 14$, df = 3, $P = 0.0651$). The length of smelt sampled using this method varied seasonally (ANOVA: $F_{1,3} = 50.42$, $P < 0.0001$, Tukey's HSD test: autumn > all other seasons). Long transects showed that the highest smelt density occurred in autumn, and that spring and autumn densities were significantly different (K-W test: $H = 10.858$, $n = 15$, df = 2, $P = 0.004$). Smelt that were sampled by long EF transects in the pelagic zone were notably smaller than those sampled using other methods (Table 3.1b; ANOVA: $F_{1,3} = 439.7$, $P < 0.0001$, Tukey's HSD test: long transects < beach seine < littoral and pelagic boat EF). Further comparisons of sampling methods can be found in Chapter 2.

Long EF transects in the pelagic zone showed that the density of smelt varied spatially as well as seasonally (Fig. 3.5). In September 2010 and January 2011, smelt density increased towards the eastern end of the lake. In contrast, in April 2011, smelt density was variable and showed no clear spatial pattern.

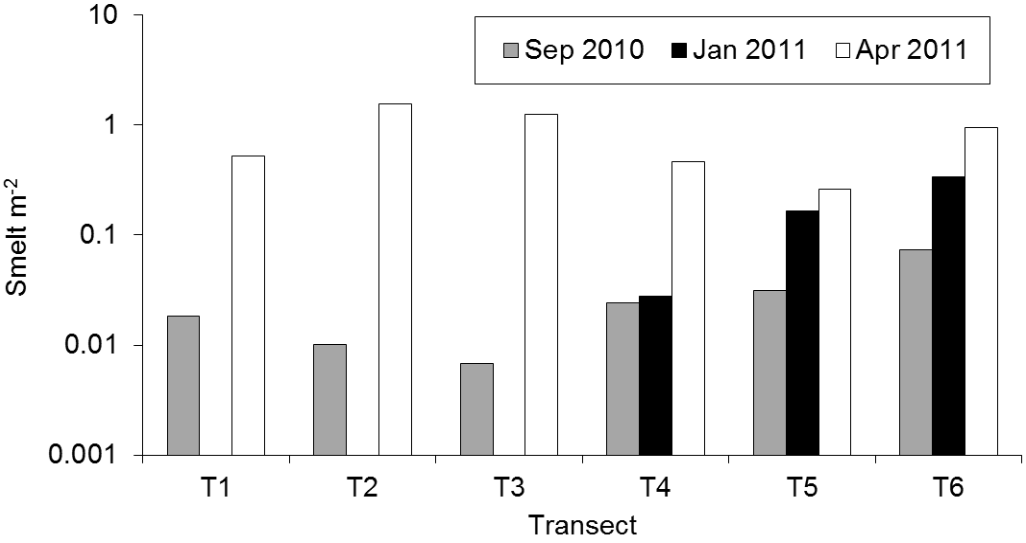

Fig. 3.5. Smelt densities in the pelagic zone of Lake Rotoiti , September 2010-April 2011, measured using long electrofishing transects sampling water depths of 0–2 m (mean area = 5390 m^2; see Fig. 3.2 for transect locations). Transects 1–3 not sampled in January 2011.

Table 3.1. (a) Number of samples, area sampled, depth sampled, and density, numbers and fork length of smelt in the littoral zone of Lake Rotoiti. Boat electrofishing transects were 117–487 m long and sampled water depths of 0–2 m; beach seine transects were 30 m long and sampled water depths of 0–1 m.

a) Littoral zone

	Number of samples	Mean area sampled (m^2) ± SE	Range of bottom depths (m)	Maximum effective sampling depth (m)	Total number of smelt caught	Smelt density (fish m^{-2})			Smelt length (mm)		
						Mean	SE	Range	Mean	SE	Range
Day- beach seine											
Spring	60	160.0 ± 0.0	0.9–1.2	1.2	2346	0.23	0.16	0.00–10.20	44	0.17	31–69
Summer	33	160.0 ± 0.0	0.9–1.2	1.2	9314	1.71	0.55	0.00–15.57	40	0.14	16–63
Autumn	35	160.0 ± 0.0	0.9–1.2	1.2	3963	0.69	0.25	0.00–8.36	42	0.16	29–57
Winter	64	160.0 ± 0.0	0.9–1.2	1.2	2414	0.25	0.05	0.00–1.72	43	0.11	31–64
Total	192	160.0 ± 0.0	0.9–1.2	1.2	18037	0.43	0.09	0.00–15.57	42	0.08	16–69
Night- boat electrofishing 10 min transects											
Spring	5	785.7 ± 147.9		2	681	0.18	0.03	0.13–0.28	45	0.20	37–100
Summer	10	490.6 ± 53.1	0.8–2.8	2	1737	0.44	0.11	0.03–1.14	43	0.19	21–85
Autumn	11	803.1 ± 37.3	0.8–5.5	2	115522	1.30	0.22	0.06–2.28	47	0.18	33–82
Winter	5	641.2 ± 25.9	0.9–2.6	2	491	0.16	0.03	0.09–0.28	44	0.31	31–73
Total	31	673.4 ± 39.4	0.8–5.5	2	14431	0.64	0.13	0.09–2.28	45	0.11	21–100

Table 3.1. (b) Number of samples, area sampled, depth sampled, and density, numbers and fork length of smelt in the pelagic zone of Lake Rotoiti. Boat electrofishing transects sampled water depths of 0–2 m. Ten-minute transects were 117–487 m long; longer (25–81 min) transects were 666–3000 m long and spanned from lake shore to lake shore.

b) Pelagic zone

	Number of samples	Mean area sampled (m^2) ± SE	Depth range of water sampled (m)	Maximum effective sampling depth (m)	Total number of smelt caught	Smelt density (fish m^{-2})			Smelt length (mm)		
						Mean	SE	Range	Mean	SE	Range
Night-boat electrofishing 10 min transects											
Spring	3	637.5 ± 4.9		2	5	0.0026	0.0005	0.0015–0.0032	42	0.37	41–43
Summer	2	837.2 ± 2.8	16.0–24.0	2	185	0.12	0.06	0.03–0.04	47	0.41	25–59
Autumn	4	760.9 ± 154.3	20.0–35.0	2	129	0.04	0.01	0.00–0.06	41	3.12	31–68
Winter	5	591.4 ± 43.7	20–34.4	2	7	<0.01	<0.01	0.00–0.01	46	0.42	25–48
Total	14	663.4 ± 52.8	20.0–35.0	2	326	0.01	0.01	0.00–1.26	46	0.25	25–68
Night- boat electrofishing 25–81 min transects											
Spring	6	5323.3 ±1035.3		2	1053	0.03	0.01	0.01–0.07	30	0.35	13–67
Summer	3	6626.7 ± 373.3		2	3345	0.18	0.09	0.03–0.34	42	0.27	16–70
Autumn	6	4837.5 ± 1002.4	9.6–62.0	2	21405	0.84	0.21	0.26–1.57	40	0.15	31–94
Total	15	5389.6 ± 575.6	9.6–62.0	2	25803	0.38	0.13	0.01–1.57	37	0.42	13–94

3.4.2 Body condition

Relative differences in body condition were evident between adult and juvenile smelt, and among groups of smelt that were caught in different areas of the lake and in different seasons (ANCOVAs of smelt mass with smelt length as a covariate; Tables 3.2 and 3.3). *W-L* regressions are plotted in Fig. 3.6 to give a visual indication of the relationships among groups. Juvenile smelt showed a faster rate of mass increase with length, evidenced by the steeper slope of the *W-L* regression of juvenile smelt compared to adult smelt (Fig. 3.6a, Table 3.2). Differences in body condition of adult smelt (i.e. body mass at given fork lengths) were evident among sampling methods (Fig. 3.6b, Tables 3.2 and 3.3, Tukey's test: boat EF long transects < beach seine < littoral and pelagic boat EF). Body condition was higher in autumn and spring than in summer and winter for smelt caught by boat EF in the littoral zone at night (Fig. 3.6c, Tables 3.2 and 3.3, ANCOVA: winter 2010 < summer 2010 < spring 2010 and autumn 2011 < autumn 2010). Body condition of adult smelt caught by beach seine in the littoral zone during the day was also lowest in winter, but peaked in spring, and was lower in autumn (Fig. 3.6d, Tables 3.2 and 3.3, ANCOVA: winter < autumn < summer < spring). Regression parameter estimates are given in Appendix 3.1.

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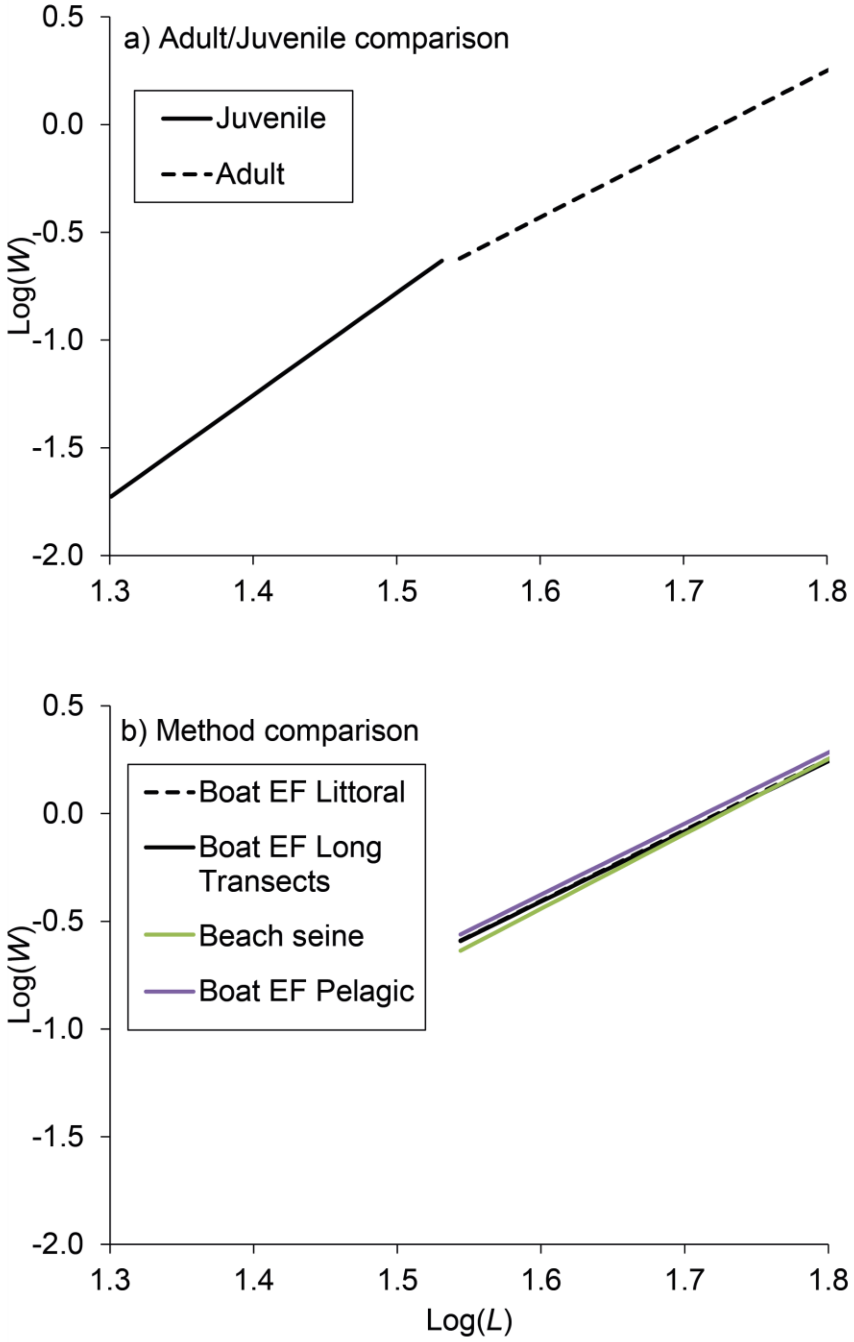

Fig. 3.6. (a, b) Regressions of $\log_{10}$-transformed smelt length (*L*; mm) vs. $\log_{10}$-transformed mass (*W*; g) for different (a) life stages and (b) sampling methods, calculated using the following formula: $\log_{10}(W) = a + b(\log_{10}(L))$. *X*-axis range ~ 20–65 mm, *y*-axis range ~ 0.01–3.16 g. Only adult smelt were used for comparison (b). See Table 3.2 for ANCOVA of this data. Regression parameter estimates are given in Appendix 3.1. *W*-*L* relationships are plotted only for the size range of fish that was sampled.

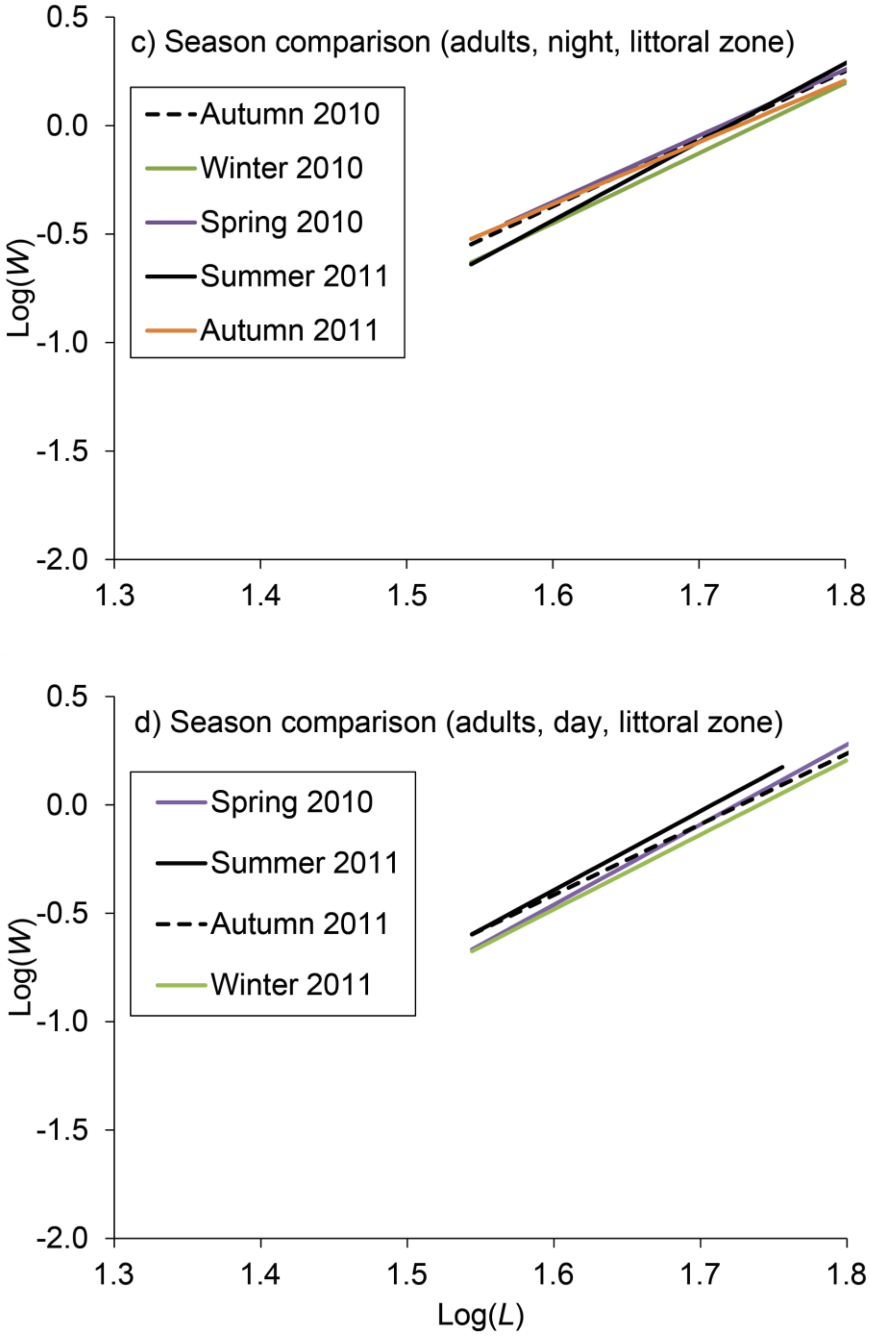

Fig. 3.6 (c, d). Regressions of $\log_{10}$-transformed adult smelt length (L; mm) vs. $\log_{10}$-transformed mass (W; g) for different seasons, for smelt captured in (c) the littoral zone at night and (d) the littoral zone during the day. Regressions calculated using the following formula: $\log_{10}(W) = a + b(\log_{10}(L))$. X-axis range ~ 20–65 mm, y-axis range ~ 0.01–3.16 g. See Table 3.2 for ANCOVA of this data. Regression parameter estimates are given in Appendix 3.1. W-L relationships are plotted only for the size range of fish that was sampled.

Table 3.2. Results of ANCOVAs of smelt mass, with length as a covariate, and (a) life stage (juvenile/adult; <35 mm or >35 mm), (b) capture method (beach seine, boat EF littoral, boat EF pelagic), and (c, d) season as categorical variables.

	SS	df	*F*	*p*
a) Life stage (juvenile/adult)				
Intercept	172.21	1	25404	<0.001
Life stage	3.69	1	545	<0.001
log(L)	135.39	1	19972	<0.001
Life stage × log(L)	3.65	1	539	<0.001
Error	33.90	5001		
b) Method comparison- adults				
Intercept	27.93	1	4659	<0.001
Method	0.15	3	8	<0.001
log(L)	25.47	1	4249	<0.001
Method × log(L)	0.13	3	7	<0.001
Error	27.64	4611		
c) Seasonal comparison- adults, littoral, night				
Intercept	25.19	1	6560	<0.001
Season, year	0.14	4	9	<0.001
log(L)	23.49	1	6117	<0.001
Season, year × log(L)	0.13	4	8	<0.001
Error	3.14	817		
d) Seasonal comparison- adults, littoral, day				
Intercept	79.68	1	16946	<0.001
Season	0.13	3	9	<0.001
log(L)	71.28	1	15160	<0.001
Season × log(L)	0.14	3	10	<0.001
Error	14.81	3149		

Table 3.3. Results of Tukey's HSD tests showing homogenous groups from ANCOVA analyses of smelt mass, with smelt length as a covariate, and (b) capture method (beach seine, boat EF littoral, boat EF pelagic), and (c and d) season as categorical variables.

Treatment	Mean log(W)	Group
b) Method comparison- adults		
Boat EF long transects	-0.361	1
Beach seine	-0.336	2
Boat EF Littoral	-0.227	3
Boat EF Pelagic	-0.223	3
c) Season comparison- adults, littoral, night		
Autumn 2010	-0.097	1
Winter 2010	-0.344	2
Spring 2010	-0.186	3
Summer 2011	-0.237	4
Autumn 2011	-0.176	3
d) Season comparison- adults, littoral, day		
Spring	-0.285	1
Summer	-0.302	2
Autumn	-0.342	3
Winter	-0.378	4

3.4.3 Reproduction

More smelt eggs were present in benthic samples collected in autumn than in spring, though egg numbers were not significantly different between the two seasons (Table 3.4; M-W *U* test: $Z = 1.00$, $P = 0.239$). The number of smelt eggs per sample varied significantly among sites (Table 3.4; K-W test: $H = 56.30$, $n = 369$, df = 6, $P < 0.001$). No smelt eggs were found at sites 1, 2, or 3. These sites were situated at the western end of the lake and were characterised by high conductivity, a low proportion of coarse sediment and narrow beach widths. In contrast, smelt eggs were found at sites 4–7 in varying numbers. These sites were situated in the main eastern basin of the lake, and had lower conductivity, higher proportions of coarse sediment, and wider beaches than sites 1–3.

Peaks in smelt gonadosomatic index (GSI) usually coincided with peaks in egg counts in benthic samples, except for a peak in GSI in January that was not reflected in smelt egg samples (Fig. 3.7). Spawning peaks in September-October, January, and April were evident from either GSI, egg counts, or both. Smelt GSI was lowest in winter, coinciding with poor body condition of smelt (Figs. 3.6c, 3.6d and 3.7).

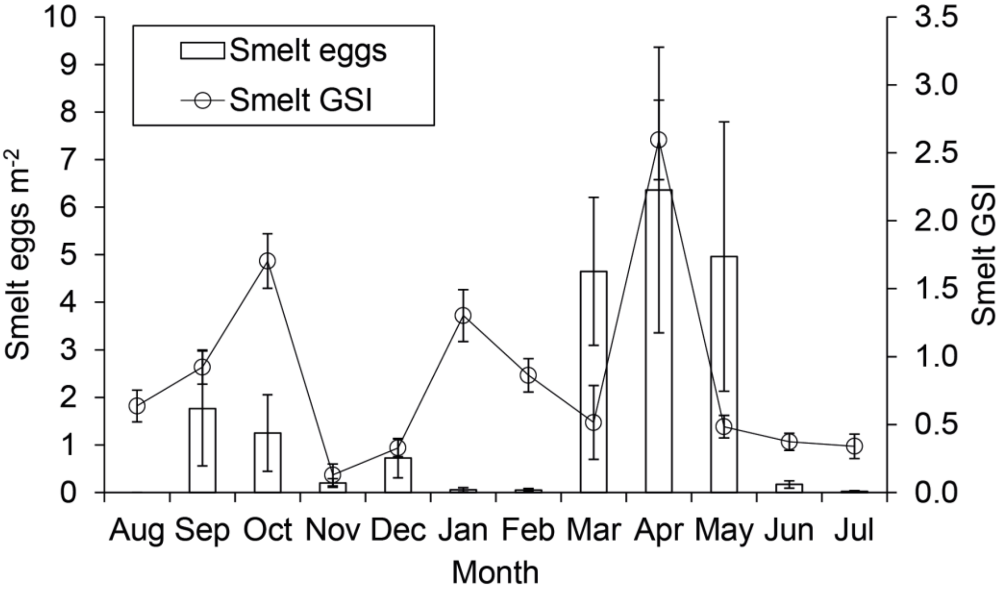

Fig. 3.7. Mean density of smelt eggs in benthic samples in littoral zone (bars) and gonadosomatic index (GSI; points) of smelt sampled in the littoral zone of Lake Rotoiti by beach seining and boat electrofishing, August 2010-July 2011. Error bars show ± 1 SE.

Table 3.4. Densities of smelt eggs in spring (Sept–Nov 2010) and autumn (March–May 2011) at sample sites in Lake Rotoiti, with overall site characteristics. Smelt eggs measured as egg density in 20 m benthic samples, by site, in spring and autumn (mean per sample ± SE) with number of samples taken (*n*).

	Eggs m^{-2} (spring)		Eggs m^{-2} (autumn)		Specific conductivity (µS cm^{-1})				
Site	Mean ± SE	*n*	Mean ± SE	*n*	Mean ± SE	*n*	% sediment >1 mm diameter	Estimated beach width (m)	Aspect
1	0 ± 0	6	0 ± 0	12	163.1 ± 4.2	8	9.6	5.8	W
2	0 ± 0	6	0 ± 0	6	170.4 ± 2.4	8	6.7	3.0	N–NE
3	0 ± 0	6	0 ± 0	12	174.4 ± 1.3	8	1.7	27.1	NE
4	3.82 ± 2.01	12	19.75 ± 5.18	20	163.0 ± 1.6	8	42.8	25.9	N–NE
5	0.39 ± 0.23	12	0.05 ± 0.03	20	151.1 ± 7.1	8	25.3	36.1	W
6	1.13 ± 0.50	6	0.71 ± 0.24	12	165.5 ± 1.6	8	28.7	33.4	S
7	0.09 ± 0.09	6	7.29 ± 3.41	12	167.2 ± 0.9	8	51.1	44.3	SW

3.4.4 Diet

The proportion of smelt with empty stomachs was highest among smelt sampled in the pelagic zone with long boat EF transects (Table 3.5). The length of smelt sampled for stomach contents analysis did not vary by season (K-W test: $H = 1.02$, $n = 124$, df = 3, $P = 0.798$), but the length of smelt did vary among methods used (K-W test: $H = 8.09$, $n = 155$, df = 2, $P = 0.018$). Specifically, the length of smelt sampled with boat EF in the littoral zone was significantly higher than the length of smelt sampled with long boat EF transects (K-W test: multiple comparisons of mean ranks).

Table 3.5. Characteristics of smelt sampled for diet comparisons, by zone, time of day, and season. Characteristics: Number of stomachs sampled (*n*), percentage of stomachs containing food, mean weight of food in stomachs, mean fork length (L) of smelt sampled, with standard error, and minimum and maximum lengths of smelt sampled.

Time	Zone	Season	*n*	% with food	Food weight (g) ± SE	Mean *L* (mm) ± SE	Range *L* (mm)
Day	Littoral	Spring	52	98	0.013 ± 0.001	45 ± 0.70	32–54
		Summer	56	91	0.011 ± 0.002	41 ± 0.97	29–55
		Autumn	105	88	0.017 ± 0.004	44 ± 0.56	29–55
		Winter	54	94	0.011 ± 0.001	43 ± 0.68	34–57
		Total	267	92	0.014 ± 0.002	43 ± 0.36	29–57
Night	Littoral	Autumn	61	71	0.018 ± 0.002	46 ± 0.73	39–57
	Pelagic	Summer	26	77	0.008 ± 0.001	39 ± 1.25	31–55
		Autumn	55	36	0.011 ± 0.001	44 ± 2.47	34–86
		Total	80	49	0.014 ± 0.001	42 ± 1.45	31–86

The amount of food in smelt stomachs (relative to body mass) varied significantly among seasons and sampling methods (Fig. 3.8). The mass of food in smelt stomachs sampled in the littoral zone during the day varied significantly among seasons (K-W test: $H = 11.14$, $n = 267$, df = 3, $P = 0.011$); however, none of the subsequent pairwise comparisons showed significant differences between seasons ($P > 0.05$). For smelt sampled in the pelagic zone at night, the mass of stomach contents varied significantly between summer and autumn (M-W U test: $Z = 3.15$, $P = 0.002$). In autumn, smelt sampled at night in the pelagic zone had significantly less food in their stomachs than smelt sampled in the littoral zone either during day and night (K-W test: $H = 40.14$, $n = 221$, df = 2, $P < 0.001$).

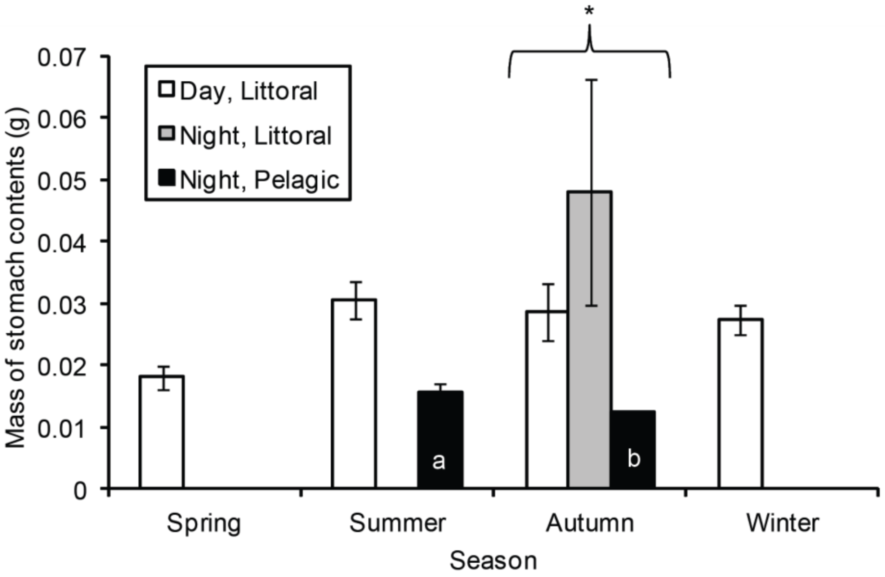

Fig. 3.8. Mean mass (± SE) of smelt stomach contents at different times and in different lake zones and seasons, standardised by smelt mass. * indicates significant differences among sampling times and locations in autumn (Kruskal-Wallis test: $P < 0.05$). Letters a and b denote significant differences between sampling occasions in the pelagic zone (Mann-Whitney *U* test: $P < 0.05$).

Smelt caught in the littoral zone during the day consumed a wide range of prey items including zooplankton, amphipods, terrestrial and aquatic insect larvae, tanaid shrimp, oligochaetes and smelt eggs (Fig. 3.9). The species found in smelt stomachs and environmental samples are summarised in Table 3.6. The diet of smelt caught in the littoral zone during the day varied with season. In spring, zooplankton, amphipods, chironomid larvae and terrestrial insects were all abundant in smelt diets (Fig. 3.9a). In summer, zooplankton and terrestrial insects were less common than in spring, and chironomid pupae and amphipods were the most commonly consumed prey species (Fig. 3.9b). A small proportion of smelt also consumed a small number of smelt eggs (Fig. 3.9b). The diet of smelt caught in autumn was much less diverse, and smelt consumed only smelt eggs, terrestrial insects, and zooplankton, with smelt eggs making up almost all of the diet by mass (Fig. 3.9c). Smelt eggs continued to be the most commonly eaten food item in winter; other species were consumed relatively rarely and made up a small proportion of the diet (Fig. 3.9d).

Differences in smelt diet were also evident among smelt sampled in autumn using different techniques at different times of day (Fig. 3.10). Smelt sampled during the day in the littoral zone consumed a wide range of prey items; smelt eggs made up the largest proportion of the diet by mass and were the most commonly eaten food item (Fig. 3.10a). In contrast, smelt sampled at night in the littoral zone consumed almost exclusively zooplankton, with chironomid pupae making up a small proportion of the diet (Fig. 3.10b). Smelt caught in the pelagic zone at night had a similar diet to those caught in the littoral zone at night, but some smelt had also consumed larval bullies (Fig. 3.10c).

Small smelt (<45 mm) caught in the littoral and pelagic zones at night consumed significantly more zooplankton than large smelt (>45 mm) (Fig. 3.11a and b; M-W *U* test: pelagic: $Z = -2.88$, $P = 0.004$; littoral: $Z = -4.66$, $P < 0.001$). Smelt caught by beach seining in the littoral zone during the day consumed much less zooplankton than smelt caught at night, but there was no difference in the amount of zooplankton consumed between large and small smelt (Fig. 3.11).

Table 3.6. Summary of most common taxa found in smelt stomachs and lake samples.

Abbreviation	Taxon	Family/species	Common name
Zooplankton	Calanoida	*Boeckella propinqua*	
	Cyclopoida	*Mesocyclops leuckarti*	
	Cladocera	*Bosmina meridionalis*	
		Ceriodaphnia dubia	
		Daphnia galeata	
Insects			
Chr larvae, chr pupae	Diptera	Chironomidae	Non-biting midge
Caddisflies	Trichoptera	*Paroxyethira* sp.	Caddisfly
Terrestrial insects	Diptera, Hymenoptera, Coleoptera		Flies, wasps, beetles
Other			
Bullies	Perciformes	*Gobiomorphus cotidianus*	Common bully
Oligochaetes	Oligochaeta		Earthworm
Tanaid shrimp	Malacostraca	*Sinelobus stanfordi*	Tanaid shrimp
Amphipod	Malacostraca	Amphipoda	Amphipod
Snail	Gastropoda	*Potamopyrgus antipodarum*	New Zealand mudsnail

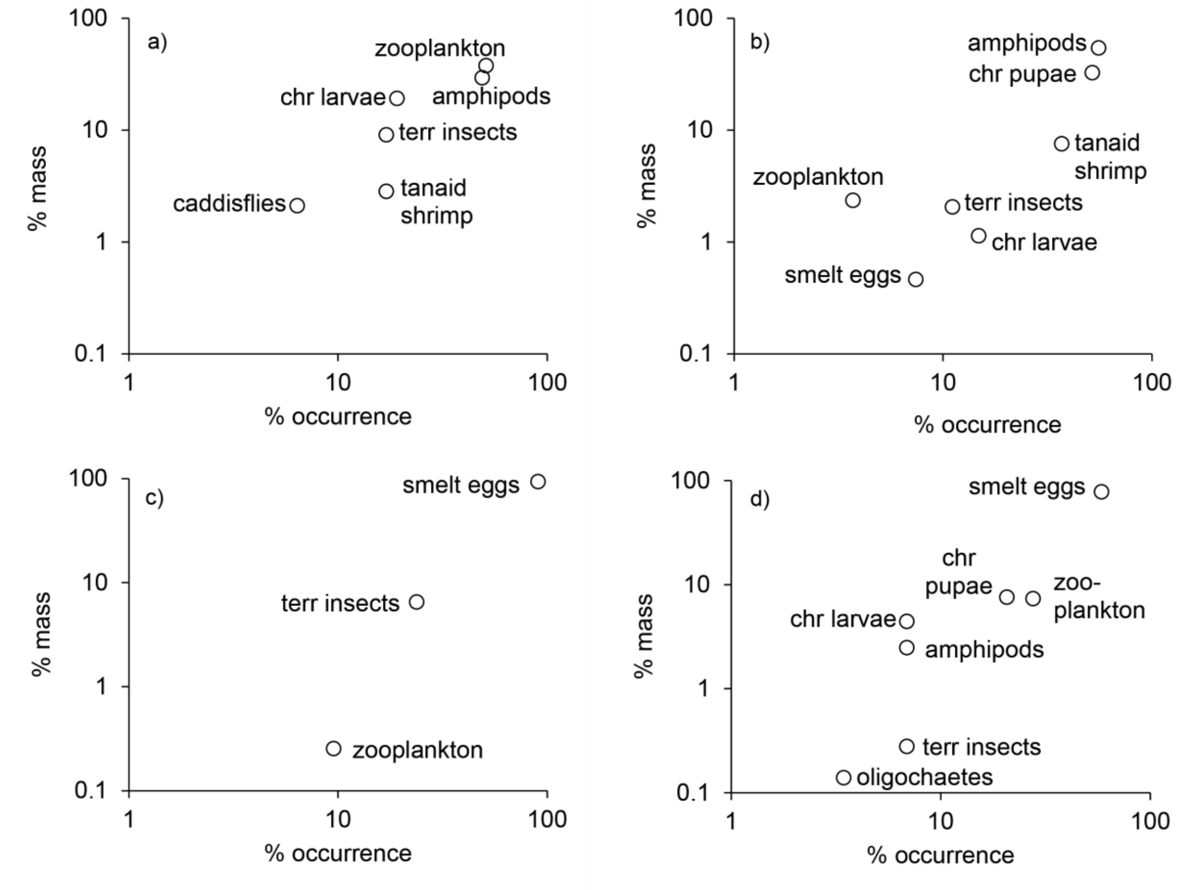

Fig. 3.9. Diet of smelt (29–57 mm) caught in littoral zone of Lake Rotoiti during the day in (a) spring, (b) summer, (c) autumn, and (d) winter, 2010–2011. Diet expressed as % mass (the percentage of each prey type by mass across all non-empty smelt stomachs), and % occurrence (the percentage of non-empty smelt stomachs containing each prey item). Refer to Table 3.5 for details of sampled smelt and Table 3.6 for diet species information.

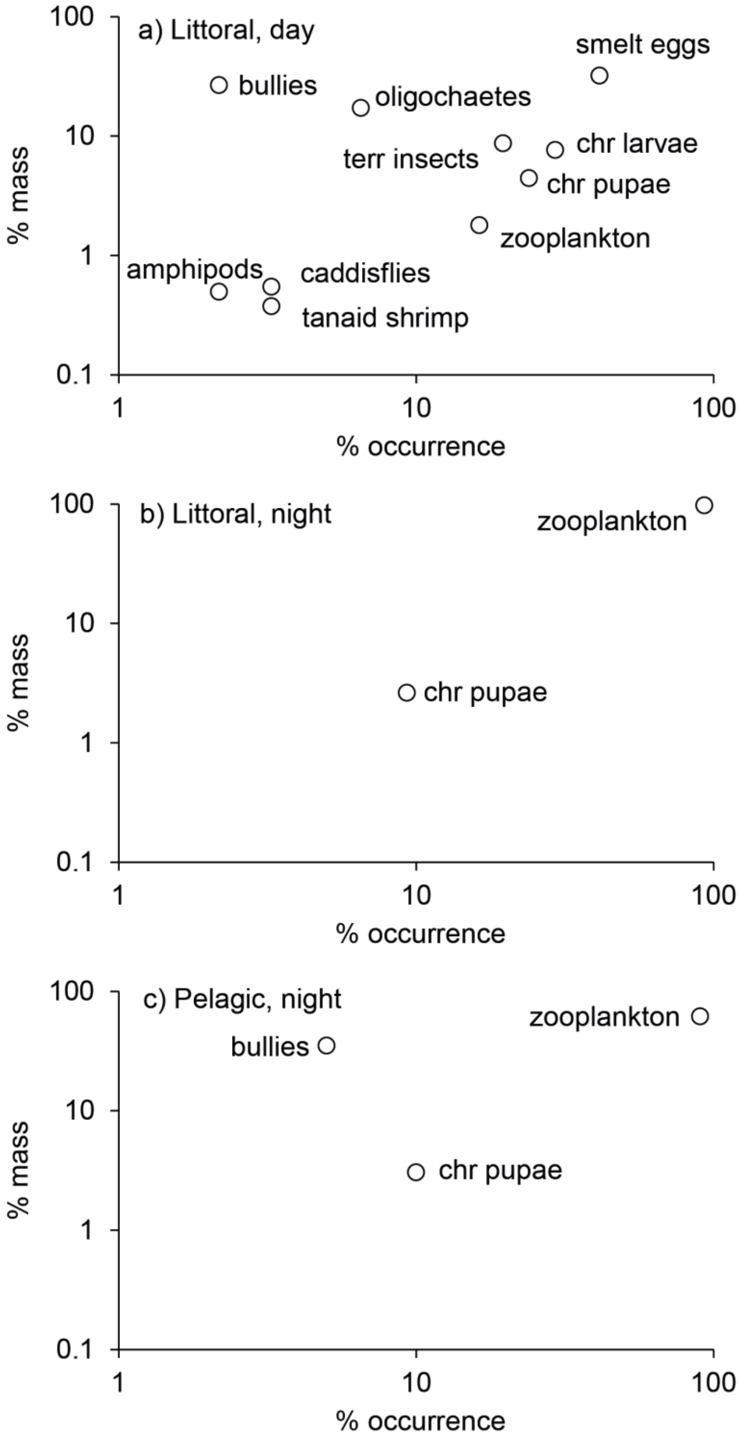

Fig. 3.10. Diet of smelt (29–86 mm) caught in Lake Rotoiti in autumn in (a) the littoral zone during the day, (b) the littoral zone at night, and (c) the pelagic zone at night. Diet expressed as % mass (the percentage of each prey type by mass across all non-empty smelt stomachs), and % occurrence (the percentage of non-empty smelt stomachs containing each prey item). Refer to Table 3.5 for details of sampled smelt and Table 3.6 for diet species information.

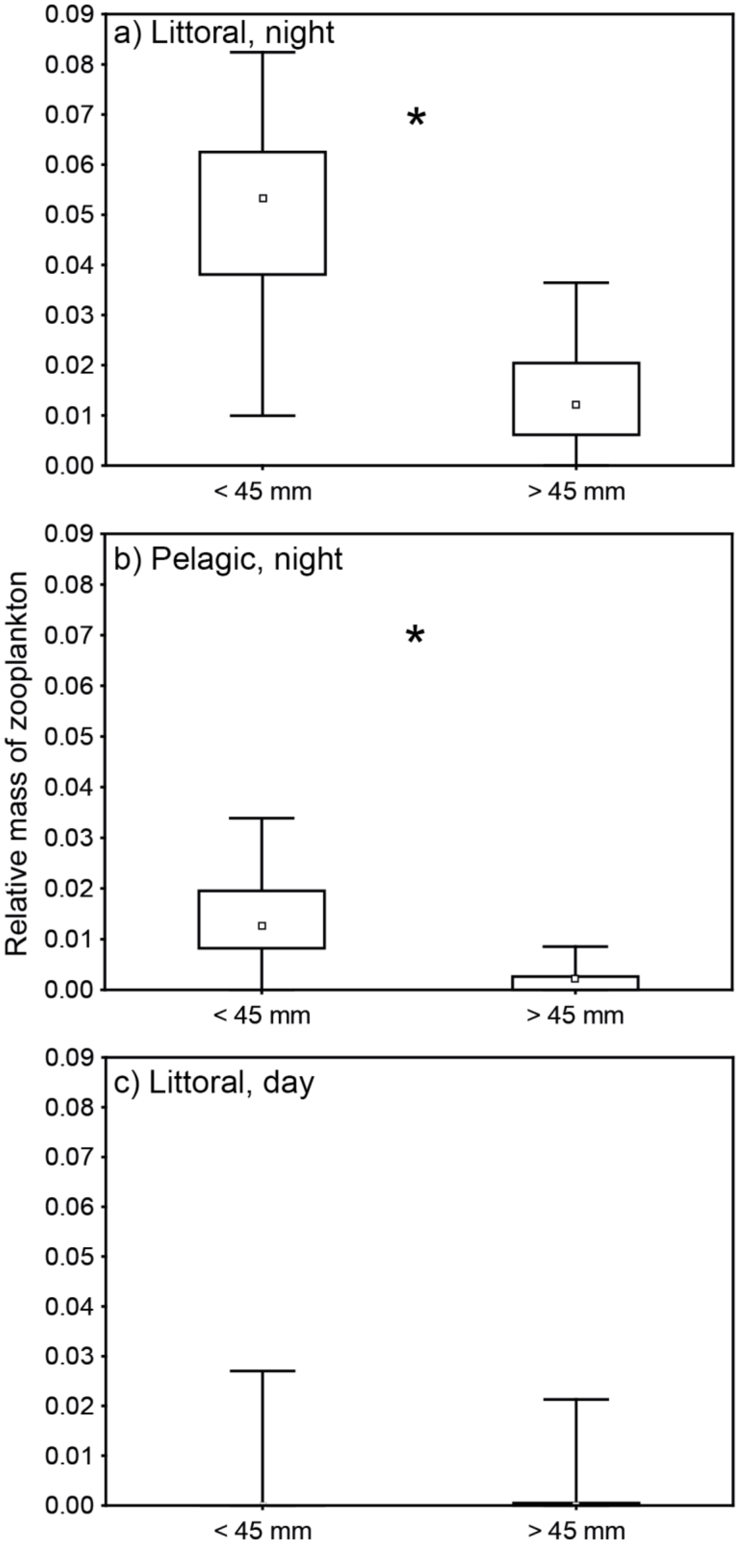

Fig. 3.11. Mass of zooplankton in smelt stomachs, relative to smelt body mass, for smelt measuring <45 mm and >45 mm. Smelt caught in autumn in Lake Rotoiti in the (a) littoral zone during the day, (b) littoral zone at night, and (c) the pelagic zone at night. Box and whisker graphs show median, 25th and 75th percentiles, minimum, and maximum. * shows significant difference between groups (Mann-Whitney *U* test: $P < 0.05$).

The relative abundance of zooplankton in the pelagic zone and benthic prey items in the littoral zone varied seasonally, and was highest in summer for littoral prey (Fig. 3.12a) and spring for zooplankton (Fig. 3.12b; refer to Table 3.6 for species summary). The relative abundance of invertebrates in the littoral zone was highest in summer, and the invertebrate assemblage was made up of several species year-round (Fig. 3.12a). The littoral invertebrate assemblage included amphipods, chironomid larvae and pupae (Family Chironomidae), oligochaete worms, caddisfly larvae (*Paroxyethira* sp.), New Zealand mudsnail (*Potamopyrgus antipodarum*), tanaid shrimp (*Sinelobus stanfordi*), and various zooplankton. Tanaid shrimp were highly abundant in summer, making up the majority of invertebrate numbers. Smelt eggs were present in littoral samples in spring, summer, and autumn, and were numerically more abundant than other prey items in autumn (Fig. 3.12a). Calanoid copepods dominated the zooplankton assemblage year-round, and were most abundant in summer and autumn (Fig. 3.12b). Cyclopoid copepods were present in small numbers year-round. Copepod nauplii and the cladoceran *Bosmina meridionalis* showed a peak in abundance in spring. Other zooplankton groups sampled included the cladocerans *Ceriodaphnia dubia* and *Daphnia galeata*.

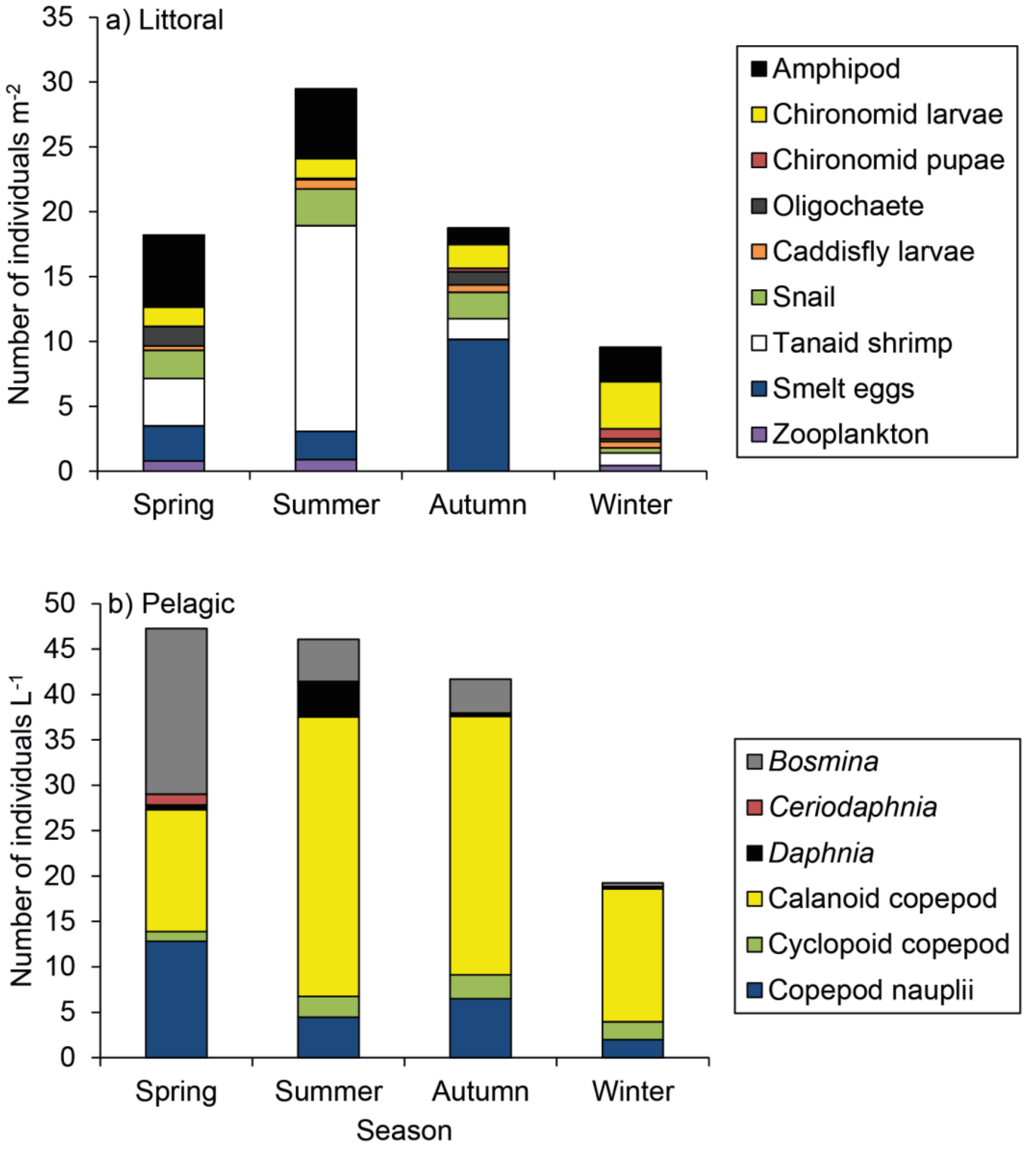

Fig. 3.12. Numbers of (a) invertebrates sampled in the littoral zone and (b) zooplankton sampled in the pelagic zone of Lake Rotoiti, by season, spring 2010-winter 2011. Refer to Table 3.6 for species details.

For smelt caught in the littoral zone during the day, tissue δ^{13}C and δ^{15}N showed little ontogenetic variation (Figs. 3.13 and 3.14). In contrast, medium (40–50 mm) and large (>50 mm) smelt caught at night in the littoral and pelagic zones were depleted in δ^{13}C compared to small smelt (<40 mm). Large and medium smelt from the pelagic zone, and large smelt caught from the littoral zone at night, showed elevated values of δ^{15}N compared to other smelt. Both smelt size and zone/time (littoral, day; littoral, night; and pelagic, night) were important determinants of δ^{13}C and δ^{15}N, and there was an interaction between size and zone/time for δ^{15}N (Table 3.7). Tukey's HSD tests showed several differences, especially in δ^{15}N, between smelt caught at night and during the day (Appendix 3.2).

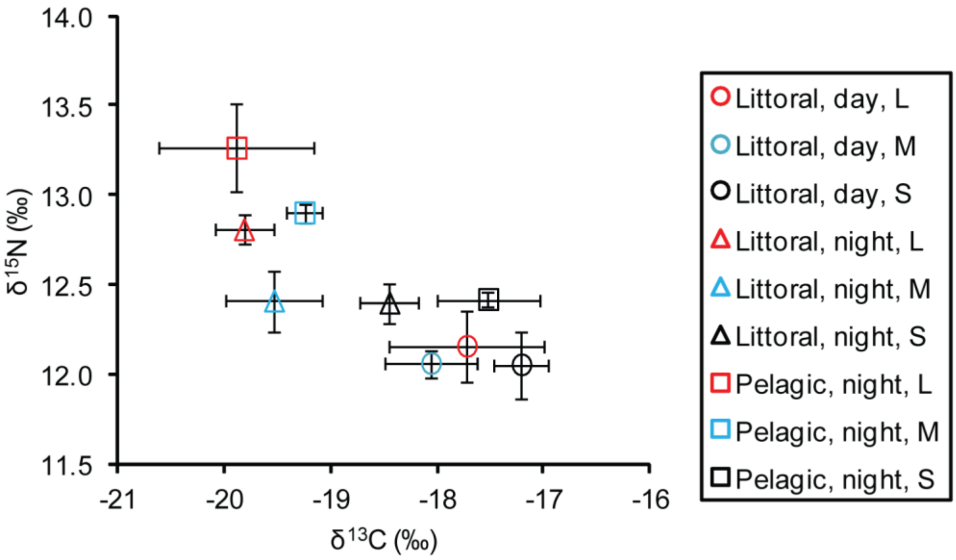

Fig. 3.13. Stable isotope ratios of C and N for smelt caught at different times in different lake zones. Error bars show ± 1 SE. S = small smelt, <40 mm FL; M = medium smelt, 40–50 mm; L = large smelt, >50 mm.

Table 3.7. Results of factorial ANOVAs comparing (a) δ^{13}C and (b) δ^{15}N between size classes of smelt (small, <40 mm FL; medium, 40–50 mm; large, >50 mm) and zone and time captured (littoral, day; littoral, night; and pelagic, night). Significant *P*-values shown in bold italics.

(a) δ^{13}C

	SS	df	*F*	*p*
Intercept	15871	1	14790	***<0.001***
Zone/time	21.07	2	9.82	***<0.001***
Size class	18.28	2	8.52	***0.001***
Zone/time × size class	4.57	4	1.07	0.388
Error	39.70	37		

(b) δ^{15}N

	SS	df	*F*	*p*
Intercept	7158	1	67878	***<0.001***
Zone/time	4.59	2	21.7	***<0.001***
Size class	1.61	2	7.6	***<0.001***
Zone/time × size class	0.85	4	2.0	***<0.001***
Error	3.90	37		

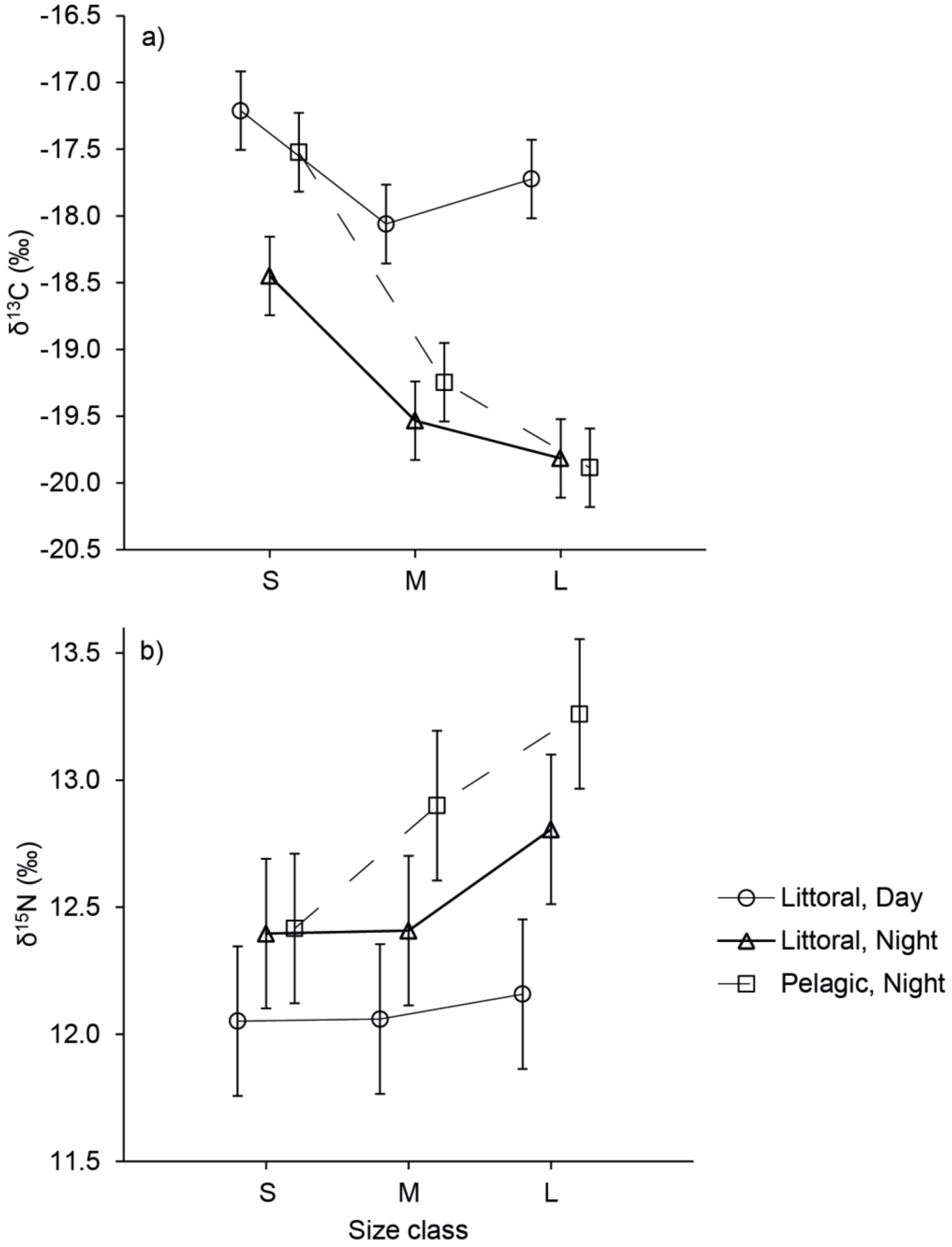

Fig. 3.14. Comparison of mean (a) δ^{13}C and (b) δ^{15}N between size classes of smelt and zone and time captured. Error bars show ±95% confidence intervals.

3.5 Discussion

3.5.1 Habitat use

Our results indicate that smelt undergo ontogenetic, diel and seasonal changes in habitat use in Lake Rotoiti. An ontogenetic habitat change between littoral and pelagic zones was evident, as we rarely caught larval smelt in littoral samples, but they were abundant in pelagic samples, especially long boat EF samples taken in September. This result concurs with findings of a study in Lake Taupo (Stephens 1984); after hatching on beaches, larval smelt moved to the pelagic zone, and made more use of the littoral zone as adults.

Smelt also undertook diel vertical migrations. In Lake Rotoiti, smelt occupy distinct layers in the water column during the day, and ascend to the surface at dusk (Rowe 1993). Diel vertical migration is a common behaviour in zooplanktivorous fish and is related to predator avoidance, feeding, and bioenergetic efficiency (Mehner 2012). However, some fish do not migrate, and numbers of these “resident” fish increase when temperature differences in the water body are low, i.e. when the water column is fully mixed (Mehner and Kasprzak 2011). Lake Rotoiti is typically fully mixed between June and October, and thermally stratified between November and April (von Westernhagen et al. 2010). The increase in smelt caught in the surface waters of the pelagic zone in April, compared to September, is consistent with a greater proportion of smelt migrating when the lake is stratified; however, hydroacoustic measurements would be needed to confirm this pattern.

Seasonal changes in smelt distribution were shown by peaks in smelt density in the littoral zone in summer and autumn; this is similar to the pattern observed in Lake Taupo by Stephens (1984), who found that littoral smelt densities peaked in summer, but were high between November and June. Smelt catches in the littoral zone were also highest in summer in lakes Ellesmere and Waihola (Glova and Sagar 2000, Kattel and Closs 2007), and in Lake Taupo (Cryer 1991). Samples taken by boat EF in depths of 0.8–5.5 m in the littoral zone at night showed that smelt densities in this area peaked in autumn. Stephens (1984) found that night time beach seining catches were approximately an order of magnitude lower than daytime catches, but densities measured by EF in the littoral zone of Lake Rotoiti were of a similar magnitude to those measured by beach seining during the day (0.9–1.2 m depth). It therefore seems likely that smelt occupying very shallow waters of the littoral zone during the day move to slightly deeper littoral waters at night.

Seasonal changes in the broad spatial distribution of smelt also occurred. Spatial patterns in smelt density within the surface waters of the pelagic zone of Lake Rotoiti conformed with patterns shown by hydroacoustics (also taken in September 2005–2010) that showed an increase in smelt density towards the eastern end of the lake than at the western end (Rowe et al. 2011). However, in April, no such pattern was observed, and overall, smelt densities in surface waters were higher than in September.

3.5.2 Body condition

The increase in body condition in smelt in spring and autumn coincided with increases in GSI and smelt egg counts. After the spawning peak in autumn, smelt body condition dropped considerably. The low abundances of prey items over winter probably make it difficult for smelt to recover body condition post-spawning.

The drop in smelt body condition and density in the littoral zone during winter and spring may have consequences for the timing of stocking of rainbow trout into the littoral zone. Rainbow trout yearlings are released in autumn (May) and spring (September); trout released in spring may be more likely to experience prey limitation due to low smelt numbers at the time of release. There is evidence of density-dependent growth in rainbow trout during their first year of lake residence, and trout released in spring experience slower growth and grow to a smaller maximum size that trout released in autumn (see Chapter 6). Bioenergetics modelling showed that a small change in smelt energy density was enough to elicit a significant increase in the consumption of prey by rainbow trout, as a drop in energy density means that more prey must be eaten to meet energetic demands (see Chapter 6).

3.5.3 Reproduction

The spatial patterns of smelt egg deposition in Lake Rotoiti indicated a preference for relatively exposed spawning sites with coarse sediments and proximity to deep water. Rowe and Taumoepeau (2004) suggested that in turbid lakes, siltation may smother smelt eggs, causing mortality and leading to lower smelt densities in turbid lakes compared to clear lakes. This may account for the fact that larval smelt abundance is highest in lakes with high water clarity (Rowe and Taumoepeau 2004). Siltation rates to beaches in Lake Rotoiti's main basin should be carefully monitored, as influxes of sediment from the lake catchment could smother smelt eggs and may cause reductions in smelt numbers.

We observed a peak in smelt spawning in autumn, in contrast to other studies of lacustrine smelt that observed spawning peaks in spring or summer (Jolly 1967, Stephens 1984, Ward and Boubée 1996). It remains to be seen whether the population in Lake Rotoiti is unique in spawning in autumn, or if this behaviour is common in other lakes. Although peaks in smelt gonadosomatic index (GSI) coincided with peaks in egg counts in benthic samples in spring and autumn, a peak in GSI in January was not reflected in smelt egg abundance. Smelt eggs were also found in smelt stomachs in winter, but not in benthic samples. This may indicate that smelt spawned in areas that were not sampled. Resorption of eggs is also a possible explanation for the discrepancy between GSI and egg abundance in January. To achieve better coverage of likely smelt spawning sites, future studies could sample a subset of the sites sampled in this study (perhaps 7 and 4) as well as other sites with coarse sediments.

3.5.4 Diet

Smelt feed on both benthic and pelagic food sources, and like many fish (Vadeboncoeur et al. 2002), integrate the benthic and pelagic food webs. Utilisation of benthic food sources can be expected in Lake Rotoiti, as the ratio of mean to maximum depth (~0.34) indicates that much of the benthic surface area is situated in shallow, littoral areas, and the relative clarity of the water likely allows adequate light penetration to the benthos, resulting in a high rate of benthic production (Vadeboncoeur et al. 2008). The amount of food in smelt stomachs and number of smelt with non-empty stomachs were higher in the littoral zone than in the pelagic zone, suggesting that the littoral zone and benthic food sources were important for smelt feeding.

Similar to previous studies, we found that smelt diet varied with size; large smelt (>45 mm) ate less zooplankton than small smelt (<45 mm). An ontogenetic shift in prey from zooplankton in small smelt to a range of prey in larger smelt has been documented in central North Island lakes (Jolly 1967, Stephens 1984). However, this pattern was not seen in smelt caught in the littoral zone during the day; zooplankton made up a much smaller proportion of the diet in these fish. Results from stable isotope analyses confirmed that small and large smelt in the littoral zone incorporated similar food sources into their body tissues. Differences in the diet and stable isotope signatures of large littoral smelt compared to large pelagic smelt suggest that littoral smelt rely more heavily on benthic food sources.

Seasonal patterns of stomach fullness align with patterns in body condition, i.e. smelt body condition was lowest in winter, which was also when the least amount of food was found in stomachs. This period coincided with low abundance of zooplankton and benthic invertebrates, suggesting that smelt are food limited during winter.

We found that zooplankton made up a significant portion of the diet of littoral smelt in spring; however, other littoral prey species such as amphipods, chironomid larvae and terrestrial insects were also important. In general, zooplankton made up a larger proportion of the diet in smelt caught at night than during the day. Previous studies have found that the incidence of zooplanktivory varies in adult smelt. For example, smelt between 30 and 69 mm long in Lake Waahi, Waikato, consumed a wide range of prey items, including zooplankton, chironomid larvae and pupae, and insects (Northcote and Chapman 1999). Chironomid larvae and pupae are the main prey item for large (50–69 mm) and small (30–49 mm) smelt at all times of year, but small smelt consumed almost exclusively zooplankton in summer (January-March) (Northcote and Chapman 1999). Stephens (1984) found that age-1 smelt continued to eat zooplankton, though similar to Lake Rotoiti, terrestrial insects, chironomid larvae and smelt eggs were also consumed. Stephens also found that age-2 smelt (≥64 mm) consumed mainly larval bullies. In Lake Rotoiti, predation on bullies was rare, but was observed in smelt caught from the littoral zone during the day and the pelagic zone at night.

To our knowledge, this study presents the first observation of significant egg predation by smelt. Egg predation was also reported by Stephens (1984), but the maximum number of smelt eggs found in smelt stomachs was 27, whereas over 100 smelt eggs were found in the stomachs of several smelt in this study (J. Blair, unpubl. data). This may reflect differences in egg density between the two lakes, though we cannot compare our egg density measurements with those of

Stephens (1984) because different sampling methods were used (net vs. corer). Smelt eggs were the most commonly eaten prey item and made up the bulk of food consumed by mass in autumn and winter. It was likely that smelt ate a higher proportion of smelt eggs in winter due to the relative scarcity of alternative prey such as benthic invertebrates and zooplankton. However, we cannot be sure that smelt prey upon smelt eggs at such a high rate every year; our results may have represented atypical conditions influenced by scarcity of food. Long-term monitoring of smelt diets is needed to answer this question.

3.5.5 Management implications

In 2008, the Ohau Channel Diversion Wall was installed to improve water quality in Lake Rotoiti by diverting inputs of water from Lake Rotorua, which usually reach Lake Rotoiti via the Ohau Channel, to the Kaituna River. Some uncertainty existed as to whether installation of the diversion wall would interrupt smelt migrations and affect smelt abundance in Lake Rotoiti (Rowe et al. 2006). Our field surveys indicate that smelt are highly abundant in Lake Rotoiti, and surveys of smelt eggs and larvae in the pelagic zone suggest that smelt reproduce within Lake Rotoiti. Because of local reproduction and littoral abundance, the impact of the Ohau Channel diversion wall on smelt populations should be limited. Additionally, recent trapping surveys in the Ohau Channel show that smelt migrations have taken place between Lake Rotoiti and Lake Rotorua after the installation of the wall (Rowe et al. 2011). Therefore, self-sustaining smelt populations should continue to support Lake Rotoiti trout populations in the future.

Because smelt seem to thrive in clear, oligotrophic lakes, probably due to improved egg survival (Rowe and Taumoepeau 2004), and increased ability to feed visually ((Rowe and Dean 1998), the Ohau Channel Diversion Wall is likely to have a positive effect on smelt abundance by improving lake water quality in the long-term. Although fish production in lakes is generally positively correlated with indicators of lake productivity, such as Secchi depth and concentrations of phosphorus, chl *a*, and dissolved solids (Bachmann et al. 1996, Downing and Plante 1993, Lee and Jones 1991, Plante and Downing 1993), severe eutrophication in lakes may create unsuitable conditions for certain fish species through impairment of visual predation or reduction of habitat due to hypolimnetic oxygen depletion (Lee and Jones 1991). As smelt are sensitive to low dissolved oxygen levels (Dean and Richardson 1999), it is likely that hypolimnetic deoxygenation caused by eutrophication would reduce the amount of useable habitat. Therefore, lake restoration measures are likely to benefit smelt populations in Lake Rotoiti in the long term by preventing severe eutrophication and hypolimnetic oxygen loss.

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3.7 Appendices

Appendix 3.1. Details of regressions of length (*L*; mm) vs. mass (*W*; g) calculated using least-squares regression using the following formula: $\log_{10}(W) = a + b(\log_{10}(L))$. Refer to Fig. 3.6, Tables 3.2 and 3.3 for comparisons. Adult: >35 mm, juvenile: <35 mm.

							W-*L* regression parameters				Regression statistics			
Comparison	Year	Season	Adult/ juvenile	Method	*n*	Size range (mm)	*a*	SE of *a*	*b*	SE of *b*	*r*	r^2	*F*	*P*
a)	All	All	Adult	All methods	384	35–100	-7.906	0.095	4.750	0.064	0.914	0.836	23468	<0.001
	All	All	Juvenile	All methods	4616	14–34	-5.879	0.037	3.405	0.023	0.967	0.934	5448	<0.001
b)	All	All	Adult	Boat EF Littoral	830	35–100	-5.675	0.069	3.293	0.041	0.940	0.884	6323	<0.001
	All	All	Adult	Boat EF (L)	587	35–94	-5.630	0.090	3.263	0.056	0.924	0.854	3430	<0.001
	All	All	Adult	Beach seine	3156	35–69	-6.003	0.049	3.476	0.030	0.899	0.808	13264	<0.001
	All	All	Adult	Boat EF Pelagic	43	35–68	-5.656	0.312	3.299	0.189	0.939	0.881	303	<0.001
c)	2010	Spring	Adult	Beach seine	596	35–69	-6.372	0.111	3.695	0.067	0.914	0.835	3013	<0.001
	2011	Winter	Adult	Beach seine	1198	35–63	-5.995	0.080	3.446	0.049	0.897	0.805	4944	<0.001
	2011	Summer	Adult	Beach seine	723	35–57	-6.218	0.066	3.641	0.040	0.958	0.918	8092	<0.001
	2011	Autumn	Adult	Beach seine	639	35–64	-5.633	0.105	3.261	0.065	0.895	0.800	2552	<0.001
d)	2010	Autumn	Adult	Boat EF Littoral	78	35–82	-5.358	0.154	3.116	0.091	0.969	0.939	1173	<0.001
	2010	Winter	Adult	Boat EF Littoral	236	35–73	-5.620	0.101	3.231	0.062	0.960	0.922	2754	<0.001
	2010	Spring	Adult	Boat EF Littoral	196	37–100	-5.235	0.143	3.052	0.086	0.930	0.866	1249	<0.001
	2011	Summer	Adult	Boat EF Littoral	109	35–85	-6.227	0.183	3.619	0.110	0.954	0.910	1075	<0.001
	2011	Autumn	Adult	Boat EF Littoral	208	35–63	-4.935	0.152	2.858	0.091	0.909	0.826	981	<0.001

Appendix 3.2. *P*-values from Tukey’s HSD test showing significant differences in (a) δ13C between lake zones and times, and size classes of smelt. Significant *P*-values shown in bold italics (α = 0.05).

$\delta^{13}C$

		Littoral, day			Littoral, night			Pelagic, night	
Zone, time	Size class	S	M	L	S	M	L	S	M
Littoral, day	S								
Littoral, day	M	0.926							
Littoral, day	L	0.997	1.000						
Littoral, night	S	0.624	1.000	0.969					
Littoral, night	M	***0.027***	0.397	0.161	0.769				
Littoral, night	L	***0.009***	0.190	0.063	0.498	1.000			
Pelagic, night	S	1.000	0.994	1.000	0.858	0.061	***0.020***		
Pelagic, night	M	0.077	0.675	0.354	0.948	1.000	0.993	0.166	
Pelagic, night	L	***0.006***	0.154	***0.049***	0.432	1.000	1.000	***0.015***	0.986

Appendix 3.3. *P*-values from Tukey’s HSD test showing significant differences in (b) δ^{15}N between lake zones and times, and size classes of smelt. Significant *P*-values shown in *bold italics* (α = 0.05).

δ^{15}N

		Littoral, day			Littoral, night			Pelagic, night	
Zone, time	Size class	S	M	L	S	M	L	S	M
Littoral, day	S								
Littoral, day	M	1.000							
Littoral, day	L	1.000	1.000						
Littoral, night	S	0.757	0.779	0.960					
Littoral, night	M	0.723	0.746	0.947	1.000				
Littoral, night	L	***0.019***	***0.021***	0.069	0.555	0.593			
Pelagic, night	S	0.647	0.673	0.920	1.000	1.000	0.566		
Pelagic, night	M	***0.006***	***0.006***	***0.022***	0.287	0.316	1.000	0.285	
Pelagic, night	L	***0.000***	***0.000***	***0.000***	***0.005***	***0.005***	0.420	***0.004***	0.711

4 Diet of rainbow trout in Lake Rotoiti: an energetic perspective[1]

4.1 Abstract

To better understand the prey requirements of trout in central North Island lakes, we characterised seasonal and ontogenetic changes in diet and prey energy density of rainbow trout (*Oncorhynchus mykiss*) in Lake Rotoiti. Common smelt (*Retropinna retropinna*) was the dominant prey item of rainbow trout larger than 200 mm (77.8% of diet by mass), followed by koura (freshwater crayfish *Paranephrops planifrons*; 6.3%), common bully (*Gobiomorphus cotidianus*; 5.5%), and koaro (*Galaxias brevipinnis*; 3.4%). Juvenile rainbow trout (<200 mm) consumed amphipods, aquatic and terrestrial insects, oligochaetes, tanaid shrimps, and smelt. Trout consumed koaro 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 (koaro and koura) 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 bioenergetics modelling of rainbow trout populations in lakes of the central North Island of New Zealand.

4.2 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,

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and may include small fish such as common smelt (*Retropinna retropinna*), common bully (*Gobiomorphus cotidianus*), koaro (*Galaxias brevipinnis*), koura (freshwater crayfish *Paranephrops planifrons*), terrestrial invertebrates, and gastropod molluscs (Cryer 1991, McCarter 1986, Rowe 1984, Smith 1959). However, rainbow trout in the deep lakes of the central North Island of New Zealand consume mainly common smelt (McBride 2005, Rowe 1984, Smith 1959). Trout and smelt dynamics have been examined in Lake Taupo (Cryer 1991, Stephens 1984), 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.

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 (Cucherousset and Olden 2011). Quantifying trout predation on various prey species is a necessary initial step in understanding trophic linkages in the food web and will provide a starting point for 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 the diet of adult fish during 1 to 3 seasons (Rowe 1984, Smith 1959). 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. Bioenergetics models are a useful tool for quantifying predator-prey relationships, and can be used to assess predator demand for prey (Chipps and Wahl 2008), to determine if 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). Bioenergetics models require an estimate of relative proportions of prey types by mass 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.

4.3 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 km^2, 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 4.1). 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 stocked and wild fish (*n* wild = 96; *n* stocked = 86). The mean fork length (FL) of sampled trout was 444 mm, with a length range of 27–646 mm. Stocked fish were identified by fin clips. Stocked trout 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 mass 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 mass (the proportion by mass of each prey species averaged across all non-empty stomachs). If smelt were intact, the FL was measured, otherwise FL was estimated 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 ($FL = 1.0641 \times SL - 0.3889$; $n = 40$; $R^2 = 0.9912$; data not shown).

Table 4.1. 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 size classes. EF = boat electrofishing.

	Season				Method			
Length (mm)	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%	23.6%	16.1%	12.5%	18.2%	0.0%	20.1%	19.1%

To measure the energy density of trout prey, the principal prey items of adult trout (smelt, common bully, koaro, and koura) 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 hours until a constant mass was reached. Several common bullies and smelt were included in each sample in order to obtain enough material for bomb calorimetry, but koura and koaro were processed individually because few specimens were captured (mean number of individuals per sampling unit: smelt, 12; common bully, 9; koaro, 1; koura, 1). 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 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.

4.4 Results

The percentage of trout with empty stomachs varied slightly with season and was highest in summer, at 23.6% (Table 4.1). Rainbow trout smaller than 200 mm FL consumed mainly invertebrates, including amphipods (*Paracalliope fluviatilus*), tanaid shrimps (*Sinelobus stanfordi*), aquatic insects, and terrestrial insects (Tables 4.2 and 4.3). 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. Koaro and koura were eaten only by trout over 400 mm long. Koura 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 mass method in most cases, but for trout between 100–199 mm FL, the occurrence method overestimated the importance of smelt (75.0%) compared to the mass method (36.1%). For trout <100 mm, the occurrence method attributed greater importance to oligochaetes, aquatic insects, and terrestrial insects than the mass method (Tables 4.2 and 4.3).

The percent composition by mass of smelt, koura and common bullies in the diet of trout (>400 mm long) did not vary seasonally (Fig. 4.1; Kruskal-Wallis (K-W) test: $n = 116$, $P > 0.05$). Koaro were only detected in trout stomachs in autumn and winter, and the percent composition by mass of this species was significantly different between seasons (K-W test: $n = 116$, $P = 0.018$). Specifically, masses were different between summer and autumn and between spring and autumn (K-W test: multiple comparisons of mean ranks). The mass of unidentified material was significantly different between summer and autumn (K-W test: multiple comparisons of mean ranks).

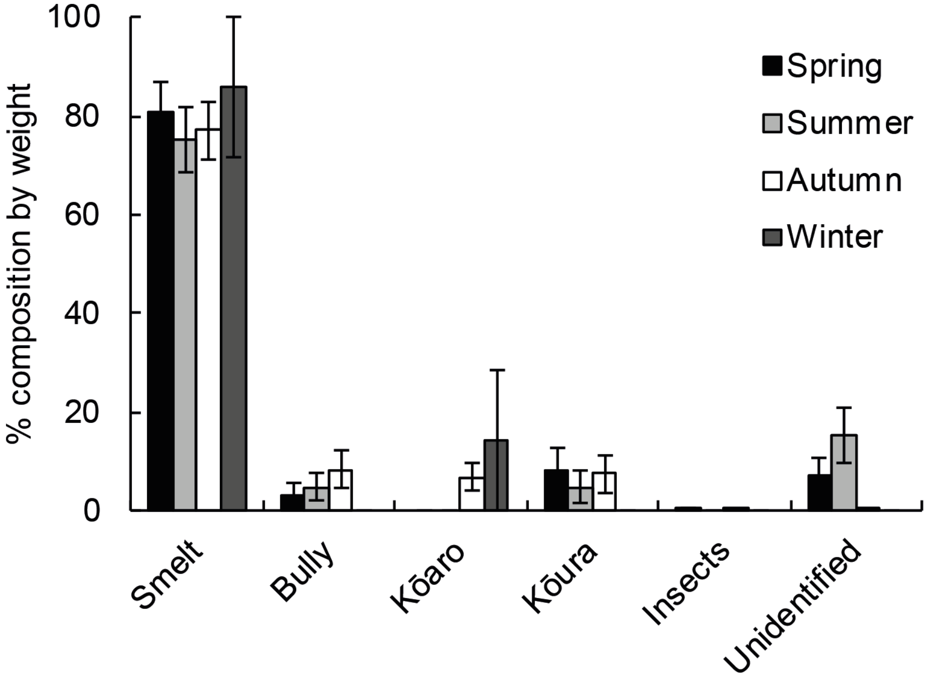

Fig. 4.1. Seasonal changes in percent composition of prey by wet mass eaten by adult rainbow trout (>400 mm) from Lake Rotoiti (mean ± 1 SE).

Table 4.2. Percent frequency of occurrence of prey items eaten by rainbow trout of different length classes in Lake Rotoiti.

Trout length (mm)	*n* (Smith 1959)	*n*	Prey items (percent frequency of occurrence)										
			Smelt	Koura	Common bully	Koaro	Amphi-pod	Tanaid shrimp	Aquatic insect	Terrestrial insect	Oligo-chaete	Mollusc	Un-identified
<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	25.0	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	1.5	3.0	0.8	0.8	7.6
Smith (1959)		119	58.0	10.0	12.0[2]		0.0	0.0	2.0	19.0	0.0	21.0	12.0

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[2] This study did not distinguish between bullies and koaro.

Table 4.3. (a) Mass of prey eaten by rainbow trout of different length classes in Lake Rotoiti (mean ± 1 SE).

Trout length	Mean trout mass (g)	*n*	Prey items									
			Smelt	Koura	Common bully	Koaro	Amphipod	Tanaid shrimp	Aquatic insect	Terrestrial insect	Oligo-chaete	Un-identified
a) Wet mass												
<100	0.006	16	0	0	0	0	0.07 ± 0.02	0	0.04 ± 0.01	0.03 ± 0.01	0.01 ± 0.01	0
100–199	0.175	4	0.20 ± 0.09	0	0.50 ± 0.50	0	0	0.06 ± 0.06	0.01 ± 0.01	0	0.01 ± 0.01	0.02 ± 0.02
200–299	0.163	7	3.35 ± 1.10	0	0.14 ± 0.14	0	0	0	0	0	0	0
300–399	0.672	5	4.47 ± 1.97	0	0	0	0	0	0	0	0	0
400–499	1.218	39	5.61 ± 1.16	0.19 ± 0.14	0.13 ± 0.08	0.44 ± 0.44	0	0	0	0	0	0.23 ± 0.12
500–599	2.213	66	7.09 ± 0.91	1.39 ± 0.74	0.31 ± 0.12	0.56 ± 0.30	0	0	0	0.01 ± 0.01	0	0.09 ± 0.07
600–699	3.142	11	8.05 ± 2.45	1.78 ± 1.78	0	4.46 ± 3.36	0	0	0	0	0	0.14 ± 0.14
Total	4.323	148	5.79 ± 7.04	0.84 ± 4.43	0.20 ± 0.75	0.73 ± 3.85	0.01 ± 0.03	0.00 ± 0.02	0.00 ± 0.02	0.01 ± 0.05	0.00 ± 0.00	0.12 ± 0.57

Table 4.3. (b) Percent composition by mass of prey eaten by rainbow trout of different length classes in Lake Rotoiti (mean ± 1 SE).

b) Percent composition by wet mass

	Prey items									
Trout length	Smelt	Koura	Common bully	Koaro	Amphipod	Tanaid shrimp	Aquatic insect	Terrestrial insect	Oligochaete	Unidentified
<100	0	0	0	0	44.1 ± 11.3	0.0 ± 0.0	29.9 ± 10.0	19.1 ± 7.9	6.9 ± 4.0	0
100–199	36.1 ± 22.2	0	21.7 ± 21.7	0	1.9 ± 1.9	14.7 ± 14.7	8.0 ± 8.0	0.2 ± 0.2	2.5 ± 2.5	14.9 ± 14.9
200–299	85.7 ± 14.3	0	14.3 ± 14.3	0	0	0	0	0	0	0
300–399	100.0 ± 0.0	0	0	0	0	0	0	0	0	0
400–499	75.3 ± 6.8	5.1 ± 3.6	4.3 ± 2.9	1.4 ± 1.4	0	0	0	0	0	13.9 ± 5.5
500–599	78.7 ± 4.5	8.0 ± 3.1	6.6 ± 2.6	3.5 ± 1.9	0	0	0	0.2 ± 0.1	0	3.0 ± 2.1
600–699	81.8 ± 12.2	5.2 ± 5.2	0	12.6 ± 9.4	0	0	0	0	0	0.4 ± 0.4
Total	72.3 ± 0.0	2.6 ± 0.0	5.5 ± 0.0	3.0 ± 0.0	3.2 ± 0.0	0.1 ± 0.0	2.3 ± 0.0	1.4 ± 0.0	0.6 ± 0.0	5.7 ± 0

The energy density of smelt varied by almost a third between seasons and was lowest in winter (Table 4.4). Common bullies and smelt caught in autumn had similar energy densities, and koaro caught in autumn had the highest energy density of all prey species. The energy density of koura 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. 4.2). 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 = smelt length (mm) and x = 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 ($F_{(2,1303)} = 18.9$, $P < 0.001$).

Table 4.4. Energy density of prey items of adult rainbow trout from Lake Rotoiti.

				Mean energy density ± 1 SE	
Species	Season	Mean length (mm)	Sample *n*	J g^{-1} dry mass	J g^{-1} wet mass
Common bully	Autumn	43.7	4	13664 ± 370.3	3123 ± 151.1
Koaro	Autumn	78.5	2	15299 ± 736.3	3636 ± 403.3
Koura	Summer	113.6	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

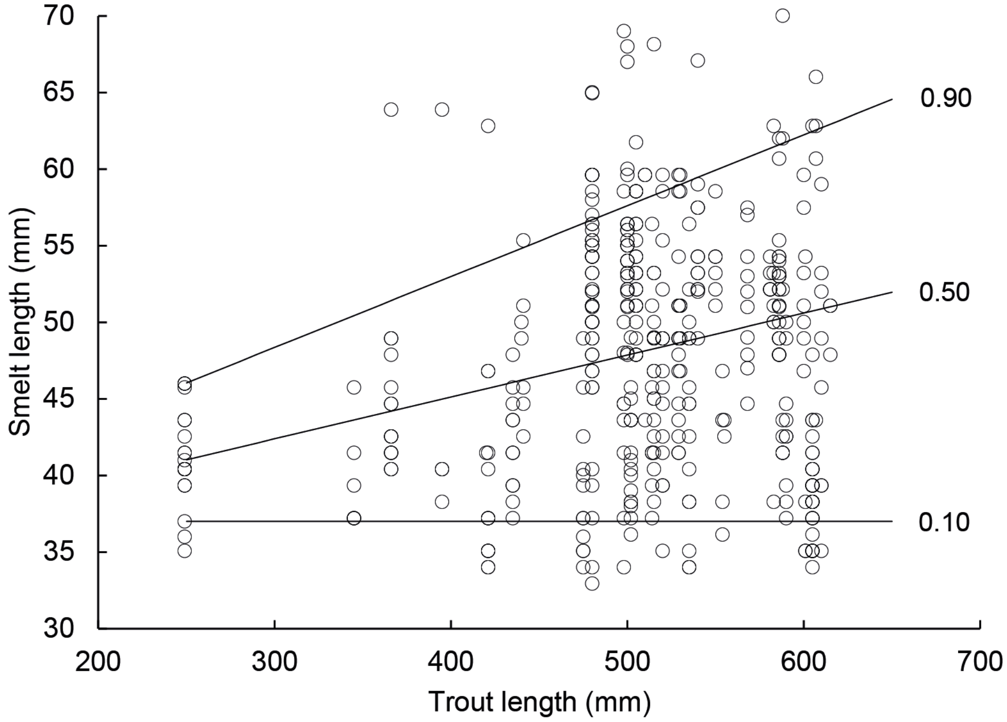

Fig. 4.2. Relationship between trout lengths and lengths of smelt in diet (fork length), with 0.10, 0.50, and 0.90 regression quantile estimates (solid lines; *n* = 435).

4.5 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 compared to 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 4.2). Rainbow trout in Lake Rotoiti, which is now mesotrophic, consumed fewer insects and more common bullies and koaro than trout in oligotrophic Lake Taupo (Cryer 1991). Nutrient inputs caused Lake Rotoiti to become more eutrophic between 1955 and the present (Scholes 2009, Vincent et al. 1984), 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) consumed a wider variety of prey items including koura and fish other than smelt, consistent with other studies of rainbow trout in central North Island lakes (Cryer 1991, Rowe 1984, Smith 1959). 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 and Ward 1997, Nilsson and Bronmark 2000, Persson 1997). Larger, benthic species such as koaro and koura 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 Taupo (Cryer 1991). In contrast, rainbow trout in Lake Rotoma displayed a seasonal dietary shift from more epibenthic prey (common bully and koura) in summer, to more pelagic prey (smelt) in winter (Rowe 1984). However, we did find seasonal differences in the percentage of empty stomachs. The proportion of empty stomachs generally increases with temperature in fish (Vinson and Angradi 2011), but the cause of increased stomach emptiness in summer in Lake Rotoiti is not known; unmeasured factors such increased gut evacuation rates in higher temperatures may have played a role. We found no evidence of prey switching in Lake Rotoiti during winter when smelt energy density was lowest, suggesting that either variation in energy density was not great enough to cause a change in the prey species eaten by trout, or that other species were not abundant enough to act as significant food sources for trout. The latter possibility could be addressed by comparing the availability of bullies, koaro and koura to trout diet (e.g. using a preference index). However, even though the proportion of smelt in the diet did not change, it is possible that the *amount* of prey eaten may change; this is a potential question to be addressed by bioenergetics modelling.

Though we have documented predation on koaro and koura by rainbow trout, the effects of trout predation on koaro and koura 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 landocked koaro 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 koaro in central North Island lakes (Rowe 1993). Bioenergetics 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 bioenergetics 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 and 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 bioenergetics model outputs (Hartman and Brandt 1995). It is also important to measure seasonal changes in diet, because model outputs may be sensitive to variation in diet composition (Lyons and Magnuson 1987). The data measured in this study will provide a basis for bioenergetics 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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5 Lake morphometry and trophic state affect growth of rainbow trout (*Oncorhynchus mykiss*) in a warm-temperate climate[3]

5.1 Abstract

The growth of rainbow trout (*Oncorhynchus mykiss*) was investigated in nine warm-temperate New Zealand lakes of contrasting morphometry, mixing regime, and trophic state to better understand the combined effects of environmental factors on fish growth in warm-temperate lakes. Mark-recapture data from stocked trout released over eight consecutive years were used to calculate growth parameters and body condition. Trout growth parameters and body condition showed a dome-shaped response to eutrophication. Growth rate was faster in lakes with greater volumes of favourable habitat (i.e. dissolved oxygen >6.0 mg L^{-1} and temperature <21°C), but slower in lakes with increased turbidity, chlorophyll *a*, and nitrogen concentrations. Variables describing habitat volume best predicted trout growth rate, and correlates of trophic state (chlorophyll *a*, conductivity) were important secondary predictors. These results suggest that lake morphometry and trophic state are important attributes structuring overall habitat quality, thus influencing rainbow trout growth in lakes in warm-temperate climates. Understanding the factors that influence the growth of coldwater fish in warm-temperate lakes allows us to predict the impact of future climate warming in cooler regions.

5.2 Introduction

The study of environmental factors affecting fish growth rates in various water bodies is of theoretical, ecological and applied importance. By characterising fish growth, we can better understand the transfer of organic material through the trophic chain to the top consumers (Gamito 1997, Lienesh et al. 2005), determine

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ecological conditions favourable for given fish species (Haddix and Budy 2005, Wells et al. 2008), and optimise fish productivity (Mazumder and Edmundson 2002). Enhancing fish growth rates and production in lakes is a common goal of fisheries management, given the economic and recreational importance of lake fisheries. To help understand the factors affecting fish production, relationships have been derived between fish growth rates or production and various physical, chemical, and biological variables, such as lake depth, nutrient loading, and lake productivity (e.g. Ryder 1965, Oglesby 1977, Leach et al. 1987, Downing and Plante 1993).

Lake morphometry influences many variables that are important for fish habitat, e.g. nutrient cycling, temperature, dissolved oxygen (DO), and sediment resuspension (Fee 1979, Genkai-Kato and Carpenter 2005, Håkanson 2005), and can therefore determine the extent of fish populations in lakes. For example, lake size (depth or area) is the principal factor controlling the persistence of some fish species in shallow Arctic lakes, due to the lack of suitable thermal habitat in both summer and winter (Hershey et al. 1999, 2006). In warm-temperate areas, refuge from warm water is likely to be important for the persistence of salmonids in lakes. Salmonids have a lower optimal range in temperature for growth than many fish, and high temperatures may have detrimental effects on several physiological processes, including feeding, growth, and reproduction (Plante and Downing 1993, Myrick and Cech 2000, Pankhurst and King 2010, Robinson et al. 2010). Fish can avoid detrimental warm temperatures in thermally stratified lakes by occupying the cooler hypolimnion, if the oxygen regime is favourable (Budy et al. 2009). However, shallow lakes usually lack such refuge habitat. Additionally, low hypolimnetic dissolved oxygen (DO) concentrations will reduce the amount of available habitat in thermally stratified lakes (Coutant 1985, Plumb and Blanchfield 2009). Hypolimnetic deoxygenation is a problem not only in deep, monomictic lakes: periodic stratification events in shallow, polymictic, eutrophic lakes can result in rapid hypolimnetic DO loss (Burger et al. 2007), which can notably shrink the fish habitat. Climate warming is predicted to cause increases in lake temperature and the duration of stratification, which will likely reduce habitat for coldwater and coolwater fish in shallow and moderately deep lakes (e.g. in North America; Schindler 2001, Fang et al. 2004). Under these conditions, enhanced nutrient input from catchments and release from bottom sediments are likely to increase eutrophication in lakes (see e.g. Jeppesen et al. 2009 (Denmark) and Trolle et al. 2011 (New Zealand)). Therefore, to predict the effects of climate warming on fish, we need to understand the combined effects of high temperatures and eutrophication, especially in shallow lakes, where these effects are likely to be most severe (Jeppesen et al. 2012).

Food supply also influences fish growth rates and production. Variables that characterise food supply, or can be interpreted as proxies for lake productivity (e.g. concentrations of chlorophyll *a* (chl *a*), phosphorus, and dissolved solids), may be positively correlated with fish production (Lee and Jones 1991, Downing and Plante 1993, Bachmann et al. 1996). In boreal lakes of British Columbia and Alaska, salmonid production increases with addition of nutrients; fertilisation of lakes with nitrogen and phosphorus increases chl *a* concentrations and zooplankton biomass, and increases survival and size of salmonids (Hyatt et al. 2004). In high-latitude (>47 ºN) lakes, salmonid production is positively correlated with phosphorus concentrations and phytoplankton productivity (Plante and Downing 1993). However, in eutrophic lakes, foraging of visual predators may be impaired by high turbidity (Beauchamp et al. 1999, Ranåker et al. 2012). The interacting effects of increased temperature, eutrophication, and reduced DO in the natural environment make it difficult to understand the mechanisms controlling fish growth rates in lakes, and require more detailed studies. Some of these environmental factors are likely to exert effects on trout growth in a non-linear way. Moreover, there is a lack of information about the factors influencing growth of lake-resident salmonids at lower latitudes, especially in warm-temperate lakes.

In this study, we aim to examine the environmental factors influencing growth rates and body condition of rainbow trout (*Oncorhynchus mykiss*) in warm-temperate lakes displaying a range of morphometries, trophic states, and mixing regimes. We examine growth rates of hatchery-raised rainbow trout bred from a single population and released into several lakes, meaning that the effects of various environmental factors on growth rates can be tested without the confounding influence of different genetic strains (*sensu* Reed et al. 2010). We also consider catchment land use, which affects productivity and water quality of lakes by influencing the allochthonous supply of nutrients and organic carbon. We hypothesise that in deeper, cooler, monomictic lakes, moderate nutrient supply may be favourable for rainbow trout growth, while in shallower, warmer, polymictic lakes, excessive external or internal supply of nutrients and organic material may negatively affect habitat quality and thus create unfavourable conditions for trout growth. This study will provide a better understanding of how environmental factors in warm-temperate lakes influence salmonid growth rates, leading to better informed management decisions involving species of high social and economic importance.

5.3 Methods

5.3.1 Data collection

Eastern Region Fish & Game stocked rainbow trout into lakes of varying size and trophic state (Fig. 5.1, Table 5.1) in austral spring (September) and autumn (May) from a hatchery facility at Ngongotaha, Rotorua. Stocking rates (Table 5.2) varied due to differences in management strategies and wild spawning populations. All hatchery parent stocks originated from the Te Wairoa Stream, a tributary of Lake Tarawera. Populations examined in this study are landlocked. Trout released in autumn were approximately 1 year old upon release (fork length = 160 ± 3 mm; mean ± SE), and those released in spring were 1.25 years old (190 ± 2 mm). There were no significant differences in trout lengths at release among lakes in spring (ANOVA; $F_{1,8} = 0.45$, $P = 0.89$) or autumn ($F_{1,3} = 0.22$, $P = 0.88$).

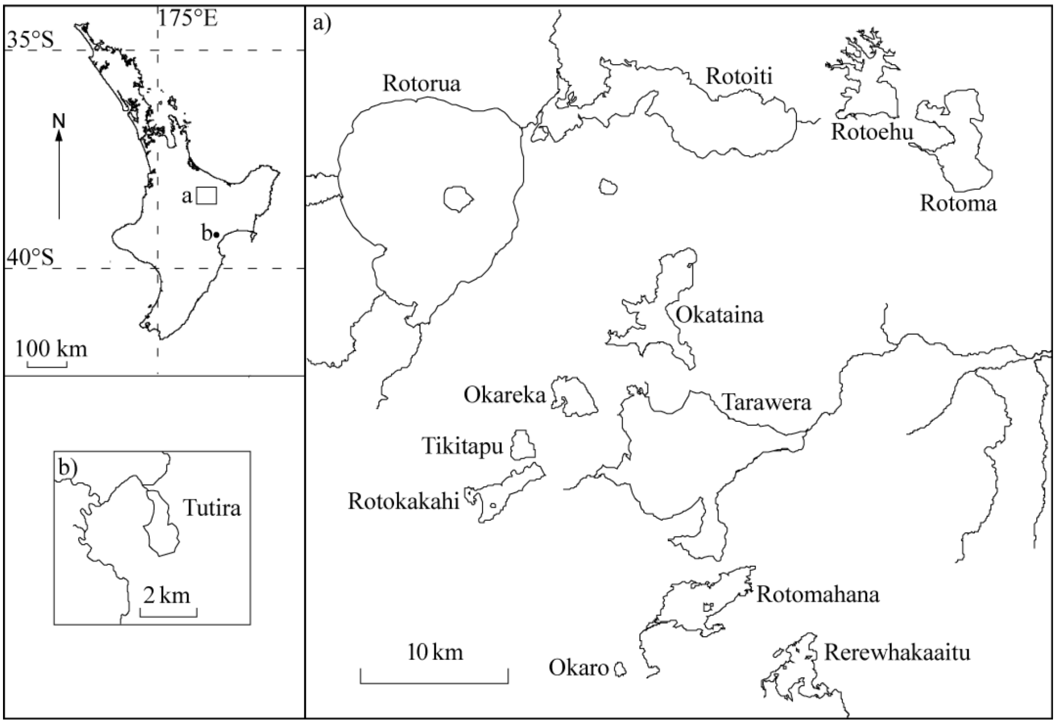

Fig. 5.1. Study areas and lakes in the North Island of New Zealand.

Table 5.1. Morphometry and mean values of physical and limnological characteristics of some lakes in the North Island of New Zealand. Values are means for 2002–2010 ± SE, except for Lake Tutira, where data represent means 2008–2010. Rere., Rerewhakaaitu; P, polymictic; M, monomictic; Ol, oligotrophic; Me, mesotrophic; Eu, eutrophic. Sources: Lake Tutira; A. Uytendaal, Hawke's Bay Regional Council, Napier, pers. comm., 2011, all other lakes; Scholes 2009, 2010.

Lake	Mean depth (m)	Area (km^2)	Mixing regime	Trophic state	Mean temperature (ºC)	Annual temperature range (ºC)	Chl *a* (mg m^{-3})	Secchi depth (m)	TP (mg P m^{-3})	TN (mg N m^{-3})
Rere.	6	5.9	P	Me	14.3 ± 0.2	8.1–21.6	3.7 ± 0.2	5.8 ± 0.2	9.7 ± 0.5	399.5 ± 7.9
Rotoehu	8	8.1	P	Eu	15.3 ± 0.1	9.2–22.6	10.8 ± 0.8	2.9 ± 0.1	39.8 ± 2.0	376.5 ± 9.6
Rotorua	11	80.8	P	Eu	15.0 ± 0.1	9.3–21.7	21.3 ± 0.9	2.4 ± 0.1	37.9 ± 0.8	458.4 ± 8.4
Okareka	20	3.3	M	Me	12.4 ± 0.2	9.3–22.2	4.1 ± 0.2	7.7 ± 0.2	8.4 ± 0.3	212.6 ± 3.8
Tutira	21	1.7	M	Me	12.1 ± 0.1	9.0–22.7	4.4 ± 1.1	3.9 ± 0.3	42.2 ± 17.4	493.9 ± 13.7
Rotoiti	31	34.6	M	Me	12.8 ± 0.1	10.8–22.1	12.2 ± 0.9	4.4 ± 0.1	40.4 ± 0.7	356.6 ± 4.5
Rotoma	37	11.2	M	Ol	12.5 ± 0.3	10.6–21.3	1.3 ± 0.1	12.8 ± 0.3	4.6 ± 0.2	141.2 ± 4.0
Okataina	39	10.8	M	Ol	12.5 ± 0.3	10.7-21.4	2.3 ± 0.1	10.5 ± 0.3	11.5 ± 0.5	135.0 ± 4.2
Tarawera	50	41.7	M	Ol	12.5 ± 0.2	10.9–21.4	1.5 ± 0.1	8.7 ± 0.2	13.9 ± 0.6	114.0 ± 4.0

Table 5.2. Stocking rates, percentage of stocked rainbow trout in recreational catch, and fork length of trout at release in lakes in the North Island, New Zealand. Values are means for 2002–2010 ± SE.

Lake	Stocking rate (fish $year^{-1}$)	Stocking rate (fish ha^{-1} $year^{-1}$)	Percentage of stocked trout caught	Length of trout released (mm)
Rerewhakaaitu	7375 ± 100	1272 ± 19	68.6 ± 5.4	Spring: 190 ± 7
Rotoehu	4380 ± 388	596 ± 54		Spring: 190 ± 7
Rotorua	1000 ± 0	12 ± 0	2.0 ± 0.6	Spring: 190 ± 7
Okareka	5000 ± 683	1515 ± 231	85.0 ± 2.7	Spring: 190 ± 7
Tutira	5346 ± 485	3168 ± 369		Spring: 200 ± 7 Autumn: 160 ± 6
Rotoiti	23812 ± 1114	688 ± 36	60.3 ± 2.6	Spring: 190 ± 8 Autumn: 170 ± 6
Rotoma	5006 ± 369	447 ± 37	64.4 ± 6.1	Spring: 190 ± 7
Okataina	3750 ± 250	347 ± 31	58.0 ± 3.3	Spring: 190 ± 8 Autumn: 160 ± 5
Tarawera	17875 ± 598	429 ± 15	69.7 ± 2.9	Spring: 200 ± 4 Autumn: 160 ± 7

We tagged 500 fish from each liberation with batch-coded t-bar anchor tags inserted at the base of the dorsal fin, and measured the fork length of a subsample of fish (mean $n = 80$) to the nearest 10 mm prior to release (mean length ± SE = 180 ± 2 mm; range = 140–260 mm). We measured some trout during creel surveys, and we encouraged anglers to provide measurements of tagged fish through a reward scheme. We calculated body condition with a different data set collected from wild and stocked rainbow trout at fishing competitions between 2004 and 2010 (see below).

5.3.2 Growth

We fitted the von Bertalanffy growth equation to length-at-age data for rainbow trout in different lakes and seasons using least-squares regression:

$$L_t = L_\infty [1 - e^{-K(t-t_0)}] \tag{5.1}$$

where t is age (yr), L_t is fork length at age t (mm), and L_∞ (mm), K (mm yr^{-1}), and t_0 (yr) are parameters. We used the mean or modal length at release as the initial data point, depending on available data, and weighted values corresponding to the actual number of measured fish. We defined the day of fish release into the lake as $t = 0$. To compare the growth rates of fish in various lakes, we calculated the instantaneous growth rate at 480 mm (the approximate fork length of fish at age 2) using the Gulland and Holt (1959) presentation of von Bertalanffy's growth equation:

$$dL/dt = A - KL_t \tag{5.2}$$

where dL/dt is fish growth rate, L_t is fork length at time t, and K and A are coefficients. Because the parameters of the von Bertalanffy equation may be influenced by the absence of older fish or by inadequate sample numbers (Knight 1968), we excluded cohorts from this analysis if the lengths of fewer than 10 fish were returned, if fewer than five fish >3 years old were returned, or if L_∞ or K fell outside of three standard deviations from the overall mean. This excluded 40% of cohorts released. Calculating the growth rate at 480 mm allowed us to match growth of a specific cohort with the conditions in the lake during the preceding year, and reduced bias associated with variation of fish length at release. We compared growth rates of trout released in autumn and spring in individual lakes with paired Student's *t*-tests. We assessed trends in growth rates over time in each lake using the Kendall rank correlation coefficient, and assessed the differences in L_∞ and growth rates between deep and shallow lakes using a Mann-Whitney *U* test.

5.3.3 Body condition of rainbow trout

Fish of the same length with greater body condition indices have more energy stored, and are in a healthier physiological state. Therefore, measuring body condition can be used to indirectly examine food availability. We calculated fish body condition using data collected from wild and stocked rainbow trout at fishing competitions between 2004 and 2010. We measured mass to the nearest 10 g and fork length to the nearest 5 mm. We used Fulton's condition factor to compare fish body condition in lakes Okataina, Rotorua, Rotoiti, and Tarawera ($(W/L^3) \times 100\,000$, where W is mass in kg and L is length in mm). We chose these lakes for the condition factor analysis because they are the most heavily fished by anglers and represent a range of trophic states. We assumed that fish with greater body condition indices have greater energy stores relative to body length, and are in a healthier physiological state. To reduce bias associated with variation of this index with fish length and gonad development, we only calculated condition of trout measuring between 425 and 474 mm caught between December and March (outside the spawning period). We compared Fulton's condition factor among lakes using a nonparametric Kruskal-Wallis ANOVA by ranks.

We also compared body condition of fish in lakes Okataina, Rotorua, Rotoiti, and Tarawera using an approach that takes into account the allometric nature of the weight- length relationship, W=aL^{b} , or in its logarithmic form

$$\log_{10}(W) = \log_{10}(a) + b[\log_{10}(L)] \tag{5.3}$$

where W is weight (g) and L is fork length (mm). We calculated regressions between $\log_{10}(W)$ and $\log_{10}(L)$ for rainbow trout caught in different lakes and years ($r^2 = 0.80$–0.87; $P < 0.001$). The calculated parameter b of these equations varied within a narrow range (2.22–2.68). This allowed us to use the calculated a coefficient as a proxy of condition factor, such that changes in a should portray the difference in fish body conditions under various environmental conditions. To accurately compare power equations, we used the procedure described by Ostrovsky (1995). In brief, the calculated W-L relationships were recalculated to “new” ones that have identical slopes equal to the overall mean b value ($\bar{b}$). The mean value of $\bar{b}$ for all regressions (± SE) was 2.46 ± 0.04. The new recalculated intercept, $\log_{10}(a')$, of each regression line at the fixed (identical) slope of $\bar{b}$ was calculated using the following formula:

$$\log_{10}(a') = \log_{10}(a) + (b - \bar{b})\overline{\log_{10}(L)} \tag{5.4}$$

where $\log_{10}(a)$ and b are best fit values of the coefficients of the specific regression line, $\overline{\log_{10}(L)}$ is its mean point. Unlike the size-specific Fulton’s factor, $\log_{10}(a')$ reflects the mean body condition of the entire fish population in a given situation (e.g. lake, year).

5.3.4 Relationships between growth rates and lake characteristics

We assessed relationships between growth rates at 208 mm and L_∞ of rainbow trout and the following environmental factors. We measured temperature, DO, and specific conductivity monthly at a mid-lake station in each of the lakes at 1 or 2 m intervals throughout the water column with a conductivity-temperature-depth (CTD) profiler (SBE 19 plus, Seabird Electronics) with CTD-mounted DO sensors (Seabird Electronics). The overall annual mean temperature of the lakes during the study period was 13.5°C, with a range of 7.0 to 23.8°C. We calculated total dissolved solids (TDS) with the following regression, which we found by comparing measurements of conductivity and TDS using a YSI EC300 meter: TDS (mg L^{-1}) = 0.5977 + 0.5652 × specific conductivity (µS cm^{-1}) ($R^2 = 0.9969$, $n = 14$). We averaged measurements from July to the following June, to provide information on average annual conditions, to incorporate the period of summer (December-February) stratification, and to coincide with the first year of trout growth in the lakes. We calculated the mid-metalimnion depth (hereafter referred to as the thermocline depth) using temperature profiles taken with the aforementioned CTD profiler during summer stratification (December-February), by finding the point at which dT/dz = maximum, where T = temperature and z = lake depth. We defined the volumes of the epilimnion and hypolimnion during summer stratification as the volumes of water above and below the thermocline (December-February); and calculated these using bathymetry data. Samples for measurement of total nitrogen (TN), total phosphorus (TP) and chl *a* were taken monthly, coinciding with CTD profiles (Scholes 2009, 2010). In lakes that stratified (Okareka, Okataina, Rotoiti, Rotoma, Rotorua, and Tarawera), we collected water samples with an integrated tube sampler that sampled water from the surface to a depth 1 m above the thermocline. We collected two additional samples from below the thermocline and 1 m above the bottom sediment with a Schindler trap. We used an average of these values in our analyses. In lakes Rerewhakaaitu and Rotoehu , which are frequently mixed, we took integrated tube samples from the surface to 1 m above the bottom sediment. We determined concentrations of TN, TP and chl *a* using standard methods (Eaton and Franson 2005). We measured water transparency with a 20 cm diameter Secchi disk. We used the Trophic Level Index (TLI) to indicate overall lake trophic state; it is analogous to the Trophic State Index (Carlson 1977) but was developed for New Zealand lakes, and incorporates TN, TP, chl *a* and Secchi depth measurements (Burns et al. 1999). We standardised the area of each catchment land use type by dividing by the lake surface area.

In this study we focused on environmental effects on trout growth, rather than density-dependent effects. Comparing density-dependent effects among lakes is difficult because differences in environmental factors among lakes may confound comparisons. Hence, density-dependent effects on trout growth in Lake Rotoiti are the subject of a current bioenergetics study (Chapter 6). Nevertheless, we incorporated the following estimates of trout density in our analyses: (1) the number of trout released from the hatchery per year in each particular lake, (2) the number of trout released per year per hectare of lake surface area, and (3) the length of trout upon release. We also calculated the ratio of stocked to wild trout in angler catches, using records gained from creel surveys every summer over the study period (Table 5.2). This provides only an approximate index of the relative abundance of wild trout. Little is known about the population abundance of wild trout or their susceptibility to fishing mortality by angling; differences in mortality rates between wild and stocked trout or among years may affect this index.

To characterise monthly changes in suitable thermal habitat volume, we calculated the volume of water in each lake that was <21ºC with monthly temperature profiles and lake bathymetry data. We then documented volume during the month when suitable habitat volume was at its minimum in each lake (i.e. the "worst case scenario" for trout). We used this temperature threshold because rainbow trout have been observed to avoid temperatures above 21ºC in lakes (Overholtz et al. 1977, Stables and Thomas 1992), and reduced growth rates were observed in rainbow trout at 22ºC and 25ºC compared to 19ºC (Myrick and Cech 2000). We calculated the minimum habitat available with DO concentrations above 6 mg L^{-1} in a similar way; we chose this concentration because salmonids begin to exhibit symptoms of oxygen stress below 6 mg L^{-1} DO (Davis 1975). We also calculated a composite measure of the habitat volume with both suitable DO and temperature. We calculated near-bottom oxygen concentration from DO measurements in the bottom 5 m of water during stratification, and in the bottom 2 m of the shallowest lakes (Rerewhakaaitu and Rotoehu).

5.3.5 Data analysis

We used Spearman's rank correlations to examine the relationships between trout growth rate, L_{∞}, and environmental factors in different lakes and years. Each year of measurements in each lake was treated as an independent data point for this analysis. Lake Tutira was not included in the correlation analyses due to insufficient environmental data.

To further determine the factors influencing trout growth rate and L_{∞} in our study lakes, we used classification and regression trees (CART) to classify data from different lakes and years. Classification and regression tree analysis is a non-parametric statistical method that has advantages over parametric regression, because it does not assume that data is homogeneous or homoscedastic, or that relationships between predictor and response variables are linear. Further, CART can deal with missing values, interactions among variables, and mixtures of continuous and categorical data, and can uncover relationships that may be missed by linear models (Breiman et al. 1984, De'ath and Fabricius 2000). We built a regression tree using the CART function in Statistica, which uses the procedure of Breiman et al. (1984). The V-fold cross-validation procedure found the optimal tree using the V-fold cross-validation procedure; this tests trees of multiple sizes by applying them to random subsets of the data, finding the tree with the highest average accuracy for cross-validated predicted classifications.

For the CART analysis, we included variables in the model only if (1) they were measured directly and were not derived from another variable (e.g. TLI was excluded, as it is a composite of TN, TP, chl *a* and Secchi depth); and (2) they directly reflected conditions in the lake (i.e. catchment area and land use variables were excluded). We showed the importance of each variable for predicting trout growth as a relative percentage. Up to four surrogate variables indicated alternative decision rules for each node; we calculated the association of surrogate variables with the variables in the final regression tree as a relative percentage.

5.4 Results

5.4.1 Relationships between growth rates and lake characteristics

The maximum age of returned fish was, on average, 4.36 yr for fish released in spring, and 4.17 yr for fish released in autumn (Table 5.4). There was a slight bias in the season when fish were caught, with slightly more fish being caught in summer or autumn in most lakes. However, in Lake Tutira, 45% of fish released in spring and 56% of fish released in autumn were caught during winter (Table 5.4).

Table 5.3. Parameters of von Bertalanffy's growth function (Eqn. 5.2) ± SE for stocked rainbow trout in different lakes in the North Island, New Zealand. Growth parameters represent mean values for the period from July 2002 to June 2010.

Lake	L_∞ (mm)	K (year^{-1})	t_0 (year)
Shallow lakes (≤11 m mean depth)			
Rotoehu	508.7 ± 6.8	1.761 ± 0.146	-0.282 ± 0.020
Rotorua	534.0 ± 7.3	1.579 ± 0.133	-0.304 ± 0.028
Tutira	540.6 ± 5.7	1.428 ± 0.107	-0.299 ± 0.023
Rerewhakaaitu	558.0 ± 10.0	1.289 ± 0.105	-0.345 ± 0.031
Deep lakes (≥20 m mean depth)			
Okareka	544.8 ± 11.0	1.519 ± 0.177	-0.311 ± 0.033
Rotoma	557.1 ± 5.8	1.671 ± 0.142	-0.268 ± 0.022
Tarawera	590.6 ± 3.2	1.515 ± 0.046	-0.232 ± 0.08
Okataina	622.8 ± 9.1	1.278 ± 0.076	-0.262 ± 0.014
Rotoiti	643.1 ± 14.9	1.259 ± 0.109	-0.243 ± 0.026

Table 5.4. Characteristics of returned stocked rainbow trout used in comparisons of growth rate and L_∞ among lakes. Values presented as means for 2002–2009. The number of fish returned by anglers is also given, as is the percentage of fish from each lake caught in each season. See Appendix 5.1 for characteristics of individual cohorts.

	Number of fish returned		Length of returned fish (mm)		Max. age of returned fish (years)	Season of capture (percentage of total catch)			
Lake	Mean	SE	Mean	SE		Autumn	Spring	Summer	Winter
Spring releases									
Okareka	33	4.80	274	7.87	4.59	30	14	26	31
Okataina	48	4.95	326	7.97	4.86	44	19	18	20
Rerewhakaaitu	35	4.79	280	6.75	4.44	41	20	16	27
Rotoehu	41	8.10	271	7.86	4.14	29	29	18	27
Rotoiti	42	3.35	304	7.47	3.72	36	25	22	18
Rotoma	21	3.40	258	7.15	5.00	28	23	32	26
Rotorua	43	5.69	290	7.46	3.88	33	17	33	20
Tarawera	55	5.83	320	4.01	4.49	34	23	26	18
Tutira	27	4.91	265	8.01	4.07	23	27	8	45
Spring Total	38	1.99	288	2.49	4.36	34	22	23	24
Autumn releases									
Okataina	35	6.88	283	4.59	4.66	52	26	19	17
Rotoiti	38	4.72	324	5.73	3.48	32	32	19	21
Tarawera	45	6.60	299	5.06	4.50	31	20	29	20
Tutira	19	4.71	220	5.44	4.13	23	25	16	56
Autumn Total	34	3.21	283	2.93	4.17	31	24	19	26
Overall Total	37	1.70	286		4.31	34	23	22	26

Our results indicate clear effects of lake trophic state and depth on trout growth rates. Rainbow trout in deeper, more oligotrophic lakes showed higher values of L_∞ than those in shallow, more eutrophic lakes (Table 5.3, Mann-Whitney (M-W) U test: $Z = -4.56$, $P < 0.001$). Growth rates of rainbow trout at ~2 years old were higher in deep lakes than in shallow lakes (M-W U test: $Z = -6.59$, $P < 0.001$). L_∞ was positively correlated with growth rates (Spearman rank $r_s = 0.909$, $P < 0.001$) and negatively correlated with the parameter K ($r_s = 0.751$, $P < 0.001$). The season in which trout yearlings were released into the lakes (spring or autumn) did not significantly affect subsequent mean growth rates in lakes Okataina, Rotoiti, Tarawera or Tutira (Student's paired t-tests, $P > 0.05$).

Changes in the growth rates of rainbow trout over time were different among lakes (Fig. 5.2). Growth rates of rainbow trout in Lake Okataina and Rerewhakaaitu increased during the observation period; though for Lake Okataina the increase in growth rate was significant only for fish released in autumn (Fig. 5.2b, c). Growth rates of rainbow trout did not change in lakes Okareka, Rotoma or Tarawera between 2002 and 2009 (Fig. 5.2a, f, h). In contrast, growth rates of rainbow trout in lakes Rotorua and Tutira declined significantly between 2002 and 2009 (Fig. 5.2g, i). Trout growth rates in Lake Rotoehu fluctuated widely during the study period but showed no clear trend (Fig. 5.2d). Rainbow trout in Lake Rotoiti were monitored from 1993 to 2009 and showed higher growth rates in the 1990s compared to the 2000s, though the growth rate had almost returned to 1990s levels by 2008–2009 (Fig. 5.2e).

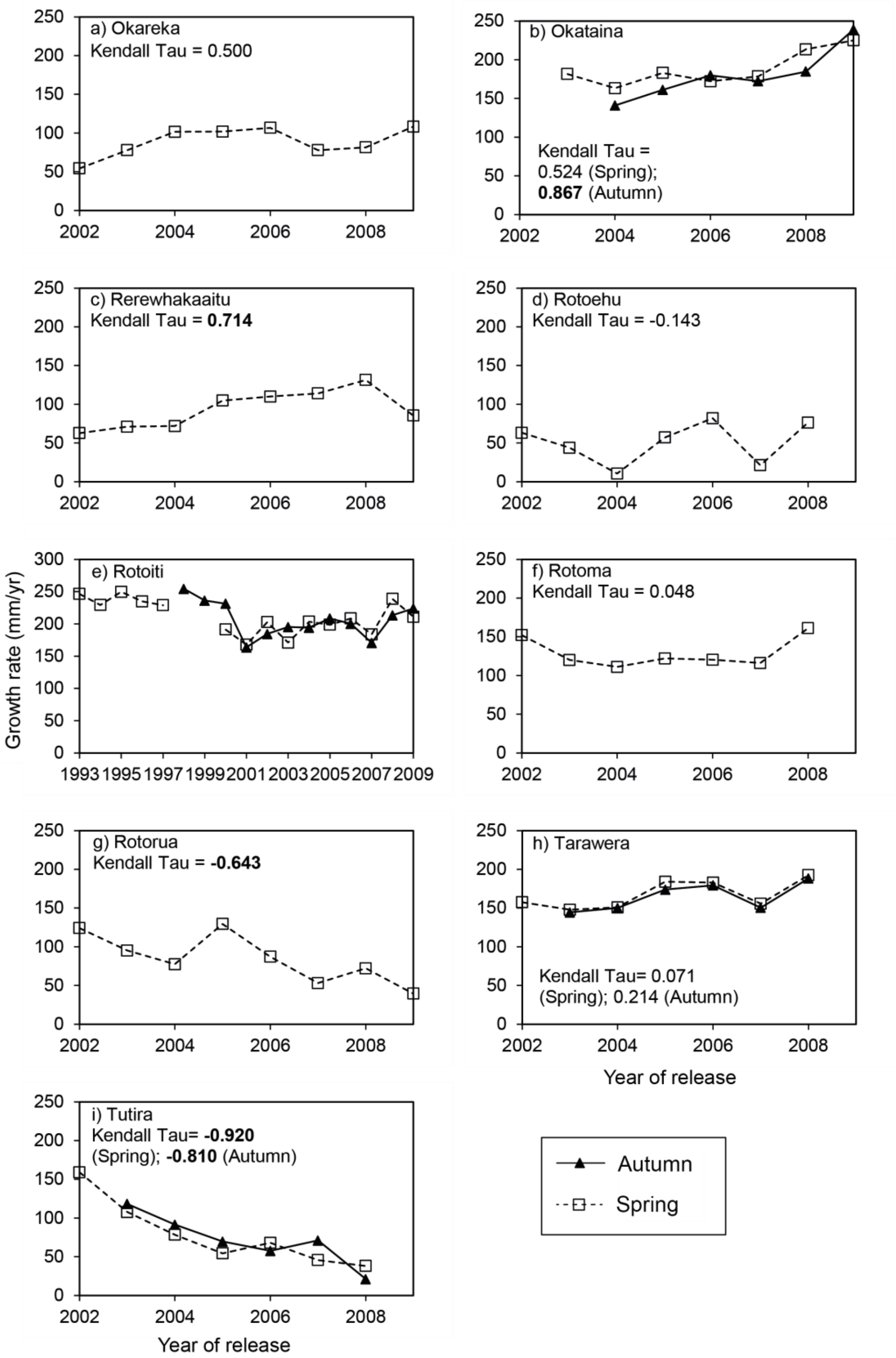

Fig. 5.2. Instantaneous growth rate at 480 mm (mean length reached at two years old) of stocked rainbow trout released in autumn and spring into lakes: (a) Okareka, (b) Okataina, (c) Rerewhakaaitu, (d) Rotoehu, (e) Rotoiti, (f) Rotoma, (g) Rotorua, (h) Tarawera, and (i) Tutira. Note different time scale used for Lake Rotoiti. Kendall Tau correlations in bold are significant at *P* < 0.05.

Some common patterns are evident in correlations between trout growth variables and variables related to lake morphometry and catchment land use. Nearly all of these correlations suggest that trout growth rates and size increase with increasing lake size (i.e. area, volume, and depth) (Fig. 5.3, Table 5.5). Additionally, trout growth rates were positively correlated with the amount of forest in the lake catchment, and negatively correlated with the amount of pasture in the catchment (Fig. 5.3, Table 5.5).

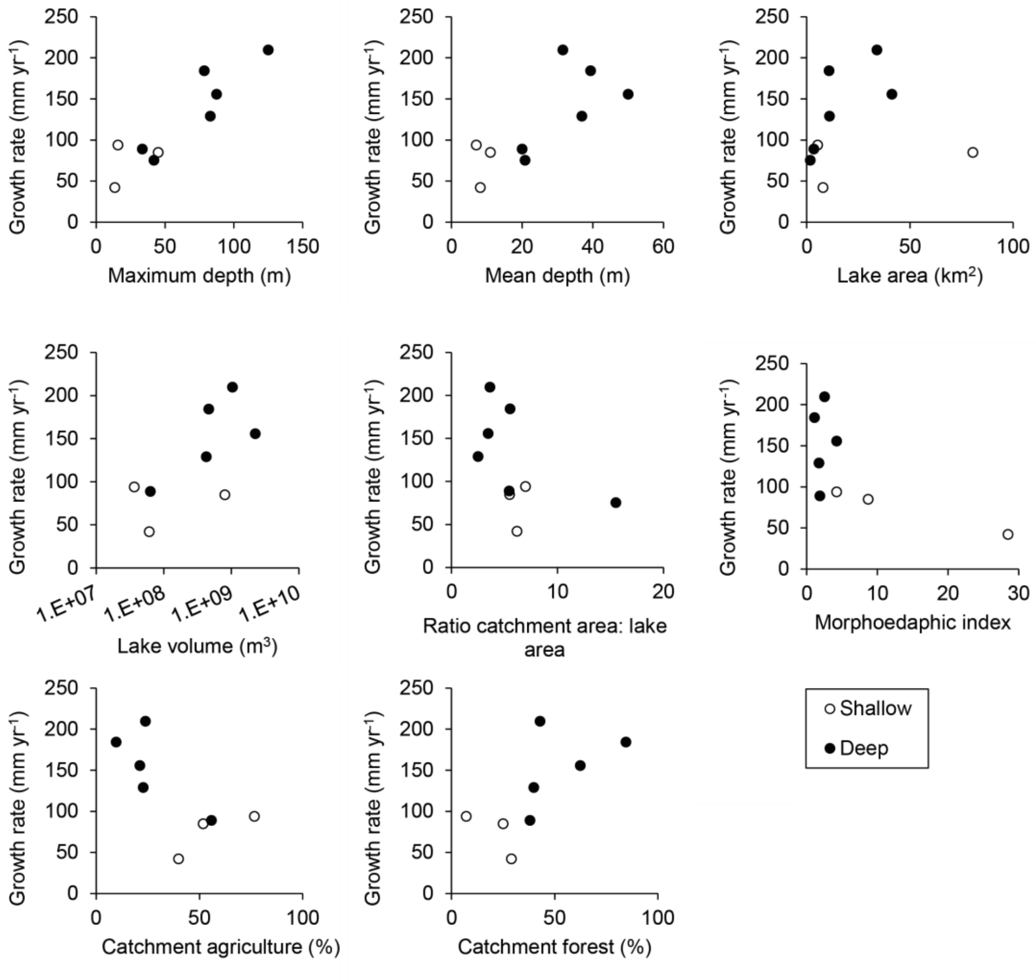

Fig. 5.3. Relationships between lake characteristics and instantaneous growth rate at 480 mm (mean length reached at two years old) of stocked rainbow trout in deep (≥20 m mean depth; ●) and shallow (≤11 m mean depth; ○) lakes in the North Island of New Zealand.

Table 5.5. Spearman rank correlations (*r*) between rainbow trout growth parameters and catchment land use and lake morphometry variables in a range of shallow and deep lakes in New Zealand (8 lakes) during 2002–2009. Growth rate was calculated for 2 year old fish, and L_∞ is a parameter of Bertalanffy's growth equation. * indicates significance at $P < 0.05$; ** indicates significance at $P < 0.01$; * indicates significance at $P < 0.001$.**

Variable (units)	Growth rate	L_∞
Catchment agriculture area: lake area	-0.629***	-0.453**
Catchment forest area: lake area	0.077	0.218
Catchment area (km^2)	0.363**	0.345**
Lake area (km^2)	0.418***	0.361**
Ratio catchment area: lake area	0.625***	0.479***
Lake volume (m^3)	0.644***	0.489***
Mean depth (m)	0.700***	0.578***
Maximum depth (m)	0.819***	0.629***

Increased trout growth rates and L_∞ were associated with both hypolimnetic and epilimnetic volume, but the positive correlations between trout growth parameters and summer thermocline depth and the epilimnion:hypolimnion ratio suggest that large hypolimnetic volumes are more important for trout growth than large epilimnetic volumes (Fig. 5.4, Table 5.6). Trout growth rates and L_∞ were positively correlated with indices measuring the absolute amount of habitat with suitable temperature and DO, but were either not correlated or negatively correlated with measures indicating average conditions throughout the water column (Fig. 5.4, Table 5.6). For example, trout growth rates and L_∞ were positively correlated with the summer minimum volume of the lake containing more than 6 mg L^{-1} DO. In contrast, trout growth rates were negatively correlated with mean DO concentrations in the entire water column and DO concentrations in the near-bottom waters during summer (Fig 5.4, Table 5.6). Growth rates and L_∞ declined with increasing eutrophication, indicated by negative correlations between trout growth parameters and TLI, turbidity, chl *a*, and TN, and a positive correlation with Secchi depth.

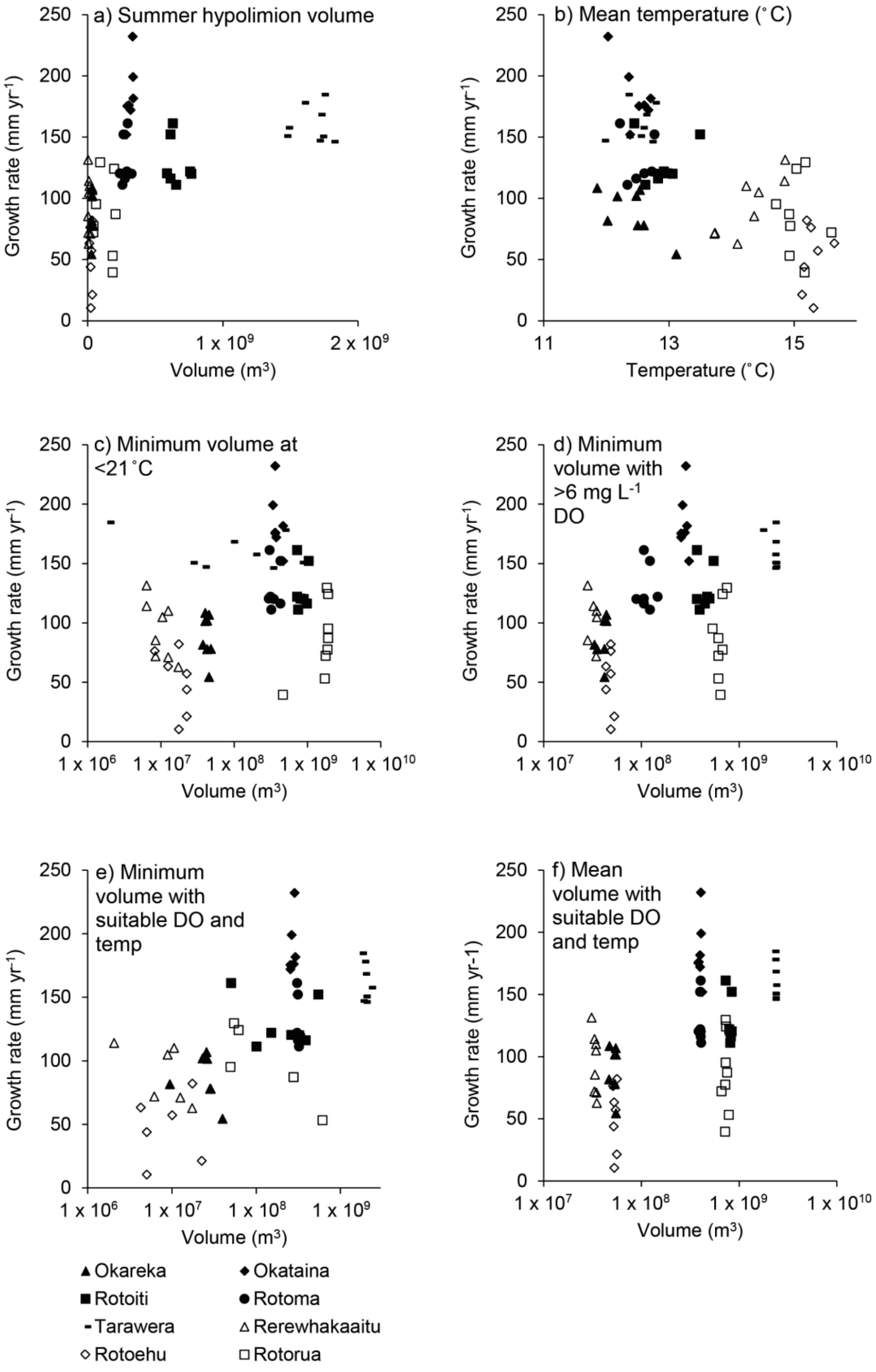

Fig. 5.4. (a-f) Relationships between lake characteristics and instantaneous growth rate at 480 mm (mean length reached at two years old) of stocked rainbow trout in deep (≥20 m mean depth; filled symbols) and shallow (≤11 m mean depth; open symbols) lakes in the North Island of New Zealand.

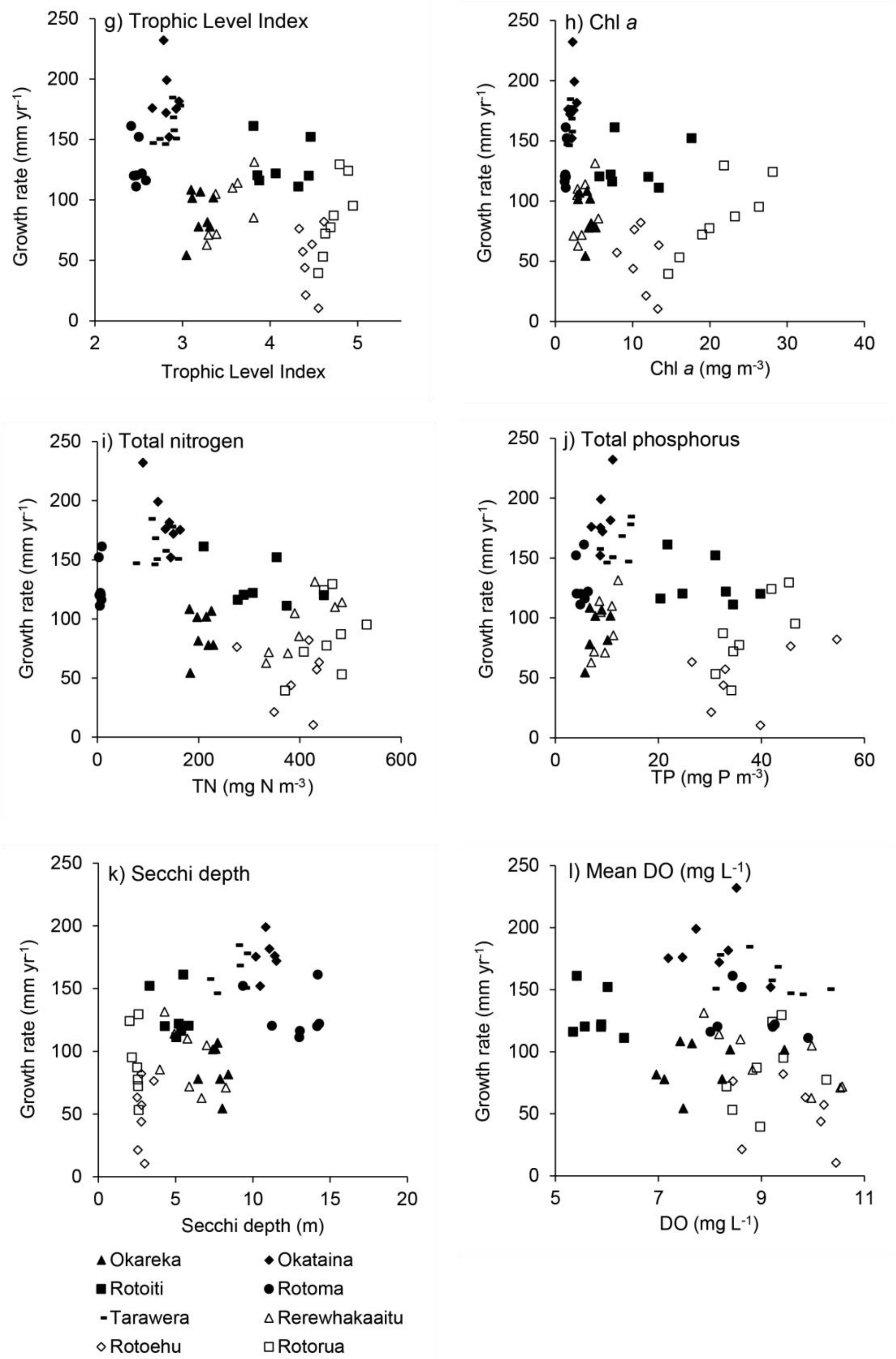

Fig. 5.4. (g-l) Relationships between lake characteristics and instantaneous growth rate at 480 mm (mean length reached at two years old) of stocked rainbow trout in deep (≥20 m mean depth; filled symbols) and shallow (≤11 m mean depth; open symbols) lakes in the North Island of New Zealand.

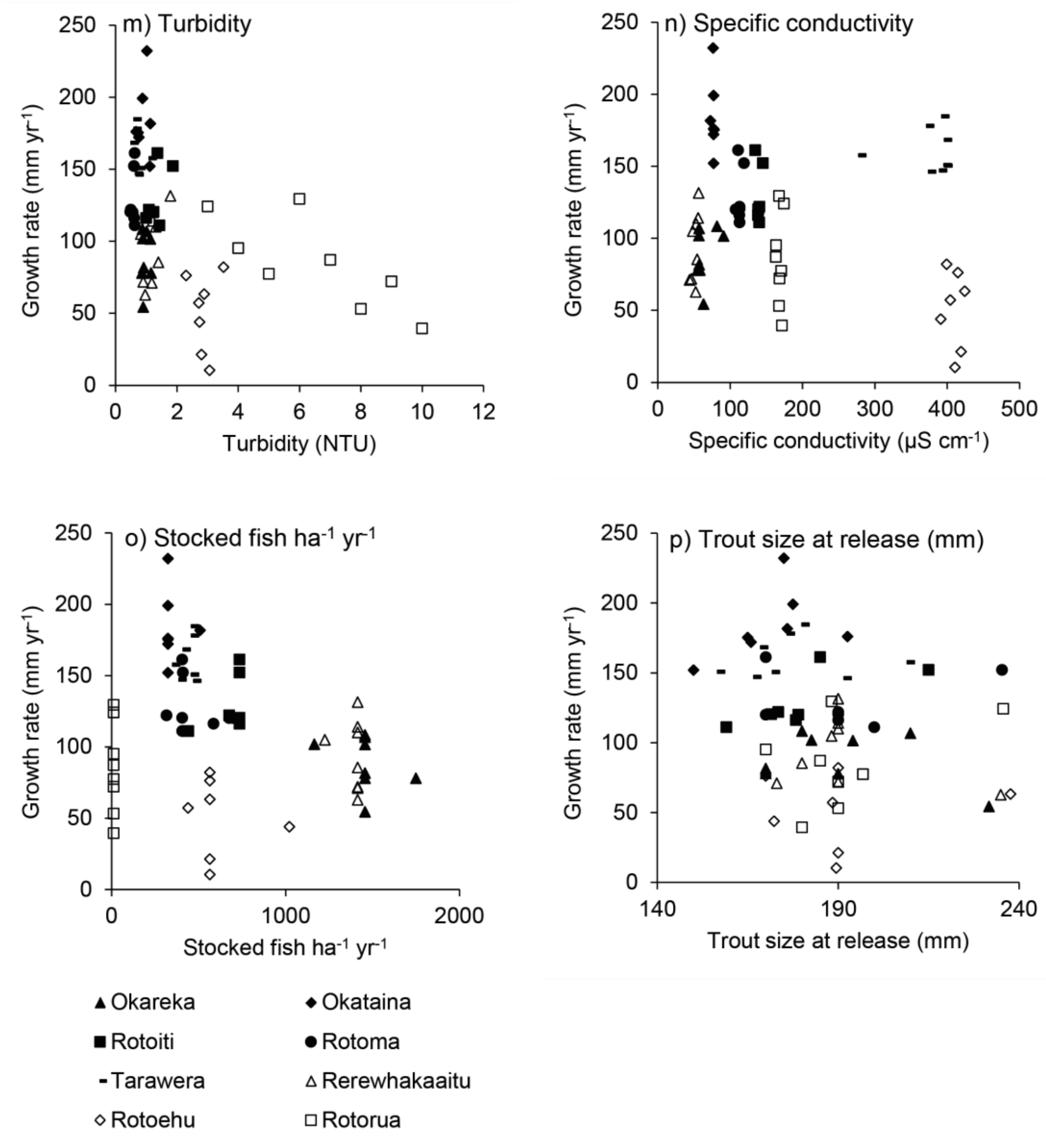

Fig. 5.4. (m-p) Relationships between lake characteristics and instantaneous growth rate at 480 mm (mean length reached at two years old) of stocked rainbow trout in deep (≥20 m mean depth; filled symbols) and shallow (<12 m mean depth; open symbols) lakes in the North Island of New Zealand.

Table 5.6. Spearman rank correlations (r) between rainbow trout growth parameters and environmental factors in a range of shallow and deep lakes in New Zealand (8 lakes, 8 years) during 2002–2009. Growth rate was calculated for 2 year old fish, and L_∞ is a parameter of Bertalanffy's growth equation. Correlations are between growth parameters and annual means of environmental factors integrated through the entire water column of each lake (where appropriate). * indicates significance at $P < 0.05$; ** indicates significance at $P < 0.01$; * indicates significance at $P < 0.001$.**

Variable (units)	Growth rate	L_∞
Lake stratification		
Summer thermocline depth (m)	**_0.581***_**	**_0.453***_**
Hypolimnetic volume (m^3)	**_0.774***_**	**_0.606***_**
Epilimnetic volume (m^3)	**_0.402**_**	0.314
Epilimnetic volume: hypolimnetic volume	**_-0.643***_**	**_-0.571***_**
Habitat suitability		
Mean water temperature (ºC)	**_-0.524***_**	**_-0.479***_**
Proportion of lake <21ºC	0.183	-0.005
Min volume <21ºC (m^3)	**_0.417***_**	0.268
Near-bottom summer DO (mg L^{-1})	**_-0.334**_**	-0.260
Minimum volume >6 mg L^{-1} DO (m^3)	**_0.477***_**	**_0.426**_**
Mean DO (mg L^{-1})	**_-0.540***_**	**_-0.465***_**
Mean volume with suitable DO and temp (m^3)	**_0.592***_**	**_0.412**_**
Minimum volume with suitable DO and temp (m^3)	**_0.621***_**	**_0.466***_**
Relative volume with suitable DO and temp	-0.120	0.090
Stocking rate (fish ha^{-1} yr^{-1})	**_-0.314*_**	-0.276
Trophic state		
Trophic level index	**_-0.367**_**	**_-0.393**_**
Turbidity (NTU)	**_-0.404**_**	**_-0.458***_**
Chl *a* (mg m^{-3})	**_-0.315*_**	**_-0.384**_**
Conductivity (µS cm^{-1})	-0.037	-0.124
Secchi depth (m)	**_0.418***_**	**_0.460***_**
TP (mg P m^{-3})	-0.055	-0.126
TN (mg N m^{-3})	**_-0.510***_**	**_-0.463***_**
TN:TP	**_-0.363**_**	-0.213

The CART analysis showed that variables associated with lake volume and the volume of suitable habitat were most important for determining trout growth rates in different lakes and years (Table 5.7). Stocking rate and mean lake temperature were also important variables, whereas trophic state indicators such as chl *a* and TP were less important. Consequently, the optimal tree design selected hypolimnetic volume as the variable most effectively separating low from high trout growth rates (Fig. 5.5). Within these two groups, indicators of trophic state were important for further partitioning of trout growth rates: in lakes with high hypolimnetic volume, chl *a* separated groups, whereas in lakes with low hypolimnetic volume, conductivity separated groups. As possible alternatives for these variables, the model also selected several surrogate variables (Table 5.8). Note that the surrogates for hypolimnion volume all relate to volume, depth, DO or temperature and hence indicate habitat quality or volume, whereas the surrogates for chl *a* are all indicators of trophic state. However, temperature was chosen as the variable that was most closely related with conductivity, and other surrogate variables for this node had little association with conductivity.

Table 5.7. Importance of variables in determining trout growth rate in classification and regression tree analysis, expressed as relative percentages.

Variable	Relative importance (%)
Hypolimnion volume (m^3)	100
Mean depth (m)	98
Minimum volume with suitable DO and temp (m^3)	86
Lake volume (m^3)	72
Minimum volume >6 mg L^{-1} DO (m^3)	72
Stocked fish ha^{-1} yr^{-1}	70
Mean volume with suitable DO and temp (m^3)	69
Mean water temperature (ºC)	66
Min volume <21ºC (m^3)	58
Mean DO (mg L^{-1})	54
Turbidity (NTU)	53
Secchi depth (m)	49
TN (mg N m^{-3})	41
Conductivity (µS cm^{-1})	40
Chl *a* (mg m^{-3})	37
Size at release (mm)	27
TP (mg P m^{-3})	24

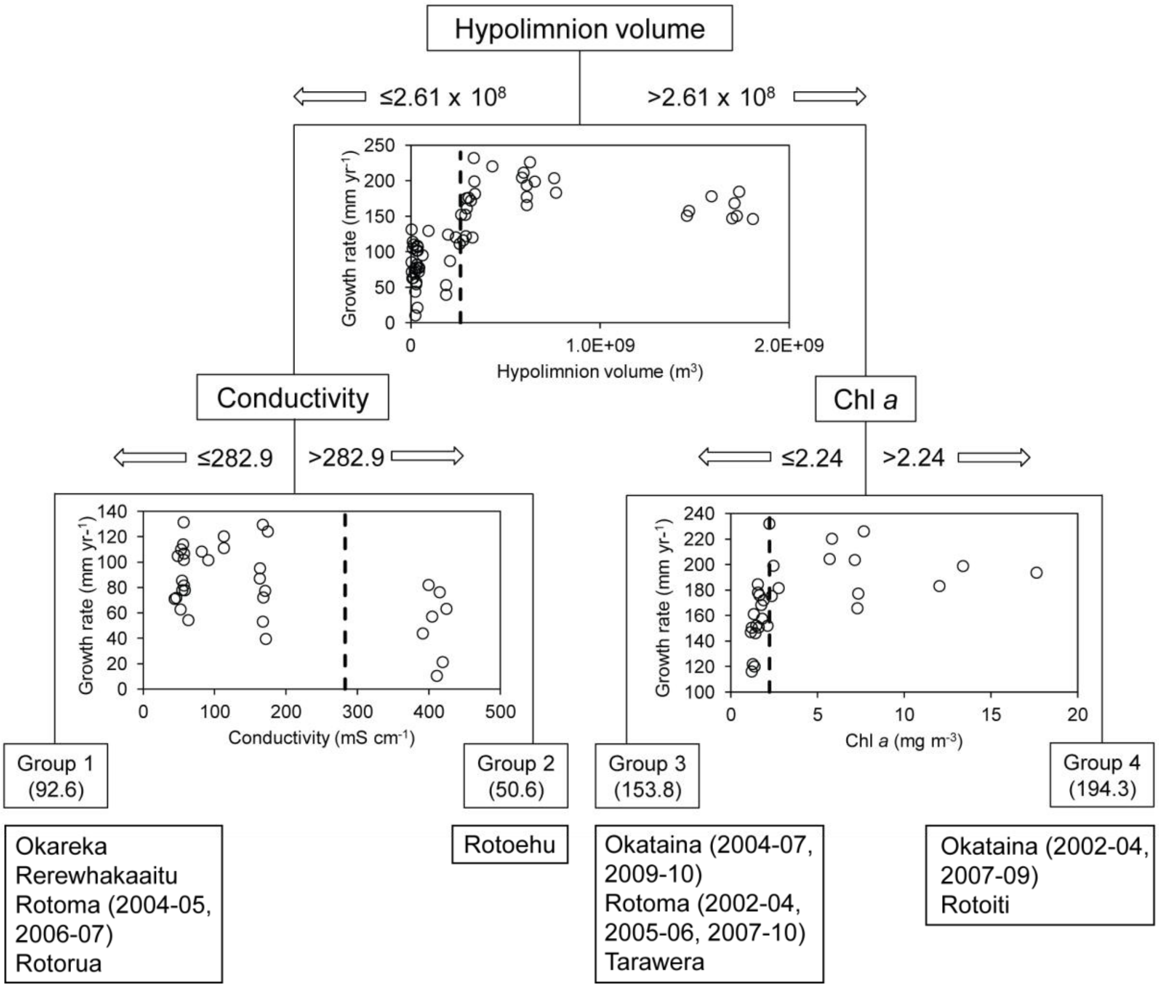

Fig. 5.5. Regression tree classifying trout growth rate on the basis of lake stratification and water quality variables, with scatterplots showing the spread of data (circles) and cut-off point separating groups (dashed lines). Decisions are given as inequalities, with the direction of sorting given by arrows. Mean growth rate (mm yr^{-1}) in the resulting terminal nodes is given below group numbers. Boxes below group numbers show the group membership of measurements from different lakes and years; where no years are given, all measurements from that lake fit were classified into one group.

Table 5.8. Surrogate values for nodes of regression tree. The association of surrogate variables with the variables in the regression tree is expressed as a relative percentage. Split sign (+ or –) indicates the direction of sorting; if negative, high values are sorted to the right, and if positive, high values are sorted to the left. The split constant is the cut-off point in the predictor variable for separating the two groups.

Node	Variable	Association with chosen variable (%)	Split sign	Split constant
1. Hypolimnion volume	Mean depth (m)	0.92	–	25.75
	Min volume >6 mg L^{-1} (m^3)	0.64	–	70806575
	Mean temperature (°C)	0.64	+	13.61
	Min. vol. suitable DO & temp (m^3)	0.80	–	81663800
2. Conductivity	TP (mg P m^{-3})	0.14	–	45.51
	Size at release (mm)	0.14	–	236.66
	Mean temperature (°C)	0.71	–	15.08
3. Chl *a*	Mean DO (mg L^{-1})	0.80	+	7.87
	Turbidity (NTU)	0.70	–	0.73
	Secchi depth (m)	0.70	+	6.46
	TP (mg P m^{-3})	0.70	–	17.30

5.4.2 Body condition of rainbow trout

Body condition of rainbow trout, measured with Fulton’s condition factor and the modified coefficient $\log_{10}(a')$ of the *W-L* relationship, was highest in mesotrophic Lake Rotoiti and lowest in oligotrophic Lake Tarawera (Table 5.9). Differences in Fulton’s condition factor were statistically significant among lakes (Kruskal-Wallis ANOVA: H = 13.99, $p = 0.003$). The two methods showed a broadly similar pattern, but gave slightly different results for Lake Rotorua and Lake Okataina; $\log_{10}(a')$ suggested that rainbow trout from Lake Rotorua were in slightly better condition than those from Lake Okataina, while Fulton’s condition factor indicated the opposite situation. Note that fish growth parameters (L_∞ and growth rate) and $\log_{10}(a')$ were closely correlated (Spearman rank correlation; r_s = 0.815 and 0.720) among the four lakes where these variables were measured simultaneously.

Table 5.9. Parameters of mass-length regression (Eqns. 5.3 and 5.4) ± 95% confidence limits, and Fulton's condition factor, ± SE, of rainbow trout in lakes of different trophic state, 2007–2011. We calculated mass (*W*, g)- length (*L*, mm) regressions as follows: $\log_{10}W = a + b \log_{10} L$, using wild and stocked trout collected December- March to avoid the spawning period. *a'* is the calculated *a* value at fixed value of *b* = 2.46 ± 0.04 (see Methods). Fulton's condition factor was calculated for rainbow trout 425–474 mm fork length. Trophic state: O, oligotrophic; M, mesotrophic; E, eutrophic.

		Length-mass regression parameters				Fulton's condition factor	
Lake	Trophic state	*n*	$\log_{10}(a)$	*b*	$\log_{10}(a')$	*n*	Mean ± SE
Tarawera	Ol	84	-6.55 ± 0.67	2.49 ± 0.25	-6.30	11	1.19 ± 0.017
Okataina	Ol	143	-6.74 ± 0.45	2.57 ± 0.17	-6.27	12	1.27 ± 0.031
Rotoiti	Me	359	-7.01 ± 0.33	2.68 ± 0.12	-6.25	24	1.35 ± 0.041
Rotorua	Eu	2351	-6.15 ± 0.14	2.35 ± 0.05	-6.29	608	1.32 ± 0.006

5.5 Discussion

5.5.1 Relationships between growth rates and lake characteristics

In this study, rainbow trout growth rate was correlated with the volume of water with favourable temperature and DO concentrations; both these factors have previously been shown to limit rainbow trout distribution in lakes (Swales 2006). Habitat availability is a key factor structuring fish populations; for example, the availability of suitable thermal habitat in lakes influences fish growth rate potential (Brandt et al. 1992, Mason et al. 1995, Budy et al. 2011). It was shown that in shallow Arctic lakes, the persistence of some fish species is constrained by a lack of suitable thermal habitat in both summer and winter (Hershey et al. 1999, 2006). In contrast, in Rotorua lakes, cold winter temperatures do not limit fish growth. In the shallow lakes in our study, near-bottom waters can exceed 20ºC during summer (Burger et al. 2007, P. Scholes, unpubl. data), exceeding the upper temperature limit of 19ºC suggested for rainbow trout in California (Myrick and Cech 2000). By providing a refuge, cold tributaries may mitigate the effects of warm temperatures in shallow Lake Rotorua: Hamurana Stream (mean flow 256 000 $m^3 d^{-1}$) and Awahou Stream (256 000 $m^3 d^{-1}$) provide inputs of water below 12ºC (Rutherford et al. 1996, Boubée et al. 2006). Thermal refuge habitats may offer the best conditions for growth for coldwater species in warm lakes during summer (Budy et al. 2011). However, loss of overall habitat volume may still have substantial effects on growth rates; these effects are not well documented yet and require further detailed investigations.

In shallow, eutrophic lakes such as Rotorua and Rotoehu, periodic stratification events cause intermittent hypolimnetic deoxygenation (Burger et al. 2007, Trolle et al. 2011) which probably limits rainbow trout habitat further, especially if high temperatures and low DO coincide. If fish are forced into areas with suboptimal temperature conditions and prey concentrations during thermal stratification, growth rate potential may be reduced (Roberts et al. 2009, Arend et al. 2011). This effect is likely to be most pronounced in Lakes Rotoehu and Rerewhakaaitu, which lack significant cold input streams. Areas of low DO and high temperature in Lake Rotoehu coincided on several occasions during summer (data not shown), which may explain the low trout growth rates in this lake.

Deoxygenation of the near-bottom waters of lakes may not be harmful for trout populations, provided there is sufficient suitable habitat outside the deoxygenated zone. Trout growth rates were negatively correlated with mean water column and near-bottom DO concentrations in our study. This seems to be paradoxical, given the positive correlations observed between trout growth rates and habitat measures; however, other studies have shown that hypolimnetic deoxygenation in deep lakes may increase fish growth when conditions in the upper water column are favourable, by concentrating prey. For example, hypoxia increased growth potential of Lake Erie walleye (*Sander vitreus*) by concentrating prey in areas with suitable light, DO and temperature conditions (Brandt et al. 2011). This may be the case for the deeper Rotorua lakes, as the main prey of rainbow trout in New Zealand lakes, the common smelt (*Retropinna retropinna*; Rowe 1984), is highly sensitive to reduced DO concentrations and are therefore is likely to avoid areas of low DO (Dean and Richardson 1999).

Our results highlight the importance of lake morphometry in mediating the effects of eutrophication in warm-temperate systems: The relationships between trout growth parameters and lake trophic state showed a non-linear or dome-shaped response to eutrophication. Increases in nutrients may be beneficial for growth of rainbow trout when sufficient habitat is present (i.e. in deep lakes), but severe eutrophication may be detrimental for trout growth where habitat is limited by high temperature (i.e. in shallow lakes). This result is in concordance with observations by Budy et al. (2011), who found that the growth rate potential of coolwater species (walleye *Sander vitreus* and crappie *Pomoxis nigromaculatus*) decreased with increasing chl *a* concentrations in a warm lake.

Habitat quality is linked to population density, and the negative correlation between trout stocking rate and growth rate (Fig. 3o) indicates possible density-dependent effects on trout growth in our study system. The spread of data evident in this relationship indicates the presence of confounding factors, such as environmental conditions and the population size of wild trout. Reliable assessment of density dependent effects requires estimates of the entire trout population, which are currently lacking. However, the reduction in growth rates in Lake Okataina between 2004 and 2007, as seen in our regression tree (Fig. 5.4) may have been due to a change in angling size regulations: during this time, the minimum catch size was raised from 35 to 58 cm, meaning that fewer trout were caught, which probably lead to higher than normal population densities and density-dependent effects on growth. Optimal fish stocking rates will depend on management goals for the fishery; currently, some lakes are managed as high-yield fisheries (e.g. Lake Rerewhakaaitu), while others are intended as low-yield trophy fisheries (e.g. lakes Tarawera and Okataina).

5.5.2 Body condition of rainbow trout

While generally consistent, the two body condition indices showed different results in some instances (see Results). Size-specific Fulton’s condition factor may be easily biased due to differences in size structure of various fish populations and the allometric nature of fish growth patterns (Pope and Kruse 2007). Though we used a limited length range to compare Fulton’s condition factor to confine this bias, small differences in size distributions between the lakes may have caused variation in the results. In contrast, $\log_{10}(a')$ averages body condition of all fish in the population, and thus more reliably reflects the state of populations under specific environmental conditions.

Differences in life history patterns between wild and stocked fish may account for some variation in body condition among lakes. Hatchery breeding can cause rapid trait divergence from wild populations (Christie et al. 2012); for example, hatchery-reared Atlantic salmon show differences in age at maturity compared to wild fish (Gross 1998), and in general, hatchery-raised salmonids are larger, heavier and grow faster than wild fish in the same cohort (Weber and

Fausch 2003, Jonsson and Jonsson 2006). Hatchery broodstock in Rotorua lakes are selected for later maturity; therefore, differences in age at maturity between stocked and wild fish are likely, and the varying proportions of wild trout among lakes (Table 2) is a possible source of variation in Rotorua lakes. Life history variation between stocked and wild-spawning rainbow trout in these lakes is not well understood, and requires more detailed investigation in the future.

5.5.3 Plasticity of rainbow trout growth rates

Adaptation to environmental change may involve distribution changes, phenotypic plasticity, or evolution, and determining the mechanism responsible for observed adaptation is important for predicting the effects of perturbations such as climate change (Gienapp et al. 2007). Determining the phenotypic plasticity of particular traits is important, because phenotypic plasticity can allow a population to adapt to environmental changes in the short term, and the degree of plasticity, along with the rate of evolution, can determine the level of adaptation to environmental change (Berteaux et al. 2004). We observed wide variation in growth rates, L_∞ and body condition of rainbow trout that originated from the same genetic source and were raised under identical hatchery conditions, providing evidence for phenotypic plasticity of growth rates and final size. Our results are similar to those of Reed et al. (2010) who found that genetically-similar, hatchery-raised sockeye salmon (*Oncorhynchus nerka*) grew larger when stocked into a warm, productive lake compared to a cooler, less productive lake. Life histories of salmonids are generally variable, and several characteristics show a high degree of phenotypic plasticity in certain species, such as growth (Reed et al. 2010) and timing of migration and maturation (Crozier et al. 2008). Future studies should clarify the effects of lake eutrophication and warm temperatures on other phenotypically plastic life history traits, such as age at maturity and timing of spawning, to help predict the consequences of global environmental change.

5.5.4 Climate change and catchment management implications

By directly examining growth of coldwater piscivores in various warm-temperate lakes such as those in New Zealand’s North Island, we can infer the likely impacts of climate change in cooler areas. In most temperate lakes, climate change is predicted to cause increases in water temperature (Gerten and Adrian 2002).

Coldwater species living in shallow lakes are likely to experience greater reductions in habitat than in deep lakes (Stefan et al. 2001, Fang et al. 2004), and this is expected to negatively affect their abundance (Jeppesen et al. 2012). Though climate change in New Zealand is predicted to be less severe than in many other locations, increases in the duration of lake stratification are likely to cause increased deoxygenation of near-bottom waters, affecting the availability of fish habitat (Hamilton et al. in press). Our results suggest that climate warming is likely to constrain growth of coldwater piscivores in shallow lakes, particularly those that lack thermal refugia. Coldwater fish populations in deep lakes are likely to be more resilient to increases in temperature, and growth may increase (up to a species' temperature threshold) if sufficient food is available to meet increased energetic demands (Elliott 1976), and if sufficient habitat is still available.

The observed decreases in rainbow trout growth rate with increasing eutrophication have important implications for ecosystem management. Trophic state of lakes is influenced by catchment land use, such that lakes where pasture is the dominant catchment land use tend to be more productive than lakes with other catchment land uses, both in New Zealand and worldwide (Taranu and Gregory-Eaves 2008, Verburg et al. 2010). In our study, lakes with more pasture in their catchments were more eutrophic and exhibited lower trout growth rates; however, the relationship between trout growth rates and lake trophic state is not linear, as was shown above. In deeper, more oligotrophic lakes, increases in productivity are likely to increase food supply and therefore growth rates of trout. However, in lakes that are already eutrophic, further eutrophication is likely to be detrimental. Slowing or reversing the effects of cultural eutrophication in these lakes is important for conserving their rainbow trout fisheries, especially since the effects of eutrophication in lakes are predicted to intensify with climate change (Jeppesen et al. 2009, Trolle et al. 2011).

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5.7 Appendices

Appendix 5.1. Spring releases. Characteristics of returned stocked rainbow trout used in comparisons of growth rate and L_∞ among lakes, 2002–2009. Season caught (% of catch) refers to the percentage of the release group caught in each season. Aut = autumn, Spr = spring, Sum = summer, Win = winter.

Lake	Year liberated	Mean length (mm)	Max. age (years)	Total fish returned	Season caught (% of catch)			
					Aut	Spr	Sum	Win
Okareka	2002	300	5.61	53	49	8	25	19
	2003	221	5.61	23	26	9	13	52
	2004	327	5.90	45	36	11	29	24
	2005	321	4.85	47	30	21	19	30
	2006	289	4.62	30	20	23	20	37
	2007	273	4.08	30	13	7	40	40
	2008	233	3.52	21	29	10	33	29
	2009	223	2.52	16	6	25	38	31
Okareka- Total		274	5	33	30	14	26	31
Okataina	2002	345	7.74	47	47	15	17	21
	2003	298	6.41	50	46	8	14	32
	2004	377	4.50	61	51	18	18	13
	2005	339	4.90	50	50	14	12	24
	2006	345	4.93	48	46	10	23	21
	2007	323	4.35	47	38	32	17	13
	2008	340	3.54	61	41	16	25	18
	2009	238	2.52	16	6	75	6	13
Okataina- Total		326	5	48	44	19	18	20
Rere-whakaaitu	2002	309	5.00	51	41	24	10	25
	2003	247	4.56	26	42	8	35	15
	2004	298	5.57	38	29	18	24	29
	2005	277	5.10	27	48	37	0	15
	2006	300	5.44	43	44	26	7	23
	2007	305	4.08	48	35	10	10	44
	2008	292	3.40	39	54	15	8	23
	2009	206	2.38	10	30	30	0	40
Rerewhakaaitu- Total		280	4	35	41	20	16	27

Appendix 5.1 (Continued). Spring releases. Characteristics of returned stocked rainbow trout used in comparisons of growth rate and L_∞ among lakes, 2002–2009. Season caught (% of catch) refers to the percentage of the release group caught in each season. Aut = autumn, Spr = spring, Sum = summer, Win = winter.

Lake	Year liberated	Mean length (mm)	Max. age (years)	Total fish returned	Season caught (% of catch)			
					Aut	Spr	Sum	Win
Rotoehu	2002	335	5.04	77	27	31	18	23
	2003	262	4.71	53	43	32	8	17
	2004	308	4.96	55	27	20	16	36
	2005	303	4.44	55	22	33	16	29
	2006	263	4.15	27	30	15	30	26
	2007	255	4.11	25	28	32	12	28
	2008	247	3.38	28	29	25	14	32
	2009	198	2.37	6	17	67	0	17
Rotoehu- Total		271	4	41	29	29	18	27
Rotoiti	2002	347	3.87	46	50	13	11	26
	2003	261	4.61	31	48	23	13	16
	2004	282	3.96	25	24	40	12	24
	2005	320	3.92	51	45	18	14	24
	2006	317	3.93	50	26	32	36	6
	2007	312	3.82	49	39	24	20	16
	2008	310	3.05	43	26	23	33	19
	2009	288	2.58	39	23	33	31	13
Rotoiti- Total		304	4	42	36	25	22	18
Rotoma	2002	318	7.50	35	29	23	31	17
	2003	237	6.57	27	30	11	37	22
	2004	298	5.54	25	16	20	28	36
	2005	267	4.78	20	40	0	25	35
	2006	273	5.35	27	15	30	30	26
	2007	256	4.29	19	26	16	26	32
	2008	226	3.51	15	20	20	40	20
	2009	192	2.51	3	0	0	67	33
Rotoma- Total		258	5	21	28	23	32	26
Rotorua	2002	319	3.60	57	26	12	42	19
	2003	306	3.63	60	30	22	23	25
	2004	329	5.57	48	42	13	25	21
	2005	323	4.34	52	37	19	23	21
	2006	290	3.92	44	36	14	36	14
	2007	289	3.87	46	35	15	39	11
	2008	247	3.55	21	38	24	33	5
	2009	221	2.58	16	13	25	63	0
Rotorua- Total		290	4	43	33	17	33	20

Appendix 5.1 (Continued). Spring releases. Characteristics of returned stocked rainbow trout used in comparisons of growth rate and L_∞ among lakes, 2002–2009. Season caught (% of catch) refers to the percentage of the release group caught in each season. Aut = autumn, Spr = spring, Sum = summer, Win = winter.

Lake	Year liberated	Mean length (mm)	Max. age (years)	Total fish returned	Season caught (% of catch)			
					Aut	Spr	Sum	Win
Tarawera	2002	279	4.91	65	35	15	29	20
	2003	301	4.29	45	38	22	24	16
	2004	375	6.57	68	35	19	32	13
	2005	348	4.50	59	32	25	25	17
	2006	335	5.14	54	39	26	24	11
	2007	322	4.46	54	33	24	22	20
	2008	363	3.48	74	28	23	22	27
	2009	234	2.57	21	24	38	29	10
Tarawera- Total		320	4	55	34	23	26	18
Tutira	2002	285	4.01	24	17	25	8	50
	2003	296	4.13	45	16	27	7	51
	2004	287	5.28	31	35	23	6	35
	2005	282	5.04	31	23	26	3	48
	2006	281	4.36	33	18	27	9	45
	2007	250	4.11	22	27	27	0	45
	2008	248	3.19	23	30	35	0	35
	2009	189	2.42	4	25	50	0	25
Tutira- Total		265	4	27	23	27	8	45
Overall Total		288	4	38	34	22	23	24

Appendix 5.2. Autumn releases. Characteristics of returned stocked rainbow trout used in comparisons of growth rate and L_∞ among lakes, 2002–2009. Season caught (% of catch) refers to the percentage of the release group caught in each season. Aut = autumn, Spr = spring, Sum = summer, Win = winter.

Lake	Year liberated	Mean length (mm)	Max. age (years)	Number of fish returned	Season caught (% of catch)			
					Aut	Spr	Sum	Win
Okataina	2003	179	5.66	1	0	0	100	0
	2004	291	4.94	42	60	14	12	14
	2005	310	6.02	39	49	8	21	23
	2006	359	5.45	48	44	25	21	10
	2007	292	4.42	47	40	34	13	13
	2008	313	3.52	49	45	18	22	14
	2009	239	2.60	19	21	42	26	11
Okataina- Total		283	5	35	52	26	19	17
Rotoiti	2002	274	5.02	26	38	12	19	31
	2003	286	3.85	49	47	24	10	18
	2004	291	3.47	47	19	45	17	19
	2005	337	3.86	48	46	29	13	13
	2006	542	3.17	30	30	13	30	27
	2007	277	2.81	18	50	33	17	0
	2008	325	3.03	54	19	37	30	15
	2009	264	2.60	29	10	52	17	21
Rotoiti- Total		324	3	38	32	32	19	21
Tarawera	2003	322	6.12	68	28	19	28	25
	2004	291	4.15	48	33	17	29	21
	2005	339	6.06	47	45	13	23	19
	2006	349	4.84	56	32	16	43	9
	2007	266	4.59	36	25	36	22	17
	2008	312	3.16	45	29	18	22	31
	2009	213	2.57	12	17	50	25	8
Tarawera- Total		299	4	45	31	20	29	20
Tutira	2002	228	4.44	20	0	10	0	90
	2003	250	4.96	26	19	31	0	50
	2004	265	4.16	45	24	18	7	51
	2005	197	5.27	16	19	19	0	63
	2006	238	5.12	25	16	32	0	52
	2007	181	3.84	6	50	33	0	17
	2008	217	3.14	12	33	17	0	50
	2009	179	2.15	3	33	0	0	67
Tutira- Total		220	4	100	23	25	16	56
Overall Total		283	4	34	31	24	19	26

6 A bioenergetic assessment of the influence of stocking practices on rainbow trout (*Oncorhynchus mykiss*) growth and consumption in Lake Rotoiti[4]

6.1 Abstract

To investigate the carrying capacity and factors affecting growth of rainbow trout in Lake Rotoiti, we employed a bioenergetics model to assess the influence of stocking rates, timing of releases, and prey abundance on growth and prey consumption. We hypothesised that stocking rates and prey abundance would affect growth and prey consumption by influencing per-capita prey availability, and that the environmental conditions encountered by fish at the time of stocking would affect growth and consumption. Prey consumption of stocked rainbow trout was calculated with the Wisconsin bioenergetics model. We calculated growth trajectories of released trout based on data from stocked trout that were released in spring and autumn from 1995 to 2009 and then re-captured by anglers. Diet, prey energy density, body mass lost during spawning and lake temperature were measured locally. Stocking timing had no effect on return rates to anglers or length or weight of caught fish. Though trout released in autumn were smaller than those released in spring, autumn-released trout grew at a faster rate and had similar lengths and weights to spring cohorts after 2 years of growth in the lake. Modelled consumption parameters were negatively correlated with trout population size, suggesting that stocking rates (347–809 fish ha^{-1} year^{-1}) caused density-dependent effects on growth. Though common smelt (*Retropinna retropinna*) accounted for 85% of total prey consumption, no significant relationship was found between prey consumption by individual trout and adult smelt abundance, possibly because trout are targeting smaller smelt that our abundance estimate did not account for. Releasing trout in autumn appears to be advantageous for growth, possibly because (1) temperature is more suitable for

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[4] Submitted as Blair, J., B. Hicks, R. Pitkethley and N. Ling, I. Ostrovsky, D. Rowe. Do stocking practices influence rainbow trout (*Oncorhynchus mykiss*) growth and consumption in a New Zealand lake? A bioenergetic assessment. *Freshwater Biology*.

growth in autumn-winter than in spring-summer, and (2) prey for small trout is abundant in autumn. Mild winter conditions appear to enhance overwinter survival and growth of rainbow trout in warm-temperate lakes compared to higher latitudes. This implies that moderately productive warm-temperate lake ecosystems are highly suitable for trout growth in winter, but less so in summer, when lake stratification and high nutrient levels may create conditions suitable for algal blooms and hypolimnetic deoxygenation. High trout growth rates of trout in warm-temperate lakes can therefore be supported by timing releases to coincide with favourable winter conditions.

6.2 Introduction

Effective fisheries management requires an understanding of the factors that influence fish growth and production. This is especially true for the optimisation of stocking sport fish in lakes, where fish abundance is primarily controlled by fishery managers and angling pressure. The success of stocked fisheries (e.g. high returns to anglers and high fish growth rates) is dependent on several factors. High natural mortality of small stocked fish due to predation or overwintering mortality can be avoided by stocking fish at appropriate sizes and times of year (Walters et al. 1997, Wiley et al. 1993, Yule et al. 2000). High growth rates of stocked fish require adequate food availability (Ney 1990), which is mediated by several interacting factors including prey density (Brandt et al. 2011), prey quality or size (Boisclair and Leggett 1989, Juncos et al. 2011, Pazzia et al. 2002), and prey encounter rate (Beauchamp et al. 1999, Brandt et al. 1992, Mason et al. 1995). Density-dependent reduction in fish growth due to excessive stocking of fish can be an important limiting factor in stocked fisheries, and can be avoided by optimising stocking rates according to the carrying capacity of the ecosystem (Lorenzen 2005, 2008). Moreover, optimal stocking rates will vary widely depending on whether the fishery is managed as a low-yield, trophy fishery or a high-yield fishery with smaller, more abundant fish (Smith et al. 2012, Walters and Post 1993).

Stocked sports fish, especially those that are top-level predators, can exert significant effects on prey abundance, and these should also be considered when assessing stocking programmes. Overstocking of piscivores can lead to an imbalance between predator consumption and prey productivity (Murry et al.

2010), and when predation pressure from stocked fish is coupled with natural fluctuations in prey abundance, a decline of prey populations can result, even when predators are stocked at constant rates (Jones et al. 1993, Stewart et al. 1981). Therefore, fish stocking rates need to be carefully evaluated to maintain an optimal balance between predators and their prey.

Fish growth is influenced by many factors, and bioenergetics models are powerful tools for quantifying predator-prey relationships in space, time, ontogeny, and linking trophic relationships to key environmental variables (e.g. temperature). The widely-used Wisconsin bioenergetics model (Hanson et al. 1997) uses mass-balance equations to estimate the proportion of the maximum theoretical consumption rate required to produce the observed growth of fish, given costs of activity, egestion, excretion, and specific dynamic action (the energy expended to assimilate food). Consumption estimates can then be scaled up to the population level and compared with the production of prey species. Obtaining accurate, unbiased, simultaneous estimates of predator and prey production is a complex task; while information on predators is often collected in recreational fisheries because of their economic and cultural importance, information on prey fishes is usually rare (Ney 1990). In such a case, bioenergetics models may be used to find the key factors influencing fish growth in a comparative way, rather than relying on estimates of absolute values for prey consumption and production that are sensitive to errors (Ney 1993, Chipps & Wahl 2008).

Rainbow trout (*Oncorhynchus mykiss* Walbaum) have been stocked into several lakes in the central North Island of New Zealand to create recreational angling opportunities. Some lakes support abundant naturalised populations of rainbow trout that rely on wild spawners, e.g. lakes Rotorua, Taupo, and Waikaremoana, but in other lakes, populations are augmented by annual or biannual stocking of hatchery-raised yearlings to supplement limited natural spawning. Growth and size of stocked trout are monitored regularly in these lakes, but the factors influencing trout growth have not yet been well investigated. In contrast to previous studies, where predation on stocked fish and overwintering mortality are common problems (Walters et al. 1997, Wiley et al. 1993, Yule et al. 2000), we examine trout stocking practices in a warm-temperate climate, in a lake lacking fish that prey on stocked rainbow trout, other than trout themselves.

In this study, we employed a bioenergetics model to explore the factors influencing rainbow trout growth and food consumption rate in Lake Rotoiti, New Zealand. We aimed to (1) assess the effect of stocking times and rates on rainbow trout food consumption rate and growth in Lake Rotoiti, and to (2) evaluate the relationship between prey abundance and consumption rates of rainbow trout to optimise trout stocking rates and timing. We hypothesised that stocking rates and prey abundance would affect growth and prey consumption by influencing per-capita prey availability, and that that the environmental conditions encountered by fish at the time of stocking would affect growth and consumption during early lake residence.

6.3 Methods

6.3.1 Study site

Lake Rotoiti (38.04º S 176.44º E) is a warm, mesotrophic, monomictic lake situated in the Taupo Volcanic Zone in New Zealand's North Island (Fig. 6.1; Table 6.1). In the late austral summer (February), typical lake temperatures range from 13°C at the lake bottom to 21°C at the lake surface. In late winter (August) the lake is isothermal, and the mean temperature is approximately 11°C (P. Scholes, Bay of Plenty Regional Council, pers. comm.). Lake Rotoiti has only a few small tributary streams and thus lacks sufficient rainbow trout spawning area to support abundant wild trout populations, although wild trout present in the lake are sustained in part by migrants originating from tributaries of the adjacent Lake Rotorua (Riceman 2008). Rainbow trout are stocked into Lake Rotoiti in spring (September) and autumn (May) from a hatchery facility at Ngongotaha, Rotorua, managed by Fish & Game New Zealand. Trout are released into the lake at approximately age 1 (autumn releases) or age 1.25 (spring releases). Rainbow trout in Lake Rotoiti are non-diadromous because of barriers to upstream-migrant adults.

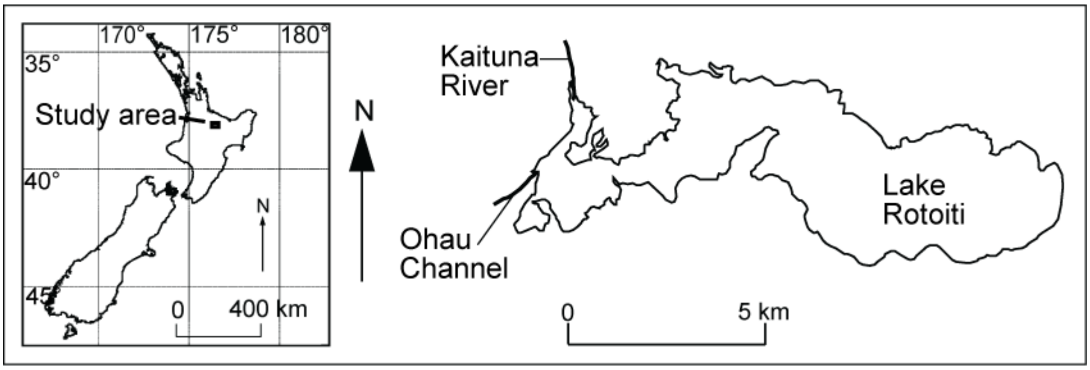

Fig. 6.1. Study area showing Lake Rotoiti and its main inlet (Ohau Channel) and outlet (Kaituna River).

Table 6.1. Physical characteristics of Lake Rotoiti, central North Island, New Zealand. Total nitrogen, total phosphorus and chlorophyll *a* values are means of monthly measurements 2002–2010 (Scholes 2009, 2010).

Characteristic	Value and units
Mean depth	31 m
Maximum depth	124 m
Surface area	34 km^2
Catchment area	123.7 km^2
Total phosphorus	29.3 mg P m^{-3}
Total nitrogen	322.8 mg N m^{-3}
Chlorophyll *a*	10.1 mg m^{-3}

6.3.2 Abundance of rainbow trout

Abundance of stocked rainbow trout was computed by applying a constant mortality rate to the known number of trout stocked into the lake from the hatchery in different years and seasons. The instantaneous rate of total mortality (Z) was calculated by regressing the natural logarithm of catch numbers of stocked trout on October 1 each year (the opening day of the fishing season) with fish age. Age of trout was inferred from fin clips unique to the year and season of release. Numbers of trout caught in each cohort and age-class were standardised to account for changes in the number of trout released by dividing the number of trout caught by the number of trout released in the cohort (Miranda & Bettoli 2007). Standardised catches of each age-class were averaged over 1995–2008 to find a mean total mortality rate for this period. Trout were considered fully recruited to the fishery at an age of 2 years.

To estimate the total population size of stocked rainbow trout, the calculated mortality rate Z was applied on a daily time step to each cohort of trout released into the lake. Trout were assumed to experience a constant rate of mortality from the time they were released into the lake. Mortality rates calculated from trout aged 2–5 years were extrapolated to trout aged 1–2 years, because no data were available on the mortality rates experienced by trout in their first year in the lake, and we were unable to find values in the literature for similar systems (i.e. landlocked populations of stocked trout that do not experience overwintering mortality and have no piscivorous predators). Trout aged 1–2 years may experience mortality as they encounter new conditions in the lake; but fishing mortality in this age class should be very low, as they are below the legal size limit for angling. Predation is relatively unlikely, as a lack of access to the sea means that only a few fish species are found in Lake Rotoiti; aside from small numbers of brown trout *Salmo trutta*, rainbow trout are the only likely predators of stocked rainbow trout. A recent diet study found no evidence of predation on stocked trout by larger rainbow trout (Chapter 4). Piscivorous birds (shags; *Phalacrocorax* spp.) are probably not significant predators of rainbow trout, as shags in nearby lakes Rotorua and Rotoehu prey mainly upon goldfish *Carassius auratus*, smelt *Retropinna retropinna*, common bully *Gobiomorphus cotidianus*, and koura (freshwater crayfish *Paranephrops planifrons*) (Potts 1972, 1977). Due to uncertainty in our mortality estimate, to check the validity of observed relationships, we calculated population size under five different scenarios: (1) mortality is constant over the entire life span ($Z = 1.2846$), (2) due to increased mortality of small, naïve fish, survival in the first year of lake residence is 50% lower than years 2–5 ($Z = 1.9778$), (3) first-year survival is 25% that observed in years 2–5 ($Z = 2.6709$), (4) due to initial mortality upon stocking, 50% mortality upon release into the lake, then constant mortality thereafter ($Z = 1.2846$), (5) 25% mortality upon release into the lake, then constant mortality thereafter ($Z = 1.2846$).

The size of the stocked trout population was calculated at the end of each calendar year by summing the abundances of all cohorts present at that time. The ratio of wild to stocked trout in the recreational catch was monitored on October 1 each year; i.e. the opening day of the fishing season and the recreational catch is intensively surveyed. Angler return rates of trout released in spring and autumn were monitored by tagging a subsample of 500 fish in each release with coded T-bar tags; anglers were encouraged to report data from these fish through a reward scheme. Mean tag return rates and lengths and masses of trout at various ages were compared between spring- and autumn-released trout between 1998 and 2008 with paired *t*-tests.

6.3.3 Bioenergetics modelling

We used the Wisconsin bioenergetics model (Hanson et al. 1997) to estimate prey consumption by stocked rainbow trout in Lake Rotoiti from 1993 to 2009. The model estimates consumption of individual fish based on the following mass-balance equation:

$$C = (R + A + S) + (F + U) + (\Delta B + G) \tag{6.1}$$

where C is consumption, R is respiration, A is active metabolism, S is specific dynamic action, F is egestion, U is excretion, ΔB is somatic growth and G is gonad production. Because the model is balanced, it can be used to find the amount of consumption required to produce the observed amount of growth. The model estimated metabolic costs based on mass and temperature dependent functions; model structure is described by Hanson et al. (1997). Required inputs included trout temperature experience, diet, growth, predator and prey energy density, and physiological parameters related to respiration, consumption, egestion, and excretion. Model inputs and outputs are summarised in Fig. 6.2 and Table 6.2. Physiological parameters for rainbow trout collated by Rand et al. (1993) were used in model simulations (See Appendix 6.1). Consumption and metabolism parameters were measured in anadromous rainbow trout in lakes Michigan and Ontario, while egestion, excretion and swimming speed parameters were measured in other salmonids including brown trout *Salmo trutta*, lake trout *Salvelinus namaycush*, sockeye salmon *Oncorhynchus nerka*, and coho salmon *O. kisutch* (Rand et al. 1993 and references therein). Predator energy density was modelled as a linear function of predator mass (Stewart & Ibarra 1991). Other inputs were measured during this study and are described below.

Trout growth simulations began at the time trout were released into the lake. Note that trout released in spring were 4 months older at the time of release than trout released in autumn; therefore, simulations were run for ages 1.25–2.25, 2.25–3.25 and 3.25–5.25 years for spring-released trout. These age classes are referred to in the text as 1–2, 2–3, and 3–5 years hereafter. Simulations of autumn released fish began on May 1 and ended on April 30, and simulations of spring released fish began on September 1 and ended on August 31. The model was run for an individual "average" fish in each cohort and age-class. Each cohort released into the lake was modelled separately based on relevant growth data. Model runs for trout aged 1–2 years and 2–3 years ran for one year, and model runs for trout aged 3–5 years ran for two years and included spawning on July 15 of the third year (day 75 for fish released in autumn, day 317 for fish released in spring). This simulation was run over two years to allow time in the model for trout to regain condition after spawning.

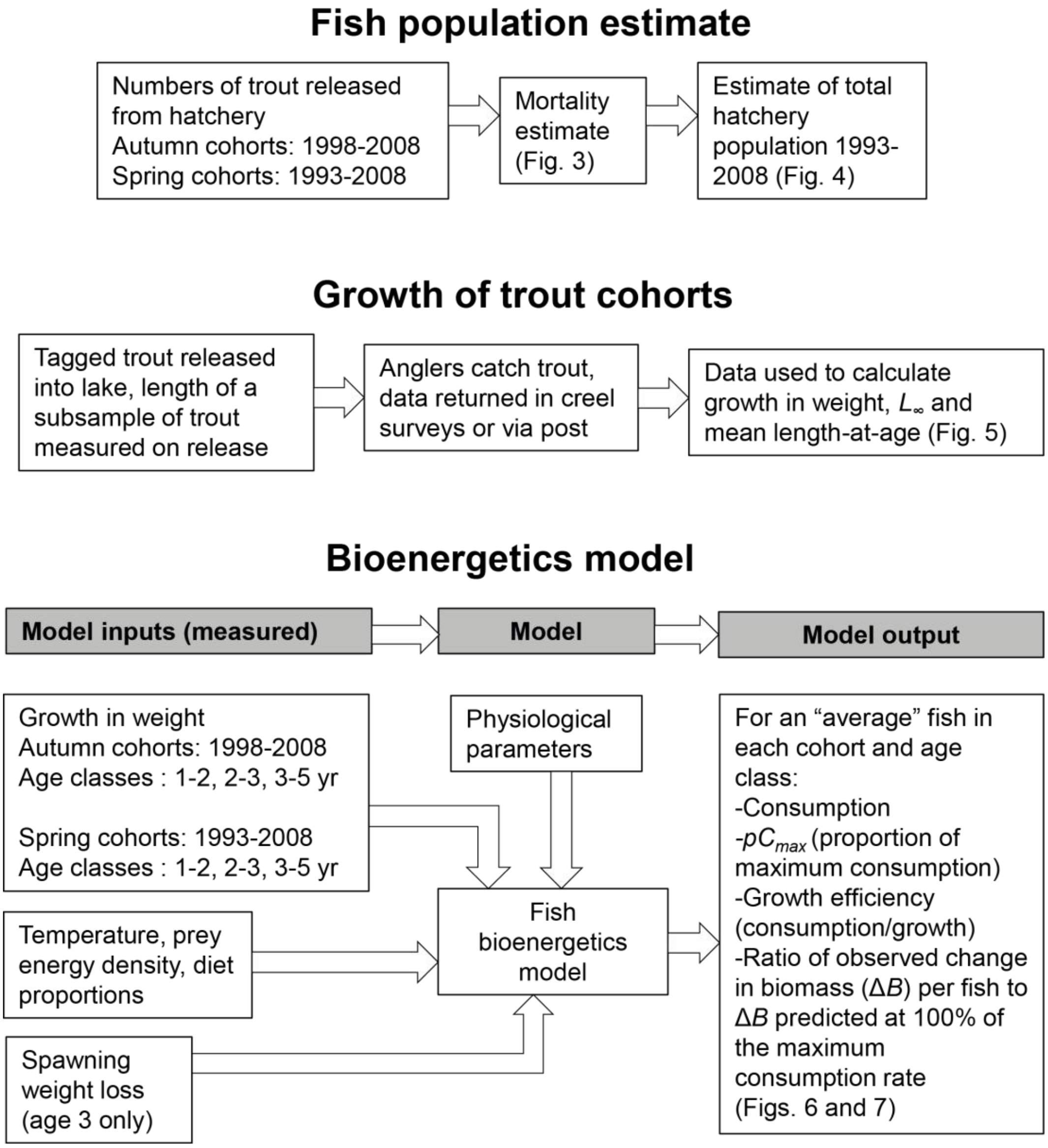

Fig. 6.2. Schematic of data analysed, including bioenergetics model inputs and outputs. See Table 6.2 for further details.

Table 6.2. Summary of bioenergetics model inputs, model outputs, trout population characteristics, and other data used in this study.

Type of data	Variable or parameter (units)	Source
Model inputs	Physiological parameters related to respiration, consumption, egestion, and excretion (see Appendix 6.1)	Rand et al. (1993)
	Temperature experience (°C)	Estimated in this study with thermal preferences of rainbow trout (M. Dedual, pers. comm.) and lake temperature profiles (P. Scholes, pers. comm.)
	Proportions of prey types in diet	Measured in this study
	Prey energy density ($J\ g^{-1}$ wet mass)	Measured in this study
	Predator energy density ($J\ g^{-1}$ wet mass)	Modelled as a function of predator mass (Stewart and Ibarra 1991)
	Growth of rainbow trout (g)	Measured in this study with tag return data from stocked rainbow trout 1993–2009
	Spawning mass loss (% body mass)	Estimated with masses of trout entering and exiting Ngongotaha Stream during peak spawning runs 1959–1962
Model outputs	Prey consumption by trout (g)	Estimated by model
	pC_{max} (proportion of theoretical maximum ration consumed by an individual fish)	Estimated by model
	Growth efficiency	Mass gained per day ($g\ day^{-1}$) divided by food consumed per day ($g\ day^{-1}$)
	% maximum growth	Observed growth as a percentage of predicted growth at maximum rations (where growth is the added biomass that is available for growth and reproduction once metabolic costs have been accounted for)
Rainbow trout population characteristics	Instantaneous rate of total mortality (Z)	Estimated with local rainbow trout catch rates
	Hatchery release numbers	Obtained from fishery managers
	Wild population catch ratio	Ratio of wild to stocked rainbow trout in recreational catch
Prey population characteristics	Adult smelt abundance (fish m^{-2})	Measured in September 2000 and 2005–2009 by hydroacoustics (Rowe et al. 2011)

Model outputs were produced on a daily time step and included the following. The proportion of theoretical maximum daily ration (pC_{max}) required for an "average" fish to produce the observed growth was calculated to give a relative indication of consumption rate between years. In the model, consumption is calculated using the following formula:

$$C = C_{\max} \times pC_{\max} \times f(T) \tag{6.2}$$

where C is consumption, C_{max} is the maximum possible consumption rate for a given species at its optimal temperature, pC_{max} is a proportionality constant that allows for the effects of ecological factors on consumption, and $f(T)$ is a temperature dependence function. pC_{max} is calculated by calibrating the model to observed growth. Values of pC_{max} range from 0 to 1; 0 indicates that no feeding is taking place, and 1 indicates that the fish is feeding at its maximum rate for a particular body size and water temperature (Hanson et al. 1997). The pC_{max} value can be used as an indicator of the degree of food availability (Railsback & Rose 1999).

We also calculated the amount of prey (g) consumed per day ("daily individual prey consumption") to produce the observed growth, trout mass (g), daily mass increment (the amount of mass gained; g), and masses of individual prey types consumed (g). Growth efficiency was calculated by dividing the daily mass increment by the daily total mass of prey consumed (i.e. the proportion of prey consumed that was converted to trout body mass). Finally, to indicate growth limitation in a way that was standardised for temperature, we calculated the % maximum growth, or the observed growth as a percentage of maximum growth predicted at maximum rations, where growth is the observed change in biomass at a given temperature regime (i.e. net production, or the biomass that is available for growth and reproduction once metabolic costs have been accounted for), and the maximum growth is the change in biomass predicted (at that same temperature regime) when fish are fed at 100% of their maximum ration (Hanson et al. 1997). This measure accounts for temperature-dependent effects, allowing the examination of the effects of density dependence without the confounding influence of temperature.

To facilitate comparison of model outputs between cohorts, we calculated yearly means of model outputs produced on a daily time step for each age-class (1–2 years, 2–3 years, and 3–5 years) in each cohort released into the lake. These means were treated as independent data points, and were used to calculate standard error of the overall mean values. ANOVA was used to compare mean pC_{max} and growth efficiency of different age-classes of trout released in spring and autumn; season and age classes were treated as categorical factors and Tukey's honestly significant difference (HSD) was used to test pairwise differences between groups. To test for density-dependent effects on growth in the first year of lake residence, we calculated Pearson correlation coefficients (r) and coefficients of determination (r^2) between the number of trout released and three indicators of trout growth and consumption of trout aged 1–2 years: (1) mean daily prey consumption per individual trout (g day^{-1}), (2) pC_{max}, and (3) % maximum growth.

Estimates of population consumption are highly dependent on the accuracy of mortality and abundance estimates (Rand et al. 1993) and on the accuracy of model parameters. Using bioenergetics models in a comparative way to test hypotheses, rather than in a quantitative way to make predictions, ameliorates the impact of uncertainty in model parameters on results (Chipps and Wahl 2008). Because several of our model parameters were measured in other populations or species, we have not attempted to estimate the absolute amount of prey consumed by the rainbow trout population, and our modelled consumption estimates are intended as relative comparisons only.

6.3.4 Model inputs

We used data collected from recaptured stocked rainbow trout to calculate growth rates between 1993 and 2009 for spring releases, and between 1998 and 2009 for autumn releases. Over this period, 500 fish from each seasonal liberation were tagged with batch-coded T-bar anchor tags inserted at the base of the dorsal fin, and anglers were encouraged to report details of recaptured tagged fish through a reward scheme. The fork length of a subsample of fish (mean $n = 80$) was measured to the nearest 10 mm prior to release. Age was estimated by adding the approximate age upon release (1.0 year old for autumn releases and 1.25 years old for spring releases) to the time spent in the lake, which was calculated using the date of release and date of capture.

To characterise growth, the von Bertalanffy growth model was fitted to length-at-age data from rainbow trout released from the hatchery in different years and seasons:

$$L_t = L_\infty[1 - e^{-K(t-t_0)}] \tag{6.3}$$

where L_t is fork length at time t, L_∞ is theoretical maximum length (mm), and K (yr^{-1}) and t_0 (years) are parameters. Least-squares regression was used to fit the model to the data. Growth in length was converted to growth in mass with the length-mass regression: $\log_{10}(W) = -7.01 + 2.68 \log_{10}(L)$, where W is mass in grams and L is fork length in mm ($r^2 = 0.84$; $n = 2019$, $P < 0.001$). The coefficients were computed by least-squares regression of length and mass data obtained from Lake Rotoiti rainbow trout at fishing competitions, where fork length was measured to the nearest 5 mm and mass was measured to the nearest 10 g. The calculated growth parameters are defined only after the fish are released, when fish are growing in the lake under natural conditions. Body condition was assumed to be approximately equal among cohorts. Student's *t*-tests were used to compare growth parameters of trout released in autumn and spring. All statistical analyses were carried out in Statistica, version 9 (Statsoft, Tulsa, USA).

Relative percentages of prey items by mass in the diet of rainbow trout were determined by stomach contents analysis of stocked and wild fish. One hundred and thirty rainbow trout >150 mm long were caught by angling, beach-seining and boat electrofishing from a range of locations in the lake between March 2009 and December 2010. Fifty-nine trout were of wild origin and 71 trout had been stocked into the lake, determined by the presence of adipose and pectoral fin clips in stocked trout. All items from the mouth, oesophagus and stomach were removed, counted and identified, and the total mass of each prey type was recorded. The relative contribution of each prey type to the diet was found by calculating the relative proportion by mass of each prey species in individual trout stomachs, and averaging these values across all nonempty stomachs. The differences in proportions of prey items in stomachs of stocked and wild fish were tested using a Kruskal-Wallis test. Proportions of each prey item making up more than 1% of the total diet were used in the bioenergetics model. Because diet varied significantly with time of year but not with trout size (Chapter 4), a single diet scenario was used in all model simulations; i.e. we assumed that diet varied slightly with season but did not change with age. Dietary proportions enumerated in 2009–2010 were assumed to be representative of the time period in which trout growth was measured (1993–2008), i.e. trout diet was assumed to be unchanged during this time. The measured dietary proportions were defined as the baseline scenario, and a sensitivity analysis was carried out to assess the effects of variation in dietary proportions on modelled consumption estimates (see below).

To estimate the energy density of prey items, smelt, common bully, koaro (*Galaxias brevipinnis*), and koura were caught from Lake Rotoiti with a beach-seine and electrofishing boat between January 2010 and November 2010. The energy density of prey items was measured with a Parr Model 1341 Plain Oxygen Bomb Calorimeter and a Parr 1108 Oxygen Bomb using standard methods (Parr Instrument Company 2008; Chapter 4). For bioenergetics modelling, 3% of the fish mass and 15% of the koura mass consumed was assumed to be indigestible (Vigliano et al. 2009). Prey energy density enumerated in 2009–2010 was assumed to be representative of the time period in which trout growth was measured (1993–2008). The effects of changes in prey energy density on model outputs were tested by means of a sensitivity analysis that compared the baseline scenario (measured values) to different energy density scenarios.

The temperature experienced by rainbow trout was estimated by assuming that trout would occupy water at 15°C if it was available (Table 3, Scenario 1). Rainbow trout in Lake Taupo, a deep oligotrophic lake near Lake Rotoiti, have been shown to prefer water at 14.5–15°C (M. Dedual, Department of Conservation, personal communication[5]). The availability of suitable thermal habitat in Lake Rotoiti was assessed with lake temperature profiles that were measured monthly with a SBE 19 plus profiler (Seabird Electronics, Bellevue, Washington, USA) at 1 or 2 m intervals as part of a lake monitoring programme (P. Scholes, pers. comm.). The lake was fully mixed each year between June and October, and water temperature was <15°C, so the mean monthly temperature in the uppermost 10 m of the water column was used over this period in model simulations. Again, we assumed that temperature conditions did not change between years, and temperature measurements confirmed this assumption. Monthly measurements of water temperatures at given depths did not vary significantly between years; 95% confidence limits calculated from temperature records for each month and depth stratum fell within 1.1°C of their respective means (P. Scholes & J. Blair, unpubl. data). A sensitivity analysis was carried out

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[5] Results of an unpublished study that monitored the horizontal and vertical movements and body temperature of rainbow trout in Lake Taupo using acoustic telemetry. Trout usually swam in the uppermost 20 m of the water column at all times of year, and spent most of their time in water between 14.5 and 15°C.

to assess the effects of variation in thermal experience compared to the baseline scenario.

Table 6.3. Temperature scenarios used in bioenergetics modelling of Lake Rotoiti rainbow trout. Scenarios inferred from observations of preferred temperature of rainbow trout (M. Dedual, pers. comm.) and monthly temperature and dissolved oxygen (DO) profiles (P. Scholes, pers. comm.). Trout were released in spring (September) and autumn (May); models ran for 1 year from September 1 and May 1, respectively.

	Temperature scenarios (°C)		
Month	(1) Preference	(2) DO limiting	(3) 15°C
January	15	15	15
February	15	17.8	15
March	15	17.3	15
April	15	15.8	15
May	15	15	15
June	12.8	12.8	15
July	11.2	11.2	15
August	10.8	10.8	15
September	11.5	11.5	15
October	12.6	12.6	15
November	15	15	15
December	15	15	15

The mean mass lost during spawning of rainbow trout was calculated from data collected from a trap in Ngongotaha Stream, a principal spawning tributary of neighbouring Lake Rotorua. Between 1959 and 1962, every fish passing through the trap was weighed, measured, sexed and the direction of movement noted (Mill 2000). Peaks in upstream rainbow trout migrations occurred between June and October, and peaks in downstream migrations occurred between August and December (Appendix 6.2). Fish masses were compared between the upstream and downstream movement peaks to find the mean total mass lost during spawning. Mass-length relationships ($\log_{10}(W) = a + b(\log_{10}(L))$, where W is mass in grams and L is fork length in mm) were derived for trout moving through the trap during the peak movement period in each year and direction. These were used to calculate the mass corresponding to the mean length of trout moving through the trap during peak runs (480 mm) in each year and direction. The total mass lost due to spawning (gonad + somatic) was estimated by subtracting the downstream mass from the upstream mass for each year, and calculating the mean of all years. This method was used to reduce bias associated with differences in length between upstream- and downstream-moving fish, as records for individual fish were not available. The mean estimated mass loss for males and females combined was 366 g, or 24% (Appendix 6.2). This is within the range of spawning mass loss reported by Fish et al. (1968) who estimated that rainbow trout in New Zealand lakes lost 22–40% of their total body mass during spawning. In model simulations, trout spawned 24% of their body mass at age 3 on July 15; this date was chosen because the spawning season of rainbow trout in New Zealand typically occurs May-August (McDowall 1990).

6.3.5 Sensitivity analysis

To assess the effects of variation in model inputs, we carried out a sensitivity analysis of modelled consumption estimates by sequentially changing individual parameters in the model. Using the mean growth rates of autumn and spring cohorts and the baseline scenario described above, we re-ran the bioenergetics model for trout aged 1–2, 2–3 and 3–5 years, varying one parameter at a time. The sensitivity of physiological parameters in similar bioenergetics models have already been assessed for lake trout *Salvelinus namaycush* and sockeye salmon *Oncorhynchus nerka* (Stewart et al. 1983; Beauchamp, Stewart & Thomas 1989), so we evaluated the sensitivity of model outputs to changes in temperature, prey energy density, and diet proportions. The model inputs used to estimate trout consumption 1993–2009 (outlined above) were defined as the baseline scenario. The sensitivity of model inputs was indicated by the percentage difference in modelled prey consumption by individual rainbow trout between the adjusted simulations and the baseline simulation, such that a positive value indicated that the test scenario resulted in a higher modelled consumption rate than the baseline scenario.

Two alternative temperature scenarios were tested in the sensitivity analysis. Since Lake Rotoiti experiences low hypolimnetic dissolved oxygen (DO) concentrations in summer, we created Temperature Scenario 2 to allow for the effects of low measured DO concentrations on the vertical distribution of rainbow trout. We examined monthly DO profiles collected at the same time as the temperature data and noted the depth at which DO typically fell below 6 mg L^{-1} in each month—a threshold of suitable habitat for salmonids (Davis 1975). We then altered Scenario 1, assuming that trout would occupy the lowest temperature possible, provided DO concentrations were above 6 mg L^{-1}. We chose to use this conservative value even though rainbow trout may tolerate lower oxygen concentrations (Matthews & Berg 1997), because trout have been observed to avoid mild levels of hypoxia when given a choice between hypoxic (80% air saturation) and fully oxygenated water (Poulsen et al. 2011), and such a case allowed us to simulate the “worst case scenario”. We also tested a temperature scenario where trout body temperature was constant at 15°C. Three prey energy density scenarios were tested: (1) the energy density of all prey items was decreased by 10%; (2) prey energy density was constant during the year and equal to the mean measured values, and (3) the energy density of all prey items was increased by 10%. The proportion of smelt in the diet was also manipulated, creating three diet scenarios. The following diet scenarios were tested: (1) the proportion of smelt was decreased by 10% to 77%; (2) the proportion of smelt remained constant at 84%; and (3) the proportion of smelt was increased by 10% to 94%. Finally, to determine the consequences of ontogenetic diet changes that have been observed in rainbow trout, we tested a scenario where trout switched to a diet of 30% koura at age 3 years; large trout consume more koura than small trout in Lake Taupo (Cryer 1991) and to some extent in Lake Rotoiti (Chapter 4)

6.3.6 Abundance of smelt

The abundance of adult smelt was measured in September 2000 and yearly in September 2005–2009 with a SIMRAD EK60 echo sounder operating at 120 Hz (Rowe et al. 2011). Twelve transects were sampled running north-south across the lake. Smelt were enumerated using echo integration. The total amount of acoustic backscatter was determined for each transect, and was divided by the mean acoustic backscatter produced by a single adult smelt to provide an estimate of smelt abundance for each transect (Rowe et al. 2011). This method enumerated adult smelt (target strength -55 dB to -45 dB), but not juvenile smelt, as juvenile smelt inhabit surface waters that are not amenable to acoustic sampling, and signals from juvenile smelt could not be distinguished from other small fish and invertebrates. Acoustic sampling methods and results were described in detail by Rowe et al. (2011). In the present study, we assessed the relationship between the mean density of adult smelt across all transects and trout consumption with Pearson’s correlation coefficient (r) and the coefficient of determination (r^2). For this comparison, we calculated the mean daily prey consumption in the year (July-

June) containing the smelt abundance measurement (September) for each separate age class of trout (1–2 2–3 and 3–5 years) present in the lake during that year.

6.4 Results

6.4.1 Trout population

Rainbow trout stocked into Lake Rotoiti experienced a yearly instantaneous rate of total mortality (*Z*) of 1.29 (r^2 = 0.81, 4 year-classes, mortality (*A*) = 27.5%; Fig. 6.3), and the coefficient of determination (r^2) of this relationship indicated that 81% of the variation in mortality was explained by fish age. Between 1993 and 1998, trout were stocked into Lake Rotoiti in spring (September), and from 1998 to 2009, trout were released in both spring and autumn (May). Hatchery releases in Lake Rotoiti were increased from 14,500 per year in 1998 and 1999 to 27,000 in 2000, and remained high except for 2004 and 2005, when 15,000 and 23,000 trout were released (Fig. 6.4a). The population of stocked trout increased dramatically in 2000 following the addition of an autumn trout release in 1998 that increased total stocking rates (Fig. 6.4a and b). The ratio of wild to stocked rainbow trout in the recreational catch declined over the study period coincident with increases in the stocked population (Fig. 6.4a). The mean tag return rate was 6.58% ± 0.95% SE for trout released in spring, and 6.35% ± 0.89% SE for trout released in autumn. These return rates were not significantly different (Student's *t*-test; *t* = 0.181, *n* = 11, *P* = 0.858).

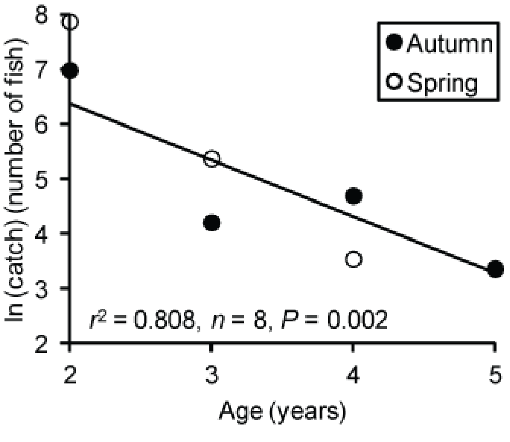

Fig. 6.3. Natural logarithm of mean catch-at-age of stocked rainbow trout released in autumn and spring into Lake Rotoiti 1995–2008. *Z* (instantaneous rate of total mortality) is the slope of the regression line. Numbers of trout caught were standardised to account for changes in the number of trout released in each cohort.

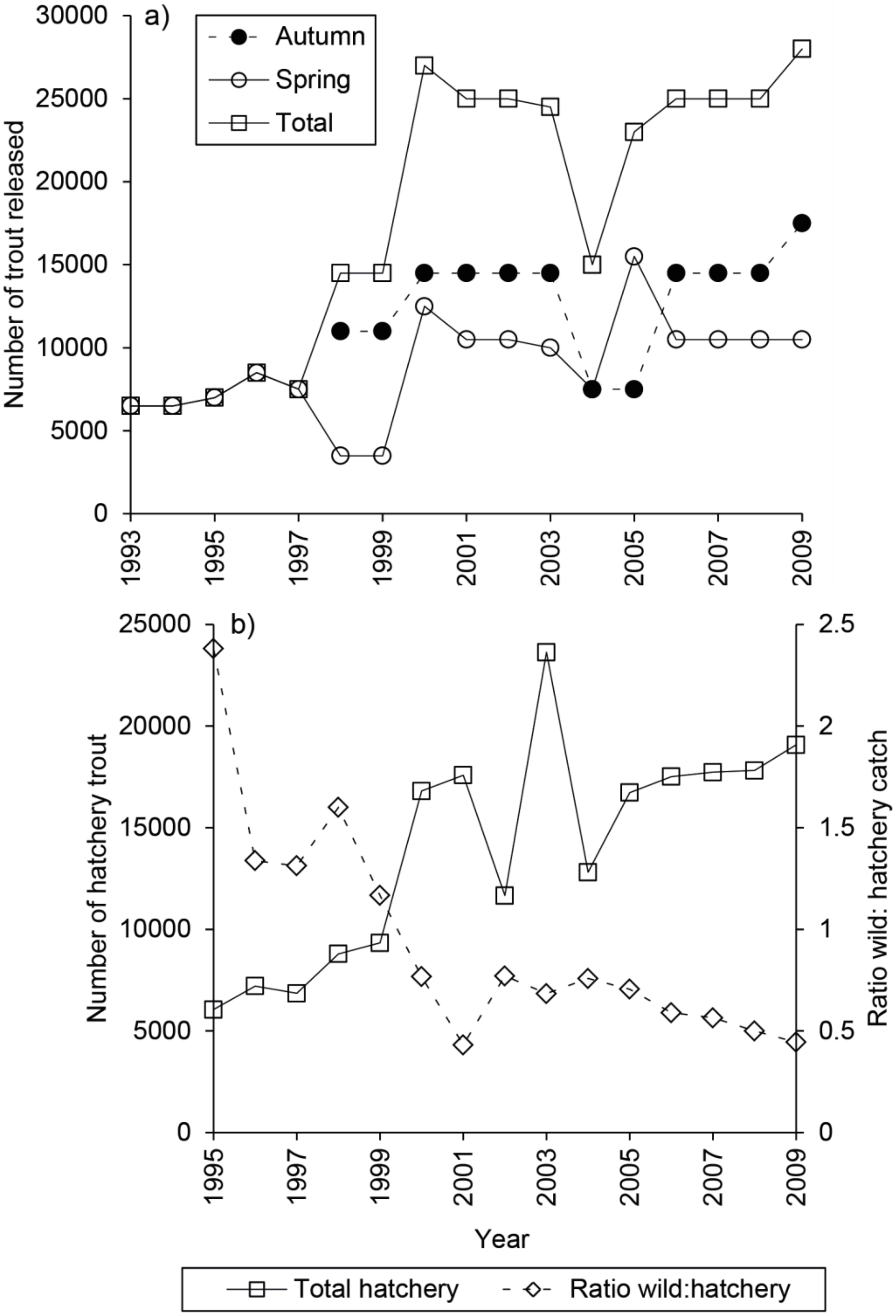

Fig. 6.4. Population parameters of rainbow trout, Lake Rotoiti 1993–2009: (a) number of trout stocked from hatchery; (b) total stocked trout population size 1995–2009, estimated at end of each year with a population model incorporating hatchery release numbers and mortality estimates.

6.4.2 Model inputs

In years when rainbow trout were released in both autumn and spring, trout released in spring had higher mean lengths at release than trout released in autumn (Fig. 6.5a; paired *t*-test; $t = -4.856$, $P < 0.001$), but the effect of release season on length was no longer present at age 3 (Fig. 6.5b; $t = 1.698$, $P = 0.118$). Trout released in spring were heavier than those released in autumn at age 1 and 2 years, but not at age 3 or 5 years (Table 6.4; age 1: $t = -3.146$, $P = 0.009$, age 2: $t = -3.278$, $P = 0.007$; age 3: $t = 1.264$, $P = 0.232$; age 5: $t = 0.500$, $P = 0.627$). Characteristics of all modelled cohorts are given in Appendix 6.3.

Table 6.4. Mean values (± 1 SE) of length, mass, and body mass lost at spawning for stocked rainbow trout released in spring and autumn in Lake Rotoiti. Spring release: 1993–2009; autumn release: 1998–2009. Calculations for body mass lost at spawning are given in Appendix 2.

Age range (years)	Initial length (mm)	Final length (mm)	Initial mass (g)	Final mass (g)	Body mass lost at spawning (%)
Spring release					
1.25–2.25	200 ± 6	520 ± 5	140 ± 11	1860 ± 46	0
2.25–3.25	520 ± 5	610 ± 6	1860 ± 46	2820 ± 74	0
3.25–5.25	610 ± 6	650 ± 9	2820 ± 74	3200 ± 256	24
Autumn release					
1.0–2.0	160 ± 5	490 ± 6	90 ± 7	1600 ± 59	0
2.0–3.0	490 ± 6	610 ± 7	1600 ± 59	2870 ± 94	0
3.0–5.0	610 ± 7	690 ± 21	2870 ± 94	3690 ± 222	24

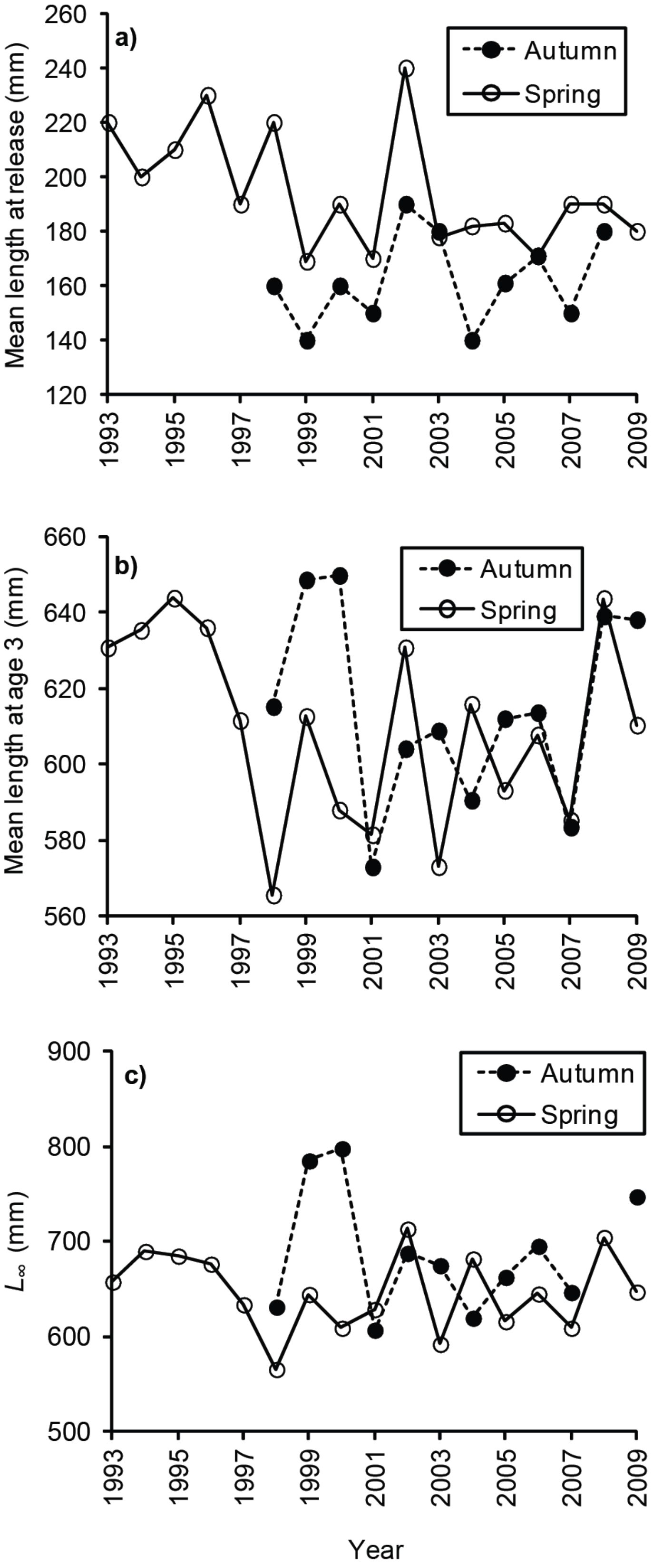

Fig. 6.5. Length and growth characteristics of stocked rainbow trout in Lake Rotoiti: (a) length at release; (b) mean length at 3 years old; (c) L_∞ parameter from von Bertalanffy growth equation. All von Bertalanffy growth equation parameters are given in Appendix 6.3.

Smelt accounted for the highest proportion of the diet of rainbow trout (Table 6.5). Seasonal means were used to characterise diet in the model because koaro were consumed by trout >150 mm only in autumn and winter (Table 6.5, Chapter 4). No difference was found between the mean mass percentages of any prey type in the diets of stocked trout compared with wild trout (smelt: Student's *t*-test; $t = -0.819$, $P = 0.415$; koaro: $t = 0.135$, $P = 0.893$; koura: $t = 1.028$, $P = 0.306$; common bully: $t = -0.441$, $P = 0.660$). Because energy density of smelt varied between seasons (Chapter 4), seasonal values of energy density were used in model simulations (Table 6.6).

Table 6.5. Diet of stocked and wild rainbow trout > 150 mm, by season (mean stomach content proportions by wet mass ± 1 SE). Prey items include common smelt (*Retropinna retropinna*), koura (*Paranephrops planifrons*), koaro (*Galaxias brevipinnis*) and common bully (*Gobiomorphus cotidianus*).

Origin	Season	Number of trout	Percentage of prey in stomach			
			Smelt	Koaro	Koura	Common bully
Stocked	Spring	11	80.6 ± 8.6	0.0 ± 0.0	16.0 ± 7.0	3.4 ± 2.2
	Summer	27	84.9 ± 13.3	0.0 ± 0.0	8.7 ± 8.0	6.4 ± 6.0
	Autumn	23	80.9 ± 7.2	6.2 ± 4.3	8.7 ± 5.5	4.2 ± 3.5
	Winter	10	80.0 ± 13.3	10.0 ± 10.0	0.0 ± 0.0	10.0 ± 10.0
Wild	Spring	16	92.0 ± 3.7	0.0 ± 0.0	4.3 ± 2.4	3.7 ± 3.0
	Summer	15	95.5 ± 10.4	0.0 ± 0.0	0.0 ± 0.0	4.5 ± 3.7
	Autumn	24	73.4 ± 10.4	7.6 ± 4.5	6.7 ± 6.0	12.3 ± 8.1
	Winter	4	100.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Stocked and Wild	Spring	27	87.6 ± 8.2	0.0 ± 0.0	8.8 ± 4.1	3.6 ± 3.5
	Summer	42	88.7 ± 6.0	0.0 ± 3.0	5.6 ± 4.0	5.7 ± 4.0
	Autumn	47	77.1 ± 4.4	6.9 ± 0.0	7.6 ± 3.4	8.3 ± 1.9
	Winter	14	85.7 ± 9.7	7.1 ± 1.3	0.0 ± 0.0	7.1 ± 7.1
Overall Mean		130	84.8 ± 3.3	3.5 ± 1.3	5.5 ± 2.0	6.2 ± 1.9

Table 6.6. Energy density of prey items of rainbow trout (mean ± 1 SE): common smelt (*Retropinna retropinna*), koura (*Paranephrops planifrons*), koaro (*Galaxias brevipinnis*) and common bully (*Gobiomorphus cotidianus*) used in bioenergetics modelling.

	Energy density (J g^{-1} wet mass)			
	Smelt	Koaro	Koura	Common bully
Spring	2604.9 ± 54.8			
Summer	2773.0 ± 14.3		2567.4 ± 14.0	
Autumn	2956.7 ± 44.8	3232.6 ± 403.3		3191.4 ± 151.1
Winter	2088.8 ± 187.2	2973.5 ± 0		3248.3 ± 0

6.4.3 Model outputs

The proportion of the theoretical maximum daily ration (pC_{max}) consumed by rainbow trout was highest in their first year of growth in the lake; values ranged from 0.79–0.98 for trout aged 1–2 years (Fig. 6.5a). Values of pC_{max} ranged from 0.58–0.82 for trout aged 2–3 years, and from 0.61–0.81 for trout aged 3–5 years. Mean pC_{max} values were not significantly different for any age class between release seasons (Fig. 6.5a). Trout 2–3 years old that had been released in autumn had higher growth efficiencies (growth per amount of food consumed) than those that had been released in spring (Fig. 6.5b). Trout aged 1–2 and 3–5 that had been released in autumn also showed higher growth efficiencies than those released in spring, but these differences were not statistically significant.

All three indicators of trout growth and consumption in the first year of lake residence were negatively correlated with estimated trout population size (Fig. 6.7). For trout released in spring 1993–2009, modelled mean daily prey consumption during the first year of lake residence showed a general decreasing trend over time, but fluctuated between 41.9 and 63.5 g d^{-1} (Fig. 6.7a). Trout released in autumn consumed between 35.3 and 56.1 g d^{-1}. Prey consumption of trout was negatively correlated with estimated trout population size for trout released in spring (Fig. 6.7b) but not in autumn (Fig. 6.7c). First-year pC_{max} values and % maximum growth showed similar trends over time (Fig. 6.7d and g). Both pC_{max} and % maximum growth declined significantly with increases in the stocked trout population; however, only 29.8 to 48.2% of the variation in these variables could be explained by stocked trout population numbers (Figs. 6.7e, f, h, i).

For mortality scenario 1 (constant mortality), trout population size on January 1 ranged from 6478–30470 during the study period. Population ranges for the alternative mortality scenarios are as follows: Scenario 2 (survival = 50% of original estimate): 6465–23910, Scenario 3 (survival = 25% of original estimate): 6453–20991, Scenario 4 (50% mortality upon release): 3239–15135, Scenario 5 (25% mortality upon release): 2859–22702 (data not shown). Despite these differences in absolute population estimates, the patterns between trout population size and consumption parameters did not change substantially among scenarios; all variables tested showed a significant relationship with population size, in the same direction as the original population estimate. For the variables shown in Fig. 6.7, values of r^2 were also broadly similar among mortality scenarios, changing by a factor of 4.8–10.4% for spring releases, and 25.5–26.2% for autumn releases (data not shown).

Mean daily prey consumption by the three age-classes of rainbow trout was not significantly correlated with density of adult smelt (Fig. 6.8; age 1–2: $r^2 = 0.064$, $n = 6$, $P = 0.584$; age 2–3: $r^2 = 0.001$, $n = 6$, $P = 0.947$; age 3–5: $r^2 = 0.491$, $n = 6$, $P = 0.079$). The lack of correlation may relate to the fact that trout consume a wide size range of smelt, and smaller smelt are not enumerated by this method (Chapter 4).

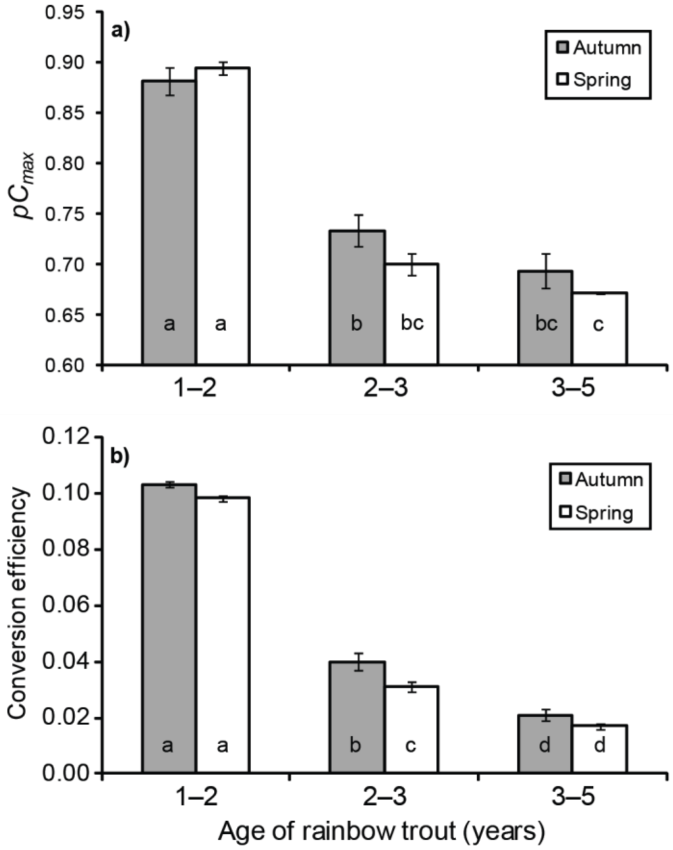

Fig. 6.6. Means (± 1 SE) of modelled (a) *pC_{max}* (proportion of theoretical maximum daily ration consumed by the "average" fish), and (b) growth efficiency (daily growth increment per mass of food consumed) by age class of rainbow trout released in autumn and spring 1998–2009 (mean ± 1 SE). Groups compared with ANOVA. Letters *a-d* denote results of Tukey's HSD tests and show homogeneous groups ($\alpha < 0.05$).

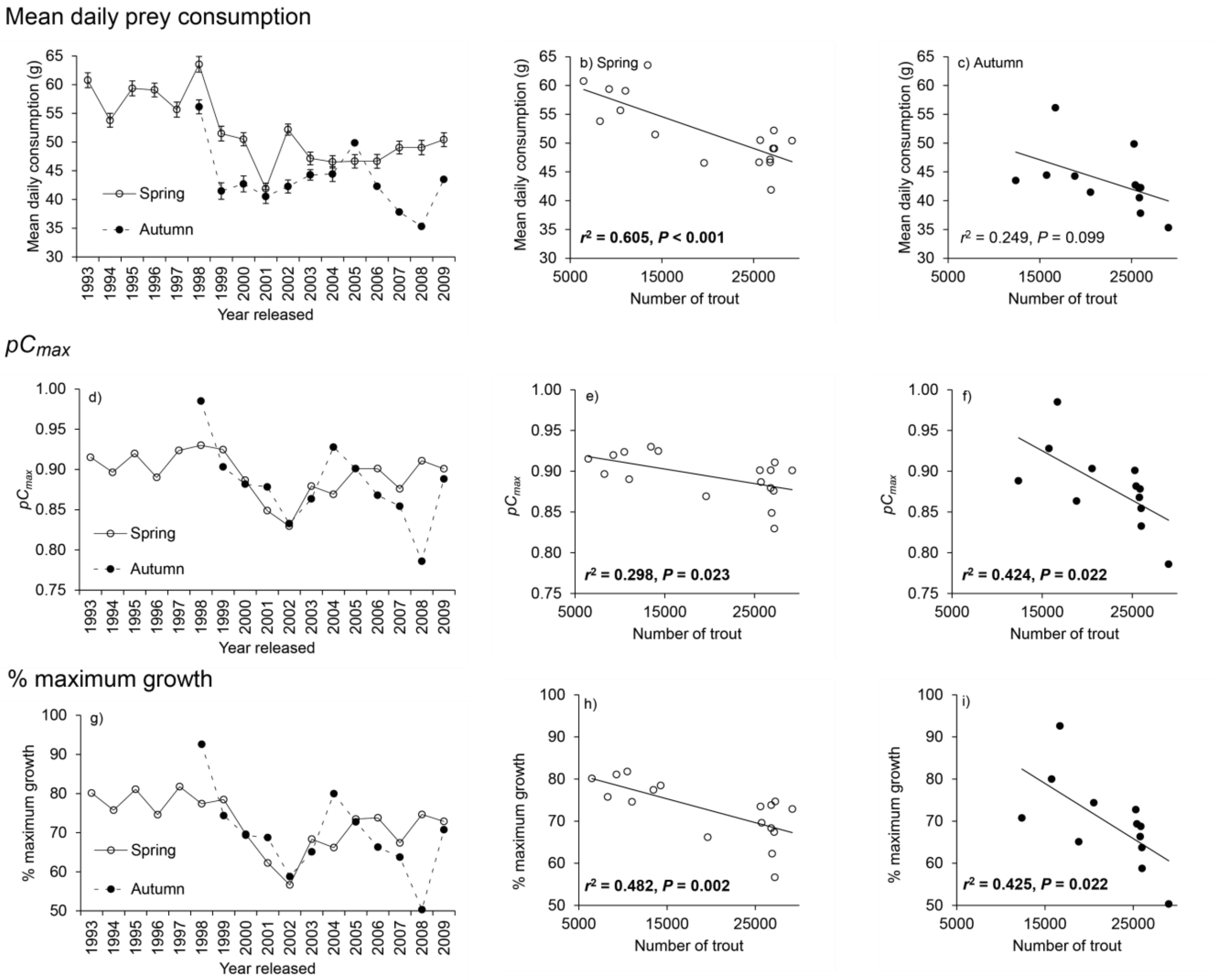

Fig. 6.7. Relationships between the number of stocked trout present in the lake and (a) observed growth as a percentage of the maximum growth possible at maximum rations, (b) mean daily prey consumption by an "average" rainbow trout during their first year in the lake (g day^{-1}), and (c) mean *pC$_{max}$* (proportion of theoretical maximum consumption rate) of an "average" rainbow trout during their first year in the lake. Each data point represents one cohort, i.e. fish released in spring and autumn of the same year (see Appendix 6.3).

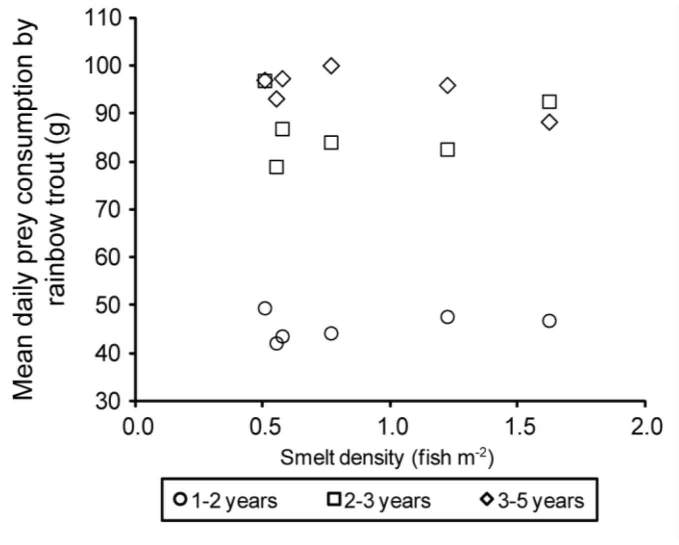

Fig. 6.8. Mean daily prey consumption by stocked rainbow trout aged 1–5 years (July-June), by age class, versus smelt density measured by echo sounding (September) in Lake Rotoiti 2000 and 2005–2009.

6.4.4 Sensitivity analysis

Modelled estimates of consumption displayed much higher sensitivity to changes in temperature and prey energy density than to changes in dietary proportions (Table 6.7). The sensitivity of consumption estimates to changes in input parameters varied according to the release season and cohort being modelled; model sensitivity was highest, on average, for trout aged 1–2 years (mean deviation from baseline scenario = 5.0%), followed by trout aged 2–3 years (4.4%) and trout aged 3–5 years (4.2%). For spring cohorts, changes in the temperature scenario had the greatest effect on modelled consumption estimates, though increasing prey energy density caused almost as great an effect. However, for autumn cohorts, changes in energy density caused, on average, greater shifts in modelled prey consumption than changes in temperature. Changing the energy density by 10% caused shifts of up to 15.7% in consumption estimates.

Table 6.7. Sensitivity analysis of input variables in bioenergetics model of rainbow trout. Results presented as the percentage change in mean individual daily consumption over the modelled period for an average individual in each age class, relative to the baseline scenario. Positive values indicate that consumption was higher in the test scenario than in the baseline scenario. Temperature scenarios are as in Table 6.3. Consumption was modelled based on mean observed growth 1993–2009 for trout released in spring and 1998–2009 for trout released in autumn. DO = dissolved oxygen, Temp = temperature, ED = energy density of prey. Mean deviation in model output = the mean of the three age classes.

Season released, test scenario	Deviation in modelled prey consumption relative to baseline scenario (%)			Mean deviation in model output (%)
	1–2 years	2–3 years	3–5 years	
Autumn releases				
Temp 2 (DO limiting)	9.7	11.1	11.7	10.9
Temp 3 (constant at 15°C)	3.7	8.2	10.5	7.7
Diet constant	–0.5	–0.4	1.8	0.3
Diet – 10% smelt	–0.7	–0.8	1.3	–0.1
Diet + 10% smelt	–0.4	0.0	2.3	0.7
Diet 30% koura			7.3	7.3
ED constant	4.6	1.7	3.1	3.2
ED – 10%	17.8	14.0	15.4	15.7
ED + 10%	–5.7	–8.1	–6.7	–6.9
Spring releases				
Temp 2 (DO limiting)	3.9	6.8	7.4	6.2
Temp 3 (constant at 15°C)	13.4	16.1	16.6	15.7
Diet constant	0.7	0.3	–4.4	–1.1
Diet – 10% smelt	–0.6	–0.7	–5.3	–2.2
Diet + 10% smelt	2.0	1.4	–3.4	0.0
Diet 30% koura			–0.4	–0.4
ED constant	–6.1	–4.2	–8.3	–6.2
ED – 10%	5.8	7.3	2.6	5.2
ED + 10%	–15.5	–13.4	–17.0	–15.3

6.5 Discussion

6.5.1 Stocking timing and size of stocked fish

Our results demonstrate that there was no effect of timing of rainbow trout liberations on returns to anglers (observed through tag return rate). Fish survival scales positively with body size (Post et al. 1999, Lorenzen 2000), meaning that we might expect higher survival rates, and thus greater returns to anglers, of larger, spring-released fish compared to smaller, autumn-released fish. However, we observed no difference in return rate between the two seasons. The reported tag return rate was ~6–7%, but approximately 40% of tagged fish caught by anglers are not reported (R. Pitkethley, pers. comm.), suggesting that the actual return rate of stocked fish to anglers was similar to that reported in colder Wyoming, USA lakes for trout stocked at <21 cm (8.4%; Wiley et al. 1993). This pattern contrasts with stocked fisheries in colder climates, where low temperatures over winter may cause high mortality of fish released from the hatchery in autumn (Strange & Kennedy 1979). For example, high overwintering mortality reduced the return rate to anglers of trout stocked into Wyoming lakes in autumn compared to those stocked in spring (Wiley et al. 1993), but another Wyoming study showed the opposite result (Yule et al. 2000), indicating that optimal strategies may differ between locations. Survival over winter is high in Lake Rotoiti, probably due to mild winter temperatures (approximately 10–14°C), which may cause differences in the optimal release strategy compared to colder climates.

The size of stocked fish can influence the success of stocking programmes. Smaller stocked fish are more vulnerable to predation than larger fish (Wiley et al. 1993, Yule et al. 2000), and in such systems, the production cost per fish landed is lowest for larger, catchable-sized fish (Wiley et al. 1993, Walters et al. 1997). However, trout stocked at a smaller size (<21 cm) yielded high angler returns in productive lakes where interspecific competitors were absent and predation risk was low (Wiley et al. 1993). This is the case in Lake Rotoiti, which lacks piscine predators of stocked rainbow trout. Therefore, in Lake Rotoiti, the timing of fish stocking can be optimised to produce highest growth rates, without the risk of predation or high overwintering mortality.

Though the season of stocking did not influence return of trout to anglers in Lake Rotoiti, stocking trout in autumn at a smaller size than spring releases appeared to benefit trout growth. Rainbow trout released in autumn were initially smaller than those released in spring, but they showed higher growth efficiencies between the ages of 2 and 3 years, had higher values of L_∞, and were heavier at ages 3, 4, and 5 years, possibly due to seasonal temperature differences. For trout released in spring, warmer lake temperatures during summer could cause elevated metabolic rate and food demand during the first few months of lake residence, compared to trout released in autumn, which would encounter cooler temperatures in their first few months of lake residence, as Lake Rotoiti is fully mixed between May and October. If sufficient food was available, trout released in spring would grow faster in their first few months in the lake, because the optimum temperature for growth in rainbow trout is 17.2°C when fed to excess (Hokanson et al. 1977). However, the optimum temperature for growth decreases with decreasing consumption of food (Elliott 1976). Depending on prey availability, rainbow trout released in spring might not be able to compensate for increased metabolic demands at higher water temperatures by increasing their food intake, resulting in slower growth.

Another possible explanation for the observed differences in growth between release seasons is related to differences between lake and hatchery conditions. Trout released in spring spend an extra four months in the hatchery, which is supplied with 10.5°C water from a spring. Trout released in autumn will experience a mean lake temperature over winter of 11.6°C; slightly higher than in the hatchery. Assuming that trout released in autumn are able to meet their metabolic demands, the warm conditions in the lake compared to the hatchery would allow a higher scope for growth and might contribute to the faster growth rates of autumn-released fish compared to fish that remain in the hatchery until spring.

Body size may also influence early growth of rainbow trout in the lake. Smaller hatchery fish may have a selective advantage over larger hatchery fish in natural environments, possibly because their lower food requirements allow them to maintain growth when food is scarce (Saikkonen et al. 2011). Similarly, Connolly & Petersen (2003) found that in mild winter conditions, the effects of low ration levels were more severe in large juvenile rainbow trout than in smaller juveniles. When food availability in Lake Rotoiti is low, smaller trout may be able to meet their metabolic needs more easily than larger trout.

Because the distribution of common smelt varies throughout the year, trout stocked in different seasons may encounter differences in prey density as well as different temperature conditions. Smelt typically migrate to the littoral zone between spring and autumn to spawn (Ward et al. 2005), and in Lake Taupo, smelt catches in the littoral zone are highest in summer (Stephens 1984). In Lake Rotoiti, smelt density in the littoral zone was highest in autumn (Chapter 3), so trout released into the littoral zone in autumn may benefit from this concentration of prey.

6.5.2 Predator-prey relationships

Contrary to our initial expectations, we did not detect a relationship between modelled prey consumption rates by rainbow trout in Lake Rotoiti and acoustic estimates of adult smelt density. Rainbow trout in Lake Rotoiti consume smelt averaging 48 mm but ranging from 33–98 mm in length (Chapter 4), while only large smelt (>45 mm) could be enumerated in echo sounding surveys, meaning that a significant proportion of the smelt population may not be quantified. Quantifying the abundance of small smelt 27–43 mm long is complex, as they often school in surface waters and are not amenable to sampling with hydroacoustics using a towed transponder, and signals from other fish and invertebrates may interfere with abundance estimates (Rowe 1993). Therefore, hydroacoustic measures of smelt abundance probably do not adequately reflect prey availability for rainbow trout. More comprehensive monitoring of smelt populations, including proper surveying of smaller size classes, is necessary to quantify the capacity of smelt populations to support continued trout stocking. This may be achieved by integrating echo sounding measurements with other techniques that sample a range of smelt size classes (including small smelt) in surface waters, such as boat-mounted nets (Chapters 2 & 3). Midwater trawling is another possibility for sampling smelt in the pelagic zone.

The effects of rainbow trout predation on other species in Lake Rotoiti have not yet been investigated; our results indicate that the native species common bully, koaro, and koura account for a small proportion of trout diet. Historical reports show that landlocked koaro populations declined dramatically in central North Island lakes after the introduction of rainbow trout (McDowall 2006), which are known to exert considerable predation pressure on native galaxiids in oligotrophic lakes in Argentina (Vigliano et al. 2009). Further investigation of the effects of rainbow trout predation on these species is recommended, given the potential magnitude of these effects and cultural significance of koaro and koura for Maori communities.

6.5.3 Stocking rates

Density-dependent effects on growth play a significant role in regulating fish populations at post-juvenile life stages (Lorenzen 2008, Lorenzen and Enberg 2002, Post et al. 1999); and relationships between consumption metrics and population size of rainbow trout suggest that density-dependent factors affected growth of trout in Lake Rotoiti. For example, % maximum growth and pC_{max} were negatively correlated with the size of the stocked trout population. These relationships correspond to patterns observed in growth rates of rainbow trout in Lake Rotoiti, which dropped after 2000, following an increase in the numbers of trout released (Chapter 5). Assuming that smelt abundance, size and energy density remain at current levels, stocking approximately 15,000 trout or fewer per year may increase growth rate of rainbow trout compared to stocking approximately 25,000 trout per year. However, management decisions will depend on desired outcomes for the fishery, because reducing the stocking rate would probably decrease angler catch rate.

Though relationships between consumption metrics and stocking density of rainbow trout were statistically significant, low values of r^2 suggest that other factors might also influence trout consumption in Lake Rotoiti. Such factors may include changes in environmental conditions in the lake (discussed below) and changes in wild trout abundance. Because stocked and wild rainbow trout have the same diet (Table 5), high stocking rates ought to reduce prey consumption by wild trout. The ratio of wild trout in the recreational catch has declined gradually since 2002, but because we lack direct information on wild trout abundance, growth rates and mortality, we cannot be certain that stocked trout are affecting wild trout. Characterising population parameters of wild trout (such as abundance, growth rates and mortality rates) would improve our understanding of density-dependent effects on growth.

6.5.4 Model sensitivity analysis

Sensitivity analyses showed that changes in prey energy density (ED) had the greatest effect on predicted consumption by rainbow trout of all variables tested.

Substantial changes in consumption were caused by changing the prey ED by as little as 10%. Smelt showed a 30% change in ED between summer and winter; model results suggested that this reduction is sufficient to trigger a requirement for greater prey intake. Previous observations show that prey ED may change significantly over inter- and multi-annual time scales (Rand et al. 1994, Bryan et al. 1996). For example, ED of alewives (*Alosa pseudoharengus*) varied twofold between seasons (Rand et al. 1994). Therefore, changes in ED during the study period could have affected actual trout consumption rates. Long-term monitoring of the ED of trout prey is needed improve our knowledge of the relationships between prey consumption and trout growth.

The sensitivity analysis showed that changing the temperature scenario had substantial effects on model output. This means that deviations in actual trout thermal experience from the estimated thermal regime (Table 3) may have led to inaccurate consumption estimates. We assumed that trout would seek out their optimal temperature within the range of available temperatures in the lake. Monthly measurements of water temperatures at given depths did not vary significantly between years (P. Scholes & J. Blair, unpubl. data), and trout should be able to regulate their thermal experience in stratified lakes by altering their swimming depth. Temperature scenario 1 used in this study represents a realistic approximation of trout thermal experience, as the estimated temperatures (assuming trout would occupy water at 15°C if it was available) were similar to the temperatures measured at the mean swimming depths of trout in Lake Rotoiti (Rowe & Chisnall 1995). It is, however, possible that differences in prey distributions or other ecological factors influenced the thermal experience of rainbow trout; for example, changes in the extent of hypolimnetic deoxygenation can influence habitat quality and growth rate potential of fish in lakes (Arend et al. 2011). Lake Rotoiti experienced increased eutrophication between 2003 and 2006 (Scholes 2009), but no change in rainbow trout growth or consumption was evident during this period (Figs. 6.5 & 6.7). Errors in estimating thermal experience may have added variability, but not a systematic bias, to the relationships between consumption and trout population density shown in Fig. 7. Quantifying temporal variation in thermal experience of trout in Lake Rotoiti would improve the accuracy of bioenergetics models.

Many uncertainties can be introduced when bioenergetics models are used to estimate consumption by predators, and in some cases model predictions may not match other measurements of consumption (Ney 1993, Bajer, Whitledge & Hayward 2004, Chipps & Wahl 2008). This study was based on direct measurements of growth, diet, and prey energy density, while some parameters used in our model were adapted based on literature data obtained for other species and in other regions to evaluate the relative change in consumption parameters among years with different stocking timing and rates. Characterisation of physiological parameters for rainbow trout in our study area would allow more accurate estimation of consumption. For example, accuracy of our model estimates could have been improved by characterising egestion and excretion, which were identified as major sources of variation in model estimates of consumption (Bajer et al. 2003). Corroborating consumption estimates in the laboratory would also help to determine the suitability of the model parameters. Model outputs were comparatively insensitive to changes in diet proportions, but were more sensitive to changes in prey ED and thermal experience. Therefore, it is important to better characterise changes in these sensitive parameters to ensure the accuracy of model outputs.

6.5.5 Conclusions and management implications

Catch rate is generally inversely related to fish size in trout fisheries, and fishery managers can maintain a compromise between high catch rates and large fish sizes by optimising stocking rates. In this study, we demonstrated that higher population levels of rainbow trout in Lake Rotoiti were associated with decreased pC_{max} and % maximum growth of trout in their first year of lake residence. It is therefore possible that at high stocking levels, trout population levels are near the carrying capacity for this lake.

Releasing trout in autumn appears to be advantageous for growth, possibly because (1) temperature is more suitable for growth in autumn-winter than in spring-summer, and (2) prey for small trout is abundant in autumn. Stocking should be timed to optimise feeding conditions for newly released trout, i.e. (1) concentrate stocking around periods of high prey abundance (e.g. autumn), and (2) stagger releases over a period of months to reduce competition for prey in the littoral zone. Autumn releases offer the best growth performance and reduced hatchery costs because the fish do not have to be reared for as long as spring releases.

Mild winter conditions appear to enhance overwinter survival and growth of rainbow trout in warm-temperate lakes compared to higher latitudes. This implies that moderately productive warm-temperate lake ecosystems are highly suitable for trout growth in winter, but less so in summer, when lake stratification and high nutrient levels may create conditions suitable for algal blooms and hypolimnetic deoxygenation. High trout growth rates of trout in warm-temperate lakes can therefore be supported by timing releases to coincide with favourable winter conditions.

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6.7 Appendices

Appendix 6.1. Physiological parameters used in bioenergetics model of Lake Rotoiti rainbow trout. Source: Rand et al. (1993).

Parameter	Parameter description	Parameter value
Consumption (Equation 3)		
CA	Intercept of allometric mass function	0.628 g g^{-1} d^{-1}
CB	Slope of allometric mass function	-0.3
CQ	Temperature where consumption rate is proportion (CK1) of maximum rate	5°C
CTO	Temperature where consumption rate is 0.98 of maximum rate	20°C
CTM	Temperature where consumption rate is 0.98 of maximum rate	20°C
CTL	Temperature for CK4	24°C
CK1	Proportion of Cmax at lower temperature threshold	0.33
CK4	Proportion of Cmax at upper temperature threshold	0.2
Respiration (Equation 1)		
RA	Intercept of allometric mass function	0.00264 g O_2 g^{-1} d^{-1}
RB	Slope of allometric mass function for standard metabolism	-0.217
RQ	approximates Q_{10}	0.06818
RTO	Coefficient for swimming speed dependence on metabolism	0.0234
RTL	Cut-off temperature at which activity relationship changes	25°C
RK1	Intercept for swimming speed above RTL	1
RK4	Mass dependence coefficient for swimming speed at all temperatures	0.13
ACT	Intercept of relationship for swimming speed versus mass at temperatures less than RTL	9.7
BACT	Temperature dependence coefficient of swimming speed at temperatures less than RTL	0.0405
SDA	Proportion of energy lost to specific dynamic action (energy cost of assimilating food)	0.172
Egestion/Excretion (Equation 3)		
FA	Intercept of proportion of consumed energy egested versus water temperature and ration	0.212
FB	Coefficient of temperature dependence of egestion	-0.222
FG	Coefficient of dependence of feeding on egestion	0.631
UA	Intercept of proportion of consumed energy excreted versus water temperature and ration	0.0314
UB	Coefficient of temperature dependence of excretion	0.58
UG	Coefficient of dependence of feeding on excretion	-0.299

Appendix 6.2. Mass (g)–length (mm) regression parameters ($\log_{10} W = a + b \times \log_{10} L$) and spawning mass loss of rainbow trout caught swimming upstream and downstream during peak spawning migrations, from Ngongotaha Stream, a tributary of Lake Rotorua, New Zealand, 1959–1962.

	Upstream				Downstream					
	Peak immigration	*a*	*b*	Mass at 480 mm (kg)	Peak emigration	*a*	*b*	Mass at 480 mm (kg)	Difference in mass (kg)	Difference in mass (%)
Female										
1959	Jun-Oct	-6.98	2.674	1.55	Sept-Nov	-6.77	2.55	1.18	0.37	23.8
1960	Jun-Oct	-7.15	2.733	1.53	Nov-Dec	-7.25	2.73	1.17	0.36	23.6
1961	Jun-Oct	-7.18	2.759	1.66	Sep-Nov	-7.83	2.95	1.21	0.44	26.8
1962	May-Aug	-7.01	2.684	1.54	Aug-Oct	-7.04	2.65	1.15	0.39	25.3
Male										
1959	Jul-Oct	-6.92	2.644	1.48	Sept-Nov	-5.86	2.20	1.13	0.35	24.0
1960	Jun-Oct	-7.30	2.783	1.46	Sept-Dec	-6.44	2.42	1.09	0.37	25.2
1961	Jun-Oct	-7.615	2.903	1.53	Sept-Nov	-7.21	2.72	1.17	0.36	23.6
1962	May-Aug	-7.46	2.836	1.43	Aug-Oct	-6.62	2.49	1.15	0.28	19.7
Mean (female and male)				1.521				1.156	0.366	24.0

Appendix 6.3. Population parameters of cohorts of stocked rainbow trout, Lake Rotoiti, with parameters fitted to the von Bertalanffy growth equation L_∞, K and, t_0.

Season, year released	Fork length at release (mm)	Number of trout released	Mean length at age 3 (mm)	L_∞ (mm)	K (mm yr^{-1})	t_0 (yr)
Autumn						
1998	160	11000	615.2	631.1	1.694	-0.172
1999	140	11000	648.6	784.7	0.778	-0.252
2000	160	14500	649.8	797.5	0.731	-0.306
2001	150	14500	572.9	606.9	1.300	-0.218
2002	190	14500	604.1	687.5	0.894	-0.361
2003	180	14500	608.8	674.6	1.008	-0.308
2004	140	7500	590.5	619.5	1.403	-0.182
2005	161	7500	612.0	662.4	1.150	-0.241
2006	171	14500	613.6	695.0	0.936	-0.293
2007	150	14500	583.4	646.5	1.031	-0.256
2008	180	14500	639.1	1053.8[6]	0.372	-0.504
2009	160	17500	638.1	747.0	0.842	-0.286
Spring						
1993	220	6500	630.7	657.4	1.397	-0.292
1994	200	6500	635.3	689.6	1.099	-0.312
1995	210	7000	643.8	684.7	1.226	-0.299
1996	230	8500	636.0	676.2	1.203	-0.346
1997	190	7500	611.5	633.6	1.500	-0.237
1998	220	3500	565.5	565.6	3.862	-0.128
1999	169	3500	612.6	644.3	1.354	-0.225
2000	190	12500	587.9	608.9	1.496	-0.250
2001	170	10500	581.4	628.5	1.138	-0.278
2002	240	10500	630.7	713.0	0.874	-0.470
2003	178	10000	573.0	592.1	1.540	-0.232
2004	182	7500	615.8	681.7	1.013	-0.306
2005	183	15500	593.1	615.8	1.474	-0.241
2006	171	10500	607.7	644.9	1.272	-0.243
2007	190	10500	585.2	608.9	1.437	-0.260
2008	190	10500	643.7	704.3	1.069	-0.294
2009	180	10500	610.3	646.9	1.272	-0.256

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[6] The L_∞ for the autumn 2008 cohort could not be estimated properly because no data were available for trout older than 3 years. The von Bertalanffy model still provided a good fit for trout of less than 3 years old, and was not used to predict the lengths of trout older than 3 years.

7 Concluding discussion

7.1 Research summary

The overall aim of this thesis was to identify the factors influencing trout growth and smelt abundance in the Rotorua lakes. Finding the influences on trout growth is important for management of the economically and socially important trout fisheries in this area, especially given that the fisheries are maintained or supplemented in most cases by regular introductions of hatchery-raised stocks. The factors influencing growth of salmonids such as rainbow trout have rarely been studied in warm-temperate lakes, and may differ from those characterised in cool-temperate systems. Prey availability is often cited as the main factor influencing predator growth, and management of prey species is an integral part of fisheries management (Ney 1990). Smelt are the main prey for rainbow trout in lakes of the central North Island (McBride 2005, Rowe 1984, Smith 1959, Chapter 4), so characterising smelt abundance is of primary importance for assessing the availability of prey for rainbow trout. Assessing the health of smelt populations in Lake Rotoiti was of particular concern, as the Ohau Channel Diversion Wall had the potential to negatively affect smelt populations, which could potentially have negative follow-on effects for the iconic rainbow trout fishery.

The objectives of this study were to (1) determine the dynamics of the abundance of common smelt, (2) determine the factors that control smelt abundance, (3) determine the relationship between smelt abundance and trout growth, and (4) examine the factors influencing trout growth in the study area.

To achieve the first objective of this study (to determine the dynamics of the abundance of common smelt), a direct sampling technique needed to be developed that is simple, repeatable, quantitative, and relatively inexpensive. Though echo sounding has been used to monitor adult smelt populations in Lake Rotoiti, small smelt in surface waters may not be detected, and confusion with other small fish species and invertebrates means that small pelagic smelt cannot be enumerated (Rowe et al. 2011). To suggest an effective capture technique for smelt, we tested purse seining, beach seining, drop netting, and boat electrofishing (Chapter 2). From the results of this trial we concluded that boat electrofishing at night is the most effective sampling method for collecting data on length frequencies, seasonal dynamics and growth of smelt, followed by scoop nets (i.e.

boat electrofishing with the current turned off). We therefore recommend the use of boat-mounted nets at night for sampling smelt in lakes. When absolute population estimates are required, we recommend combining this technique with one that enumerates fish in the deep pelagic zone, such as echo sounding or midwater trawling.

To achieve the second study objective (to determine the factors influencing smelt abundance), we examined seasonal changes in smelt habitat and resource use by measuring spatial and seasonal changes in smelt abundance, body condition, and diet (Chapter 3). We also characterised seasonal and spatial changes in smelt reproductive state and benthic egg abundance. Smelt abundance and body condition were low during winter, coinciding with the post-spawning period and low prey abundance (zooplankton and benthic invertebrates). Stomach contents and stable isotope analyses showed that smelt undergo an ontogenetic change in diet, from mainly zooplankton as juveniles to a combination of prey, including benthic invertebrates, as adults. Differences in diet and stable isotope signatures of smelt caught during the day compared to those caught at night suggest the existence of two feeding guilds; (1) a resident littoral group that feeds solely on benthic invertebrates at all life stages, and (2) a group that occupies deep water during daylight and migrates to surface waters at night, and undergoes the aforementioned ontogenetic shift in diet. Smelt are abundant in Lake Rotoiti and reproduce locally; therefore, populations should provide a sustainable prey resource for rainbow trout in the near future.

Characterising the diet of rainbow trout in Lake Rotoiti was a necessary first step for achieving the third study objective of determining the relationship between smelt abundance and trout growth rates (Chapter 4), and for further investigations of influences of prey supply on trout growth (Chapter 6). Additionally, bioenergetics models require an estimate of relative proportions of prey types by mass as well as energy density; this information was lacking for trout in central North Island lakes. Our measurements of these parameters provided a basis for bioenergetics modelling, and showed that trout undergo an ontogenetic diet shift when they reach a length of approximately 200 mm; thereafter, smelt are the principal prey item at all times of year. Rainbow trout consumed larger prey as they grew larger (i.e. koaro, koura, and larger smelt) but the minimum size of smelt consumed did not change with trout size.

The final two research chapters addressed the final research objective: to examine the factors influencing trout growth. This problem was addressed in two parts: Chapter 5 assessed habitat and environmental effects, and Chapter 6 assessed population density and stocking effects. Along with prey supply (Ney 1990), habitat availability is an important determinant of fish growth rates (Bryant 1992, Budy et al. 2011, Mason et al. 1995). Temperature and eutrophication of lakes are projected to increase in the future, so it is important to understand how higher lake temperatures and increased eutrophication will affect trout habitat and growth. To address this issue, we carried out a multivariate analysis of several lake characteristics relating to morphometry, land use, stratification, and trophic state, and assessed how these variables affected trout growth rate. Lake morphometry was an important factor structuring habitat availability in these lakes, and hypolimnetic volume was the variable that most effectively separated lakes and years with high and low trout growth rates. Within the two lake types (deep, with a large hypolimnetic volume, and shallow, with a small hypolimnetic volume), indicators of trophic state were correlated with trout growth rate in different ways. In deep lakes, increased chl *a*, an indicator of productivity, was associated with increased trout growth rates, whereas in shallow lakes, which were more eutrophic, increases in temperature and conductivity were associated with decreased trout growth rates. Therefore, future increases in water temperatures and eutrophication in these warm-temperate lakes are likely to constrain trout growth, and the effect of these increases will be greater in the shallow lakes than in the deeper lakes.

The success of stocked fisheries (e.g. high returns to anglers or high fish growth rates) is dependent on several factors, including the size of fish at stocking, and timing of stocking in relation to predation risk and changes in temperature. In addition, the stocking rate that can be supported in each lake is different, and it is important to optimise stocking rates according to the carrying capacity of the ecosystem (Lorenzen 2005, 2008). In Chapter 6, we employed a bioenergetics model to assess the effects of stocking rates and timing on rainbow trout growth in Lake Rotoiti. Higher stocking levels of rainbow trout in Lake Rotoiti were associated with decreased prey consumption by trout in their first year of lake residence. This corresponds to observations of trout growth rate, which declined following an increase in trout stocking rates (Chapter 5). It is therefore possible that at high stocking levels, the total trout population is near carrying capacity.

Releasing trout in autumn appears to be advantageous for growth, possibly because (1) suitable temperature and DO habitat is more abundant in autumn-winter than in spring-summer, and (2) prey for small trout is abundant in autumn. These results provide useful information to fishery managers on the management of stocked rainbow trout in Lake Rotoiti, and indicate that optimal stocking rates and timing in warm-temperate systems may differ to those in cool-temperate systems.

7.2 Management implications and recommendations for future work

7.2.1 Monitoring of smelt populations

This study showed that bioenergetics models can be used to retrospectively analyse the effects of stocking rates, but to use measures of smelt abundance to predict appropriate stocking rates of trout, it will be necessary to gather data on inter-annual changes in seasonal smelt abundance and condition to add to the data that is already collected on rainbow trout. Unfortunately, this was not possible in the short time frame of this study.

Two lines of evidence indicate that sampling the entire smelt population is important for predicting the carrying capacity of the lake to support trout growth. The first indication is that the minimum size of smelt consumed by trout did not change with trout size; i.e. even large adult trout consumed a wide size range of smelt, from approximately 35 to 70 mm (Chapter 4). In addition, there was no relationship between adult smelt abundance (measured by echo sounding) and consumption rates of rainbow trout of any age class, estimated using bioenergetics modelling (Chapter 6). The lack of a relationship suggests that echo sounding population estimates may not sample all the relevant size classes of smelt, and sampling small smelt in the surface waters is also necessary to estimate food supply for rainbow trout.

The apparent differences between smelt caught in the littoral and pelagic zones (Chapter 3) should also be considered when designing a smelt sampling programme. For example, samples taken by beach seine appear to only contain littoral residents of a limited size range (Chapters 2 and 3) and may not be representative of the entire population. Therefore, to ensure that the sample contains pelagic smelt of a wide range of sizes, smelt in surface waters should be sampled in both the littoral and pelagic zones at night. Suggestions for future research in this area include exploring if diet separation also exists in other lakes, and whether littoral and pelagic smelt are distinguishable, e.g. by meristic characters, as is the case in diadromous and lacustrine smelt (Ward et al. 2005).

In addition to assisting with the management of rainbow trout populations, a seasonal sampling programme for smelt in lakes in the Rotorua region would help to clarify several outstanding research questions. These questions include, firstly, whether the drop in condition and energy density observed in Lake Rotoiti smelt over winter (Chapters 3 and 4) occurs consistently in every year and lake, or whether our sampling period represented a “bad year” in terms of smelt prey availability. Sampling during a period of particularly low prey availability would explain why we observed a much higher rate of egg predation by Lake Rotoiti smelt than those in Lake Taupo (Stephens 1984). Secondly, changes in smelt spawning season among years and lakes may occur; anecdotal evidence suggests that in some years, smelt are highly abundant in the littoral zone during spring, whereas in other years, they are highly abundant in autumn (R. Pikethley, Fish & Game, pers. comm.). It is not yet known whether the autumn spawning peak observed in 2011 in Lake Rotoiti is typical, or what kinds of environmental conditions might drive a change in spawning season. Future researchers can discern these patterns either by sampling smelt eggs from beaches, or by seasonal examination of littoral smelt abundance, gonadosomatic index, and condition factor, because increases in these factors coincided with high measurements of egg abundance in benthic samples.

7.2.2 Effects of lake management interventions

Water flowing from Lake Rotorua into Lake Rotoiti via the Ohau Channel constituted a significant input of nutrients and algae and was chiefly responsible for the reduction of water quality in Lake Rotoiti (Hamilton et al. 2005). In 2008, the Ohau Channel Diversion Wall was installed to improve water quality in Lake Rotoiti by diverting inputs of water from Lake Rotorua to the Kaituna River. Most of the water flowing out of Lake Rotorua now flows directly down the Kaituna River rather than into Lake Rotoiti. It is necessary to assess the effects of diversion wall construction on fish populations, because juvenile and adult smelt regularly migrated from Lake Rotoiti into the Ohau Channel prior to wall construction (Rowe et al. 2006).

Our field surveys indicated that smelt are highly abundant in Lake Rotoiti, and surveys of smelt eggs and larvae in the pelagic zone suggest that smelt reproduce within Lake Rotoiti. Because of local reproduction and littoral abundance, the impact of the Ohau Channel diversion wall on smelt populations should be limited. Additionally, recent trapping surveys in the Ohau Channel show that smelt migrations have taken place between Lake Rotoiti and Lake Rotorua after the wall installation (Rowe et al. 2011). Therefore, self-sustaining smelt populations should continue to support Lake Rotoiti trout populations in the future. Because smelt seem to thrive in clear, oligotrophic lakes, probably due to improved egg survival compared to turbid, eutrophic lakes (Rowe and Taumoepeau 2004), the Ohau Channel Diversion Wall is likely to have a positive effect on smelt abundance by improving lake water quality in the long-term. Because smelt spawn preferentially on relatively exposed beaches with coarse sand, sedimentation of these areas should be prevented.

7.2.3 Recommendations for future fishery management

The suitability of current stocking and management regimes are best assessed on a lake-by-lake basis, since conditions in every lake are different. Results of bioenergetics modelling (Chapter 6) showed that optimal stocking rates for lake Rotoiti depend on the management goals for the fishery. Current stocking rates appear to be causing density-dependent effects on growth, so if a low-yield, trophy fishery is preferred, stocking rates should be decreased. However, if a high-yield fishery with smaller, more abundant fish is preferred, stocking rates should remain at current levels. Growth rates of stocked rainbow trout may be optimised by gradual stocking over a period of time or by releasing trout in summer or autumn, when smelt are abundant in the littoral zone and are in good condition (Chapter 3).

Stocking rates in Lake Rotoiti were increased between 2010 and 2012, and a clear reduction in condition of trout has been recorded since then (R. Pitkethley, pers. comm.). The goal of increased stocking was to increase the amount of trout available for capture by anglers, because an angling survey had indicated that fishing pressure in Lake Rotoiti had increased relative to other lakes. Because

Lake Rotoiti stocking rates already appear to be causing density-dependent effects, any reductions in prey availability could cause reductions in trout condition or growth. Managers need to balance the risk of poor trout condition with the benefit of increased catch rates. To avoid possible reductions in trout condition, it might be prudent to lower stocking rates slightly. However, if anglers are willing to accept lower trout condition, current stocking rates may be appropriate.

In general, it seems that Fish & Game's stocking practises are appropriate. Trophy fisheries are more likely to produce the desired large fish when (1) habitat quality is sufficient (i.e. suitable temperature and dissolved oxygen) and (2) stocking densities do not cause limitations in food supply. Therefore, trophy fisheries should be concentrated in lakes where habitat is suitable, i.e. deep lakes such as Tarawera and Okataina.

The effects of climate change should be considered when planning future trout stocking strategies. If the rainbow trout fisheries in shallow lakes are severely impacted by temperature increases, Fish & Game may face pressure from anglers to create a warmwater species fishery. This is likely to be a highly contentious issue, given the positive effects of the trout fishery on tourism and the cultural ecosystem services that it provides. However, environmental legislation today is very different to when trout were first introduced (around the 1900s), and introduction of a new species to New Zealand would likely face significant regulatory hurdles, especially considering the widely documented effects of introduced salmonids on native fish populations. It is possible that someone might take matters into their own hands and introduce a species already present in New Zealand; for example, perch, tench, or rudd. Introduction of these species would probably have undesirable consequences for the ecosystems of lakes in the Rotorua area, and it is important to educate the public to reduce the risk of spread of invasive species.

Although climate change may affect the success of rainbow trout in shallow lakes, trout populations in deep lakes will probably not be as badly affected, due to the presence of thermal refuges in stratified lakes during summer. Providing that further eutrophication of these lakes is prevented, trout should have sufficient habitat around and below the thermocline that is well-oxygenated and within a suitable temperature range. But if bottom water deoxygenation worsens, trout habitat will be reduced. Current programs aiming to reduce nutrient inputs into the Rotorua lakes will help to preserve trout habitat into the future.

7.2.4 Future research needs for trout bioenergetics modelling

To improve bioenergetics model estimates of rainbow trout consumption rates, several refinements to model inputs are possible. Measuring physiological parameters in rainbow trout, especially those related to excretion and egestion, would improve model accuracy. In addition, corroborating the model in the laboratory would help to determine the accuracy of the modelled consumption estimates. The sensitivity analysis of model inputs indicated that further characterisation of temperature experience and prey energy density should be prioritised, as these parameters had the largest influence on consumption estimates. Firstly, thermal experience could be better characterised by carrying out either hydroacoustic surveys throughout the year to determine seasonal changes in trout depth distributions, or a tagging study of rainbow trout in Lake Rotoiti. Temperature-logging archival tags could be used to accurately characterise thermal experience in the field. Characterising thermal experience of trout in shallow lakes that lack coldwater inputs, such as lakes Rotoehu and Rerewhakaaitu, would help to determine the detrimental effects of warm temperatures on growth. Secondly, measuring seasonal and interannual changes in smelt energy density would also help improve the accuracy of bioenergetics model estimates.

Differences in the diet of rainbow trout among lakes may contribute to variation in trout growth rates. This matter was not addressed in this study, but spatially-explicit models of fish growth rate potential show that habitat quality and prey availability interact to affect growth of fish (Bryant 1992, Budy et al. 2011, Mason et al. 1995). Though it is clear that trout growth rate in the Rotorua region is heavily influenced by lake conditions, especially habitat volume (Chapter 5), prey availability is also likely to play a role. Clarifying the relationships between lake conditions, prey availability, and trout growth rate requires regular sampling of spatial variation in smelt abundance in relation to environmental conditions in different lakes.

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