

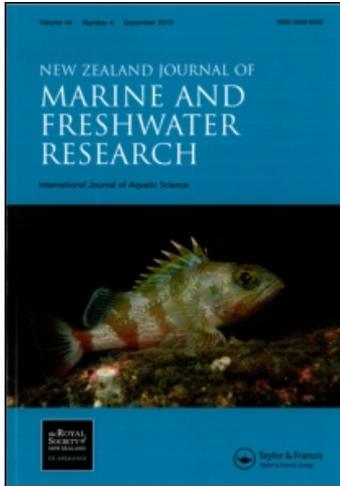
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The influence of natural variation in discharge on juvenile brown trout population dynamics in a nursery tributary of the Motueka River, New Zealand

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The effects of natural flow variation on juvenile brown trout population dynamics were investigated by biannual sampling over 5.5 years in the Rainy River, a tributary of the Motueka River. A large flood in late March (50-year return period) substantially reduced the density (by 66%) and biomass (by 73%) of 0+ trout over autumn–spring, but the cohort responded with compensatory survival to achieve similar density and biomass by spring as in other years. A low-flow event in February–April (return period >8.4 years), when 7-day low flows fell to 56% of the 7-day mean annual low flow (MALF) and were less than the MALF for 46 days, had no adverse affect on the population. We found no evidence for density-dependent growth. However, there was strong evidence for a two-phase self-thinning response in density, with no self-thinning occurring over summer (i.e. the 0+ population remained below carrying capacity) until a threshold mass of 22.08 g (length = 123.7 mm) was attained in autumn after which severe self-thinning took place over autumn to spring. The results indicate that over spring–autumn the population is insensitive to flow reduction and that over autumn–spring the effects of high (and probably low) flow events on local abundance and biomass are offset by compensatory (density-dependent) survival. However, effects on the contribution of migrants to the downstream population remain unknown. The study identified ecological redundancy, which could be exploited for flow allocation. Significantly, it has shown that minimum flows equivalent to the MALF (often advocated by New Zealand conservation and fisheries management organisations) are not always necessary for sustaining juvenile trout populations.

Keywords: brown trout; *Salmo trutta*; low flow; flood; flow variation; density; survival; mortality; growth; self-thinning, ecological redundancy, flow allocation

Introduction

The flow regime is a critical factor in determining the structure and function of stream ecosystems (Resh et al. 1988; Minshall 1988; Jowett & Duncan 1990; Poff & Ward 1994; Poff et al. 1997). Often this is most graphically illustrated during flood flows, with flood-induced mortality of the stream fauna (as inferred by reductions in the abundance of fish (e.g. Jowett & Richardson 1989) and invertebrates (e.g. Scrimgeour & Winterborun 1989) and changes to the physical habitat and

channel form being apparent once floodwaters recede (e.g. Wondzell & Swanson 1999). In many lotic systems, flooding is the primary source of disturbance and may affect community structure, and particularly fish populations, long after the floodwaters have receded (Resh et al. 1988; Biggs & Close 1989; Matthaei et al. 2003; Olsen et al. 2007; Effenberger et al. 2008; Lobón-Cerviá 2009). Such effects can result from differences in the resistance or resilience between species, or as a result of habitat modification caused by the disturbance.

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At the other end of the flow spectrum are low flow events. Unlike floods, which are mainly unavoidable natural events, low flows are regularly influenced by human use of water. Activities that abstract water from a stream or hydraulically connected groundwater, or reduce catchment water yield (e.g. conversion of pasture, tussock grassland or low scrub to plantation forestry; Fahey et al. 2004) have the potential to influence the magnitude, frequency and duration of low flows unless limited by suitable regulation, such as minimum flow rules and allocation limits.

The effects of low flows are usually more subtle than those associated with floods and arise from changes in the quantity and quality (including water quality) of in-stream habitat. Consequently, the effects of low flow are not as well understood as the effects of floods. In the case of fish, low flows can affect the area of suitable habitats of appropriate depth, velocity and proximity to food sources and food supply (reviewed in Dewson et al. 2007). The quality of available habitat may also change (e.g. physicochemical conditions such as water temperature and dissolved oxygen content; Elliott et al. 1997). Low flows may also affect the food chain, upon which fish depend, by altering the habitat available for periphyton and macroinvertebrates, and accrual periods of these communities, with the result that periphyton may proliferate (depending on nutrient availability) and this may influence grazer abundance (Poff et al. 1997; Opsahl et al. 2003; Suren et al. 2003a, b; Dewson et al. 2007). Reduced habitat and food availability during periods of low flow may increase competition, which has been found to affect the survival, movement and growth of stream-dwelling brown trout (Jenkins, Jr et al. 1999; Bohlin et al. 2002; Vollestad et al. 2002).

While biotic factors such as competition for food and space can exert control on stream salmonid populations through density-dependent survival, this mainly occurs when density is high (Elliott 1994), although density dependence may be expressed in growth at low

densities too (Lobón-Cerviá 2007). With respect to competition, density is relative to body size. Typically, as stream salmonids grow, they have increasing demands on food and space and populations self-thin accordingly (Chapman 1962; Elliott 1993a; Grant 1993). The relationship between density and body weight is used for assessing population self-thinning and has proved to be a useful index of density-dependent loss (Elliott 1993a; Lobón-Cerviá 2008). However, floods and drought have a much greater influence in controlling salmonid populations (Jowett & Richardson 1989; Harvey et al. 1999; Nislow et al. 2002), the former largely through recruitment and especially so in hydrologically variable streams (Hayes 1995; Lobón-Cerviá 2009; Nicola et al. 2009). Therefore, the highly variable flow regimes common throughout New Zealand (Jowett & Duncan 1990) ought to be the dominant influence on salmonid and native fish populations.

The highly variable hydrology of most New Zealand rivers, coupled with the flexible niches and life-history requirements of much of the freshwater flora and fauna (including introduced salmonids) ought to produce 'hydrological and ecological redundancy' in our riverine ecosystems (Olden & Poff 2003; Jowett & Biggs 2008). Hydrological redundancy refers to the fact that hydrological components of natural flow regimes are often highly correlated (Olden & Poff 2003) and therefore some must be redundant in maintaining ecosystem structure and function. A good understanding of physical processes and their relationship to aquatic biota is necessary to identify which hydrological components are important (Monk et al., 2007) and which parts of these are outside a threshold which might be necessary to achieve a benefit for the structure or functioning of the ecosystem (i.e. are ecologically redundant; Jowett & Biggs 2008). Extending the thesis of Jowett & Biggs further, within those parts of flow regimes that are ecologically important, whether a habitat-dependent ecological response ensues from

flow change will depend on whether habitat is limiting (i.e. whether populations, e.g. fish, are at carrying capacity). Hydrological and ecological redundancy offer opportunities for flow exploitation. In order to achieve improvements in environmental flow setting and flow allocation efficiency more research is needed to identify ecological redundancy, including whether (and under what circumstances) valued fish populations such as trout (which are highly influential in flow management decisions) are below carrying capacity (Becca et al. 2008). Moreover, to be useful for flow management, such understanding needs to be expressed in the context of ecologically relevant flow indices and models that allow effects of flow change, and comparisons of alternative flow regimes, to be quantified and summarised (e.g. Jowett et al. 2008).

Predictions of the effects of flow regime change on fish in New Zealand have usually been based on habitat modelling, supported by a few studies from New Zealand and elsewhere that have demonstrated expected relationships between predicted and ecological response (e.g. Stalnaker 1979; Nehring and Anderson 1993; Jowett 1992, 1995; Jowett & Biggs 2006). Empirical studies of fish population response to flow change mainly have been short term, which limits the inferences that can be made from them (Kraft 1972; Canton et al. 1984; Harris et al. 1991; Hayes 1995; Jowett 1995; Nislow et al. 2004; Jowett et al. 2005). Long-term studies are rare (Elliott et al. 1997; Bell et al. 2000; Gouraud et al. 2001; Lobón-Cerviá 2009), but are necessary to detect flow disturbance effects on recruitment and density dependence, and to understand carrying capacity limits (Bell et al. 2000; Lobón-Cerviá 2007, 2009; Elliott 2009). No such long-term studies have been conducted on fish in New Zealand, yet these are sorely needed for understanding the effects of artificial flow change against the background of natural variation in population parameters. This paper presents preliminary results of a study designed to do just that.

The ongoing study on the Rainy River, a tributary of the Motueka River, is aimed at understanding the effects of natural flow variability on juvenile brown trout population parameters, identifying ecologically relevant flow regime components and quantifying effects with respect to ecologically relevant flow indices. In this paper, we present results from biannual surveys of juvenile brown trout population dynamics undertaken over 5.5 years at three sites. We examined the influence of the magnitude, frequency and duration of high and low flow events. We were particularly interested in whether there was evidence for self-thinning and growth limitation, indicating space and food limitation (i.e. population at carrying capacity) associated with season, and low and high flow indices, including the mean annual low flow (MALF). The latter is widely recognised as an ecologically relevant low flow in environmental flow management in New Zealand (Jowett 1992; Jowett & Biggs 2006; Becca 2008).

Methods

Site description

The study was conducted within a 1760-m segment of the Rainy River, downstream of The Forks (41°42'30"S, 172°48'58"E). The Rainy River is a fifth-order tributary, located in the upper Motueka River catchment in the north of the South Island (Fig. 1). The Rainy River drains a catchment of 105 km² (420–1030 m a.s.l.) and near its confluence with the Motupiko River has a mean flow of 1.794 m³/s, a median flow of 0.882 m³/s and a 7-day MALF of 0.187 m³/s (Basher 2003). Mean width of the stream in the study segment during sampling occasions was about 5.9 m. Substratum comprises mainly cobbles (64–256 mm) and gravel (2–64 mm) with a few boulders (>256 mm), and with minor amounts of sand and silt. The relatively clean cobbles, gravels and boulders provide good spawning and rearing habitat for brown trout (*Salmo trutta* L.).

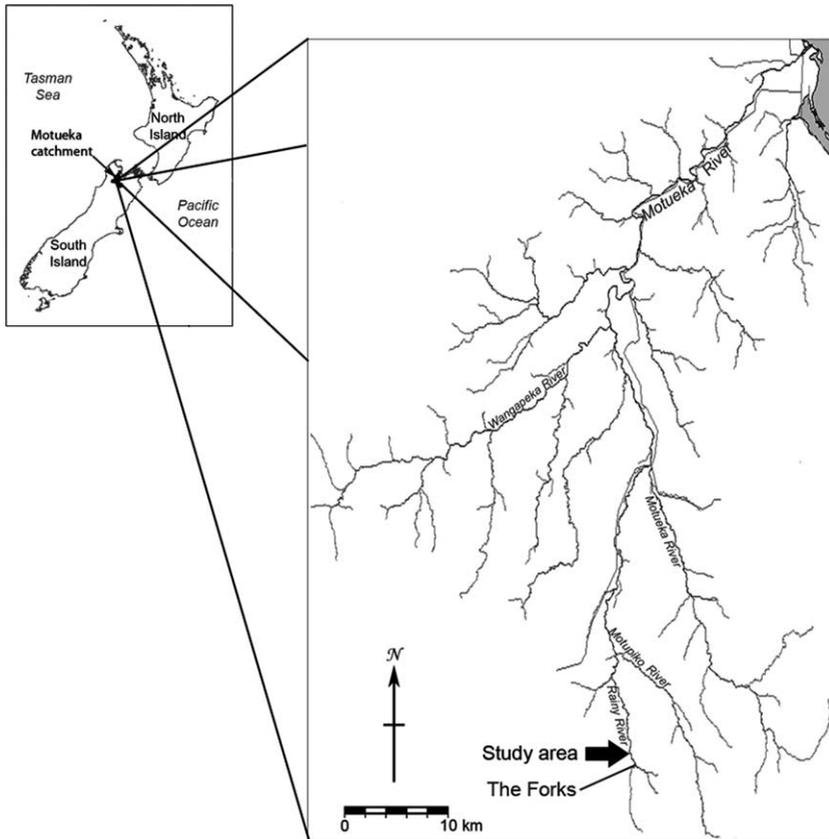


Fig. 1 Map of the Motueka Catchment showing the location of the study area.

Vegetation in the upper catchment is dominated by native forest (particularly southern beech *Nothofagus* spp.), with pasture and some areas of scrub on the floodplain below The Forks, whilst the geology of the catchment is dominated by Moutere gravels (Basher 2003). Annual rainfall is between 1200 and 1500 mm, depending on the location within the catchment with highest rainfall in the southwest (Basher 2003).

Six species of fish have been recorded from the Rainy River: brown trout (*S. trutta* L.), longfin (*Anguilla dieffenbachii* Gray) and shortfin (*Anguilla australis* Richardson) eels, upland bully (*Gobiomorphus breviceps* Stokell), dwarf galaxias (*Galaxias divergens* Stokell) and koaro (*Galaxias brevipinnis* Günther). Of these, brown trout, dwarf galaxias, upland bully and the two

eel species are common. Combined densities of these four species usually were less than 0.5 fish/m². Eels are the dominant species by biomass, with some large individuals weighing 3 kg or more, and they are the top aquatic predator.

In terms of the Motueka River trout fishery, the Rainy appears to function as a spawning and juvenile rearing tributary, having little deep-water holding habitat for adult trout year-round. The river supports mainly 0+ trout, a few yearlings and occasional 2-year old fish. We assume surviving juveniles recruit to the downstream adult population in the Motupiko River and wider Motueka catchment. A recent otolith micro-chemistry analysis of 48 adult trout sampled from the Motueka catchment indicated that only 4.2% of the fish recruited from the

Rainy River (Olley 2008), but the proportion no doubt varies over time. Ratios of Sr:Ca indicated that none of these fish migrated to the ocean (i.e. they were entirely freshwater resident). Although anglers report 'sea run' brown trout in the Motueka River, otolith micro-chemistry analysis in this, and other, rivers in South Island suggest that a sea running life history is uncommon, and freshwater residence, with extensive movement within freshwater by a large proportion of the population, is the norm (Kristensen et al. 2007; Hayes et al. 2008).

Flow and water temperature

Much of the hydrological data presented are based on measurements at a long-term monitoring station in the Motupiko River (at Christies Bridge, 23 March 1990–1 November 2006), which has a mean flow of 2.2 m³/s, a median flow of 1.1 m³/s (Basher 2003) and a 7-day MALF of 0.314 m³/s (Tasman district council, unpublished data). A temporary gauging site was established in the Rainy River from 14 February 2004 until 17 October 2004 (pressure transducer (Jumo 4–20 mA) attached to a Nomad data logger (Model GP-HR, Intech Instruments Ltd, Auckland, New Zealand)) to estimate discharge in the study reach. A regression of these data against discharge data from the Motupiko River over the same period was used to derive a relationship between mean daily flows in the study reach with mean daily flows recorded in the Motupiko River.

Water temperature was logged in the study reach at 30–60-min intervals over the period 3 December 2002–18 July 2006.

Sampling

Juvenile trout were usually sampled at three sites in the Rainy River on two occasions per year; in late November/early December and in late March/early April over the period December 2003 to March 2009. These sampling occasions correspond to late spring and early autumn. In

2005, sites were sampled on an additional occasion immediately following a large flood in late March, which occurred just after the regular March sampling. Within each site, sampling was stratified by meso-habitat, with pool, riffle and run habitats being surveyed separately. Contiguous meso-habitats were preferred, but sometimes this was not possible owing to unrepresentative or excessively long meso-habitats. An attempt was made to sample the same meso-habitats, but reworking of the channel by floods meant that we had to relocate meso-habitats and entire sampling sites on some occasions after the big flood in March 2005. Relocated sites offering a riffle, run and pool were selected as close as possible to the original site. Areas sampled were estimated from length measurements of each meso-habitat unit and mean width estimates, which were based on measured wetted widths over three to five cross-sections. The lengths sampled in meso-habitats ranged between 6.8 and 19.1 m, and widths ranged between 2.9 and 10.1 m. Distance between sites ranged between 140 and 1180 m, within the 1760-m study segment.

Juvenile trout were collected by multiple-pass electric fishing using a mains-set electric fishing machine (NIWA Instrument Systems, Christchurch, New Zealand) with two catching electrodes and stop-nets at upstream and downstream limits of each meso-habitat unit. Stunned fish were captured using hand-nets or hand-seines and placed in buckets and live boxes for processing. Fish were anaesthetised using 2-phenoxyethanol, measured to the nearest millimetre and weighed to the nearest 0.1 g. Within each meso-habitat unit, between three and five repeat catches were made without replacement for depletion abundance estimation.

Data analysis

Density, biomass and instantaneous loss rate

Abundance was estimated from the depletion counts using the maximum weighted likelihood approach of Carle & Strub (1978). Density was

then calculated by dividing abundance by the area sampled. Biomass was estimated as the product of density and mean weight for each site. Instantaneous loss rates at each site for 0+ trout between spring and autumn and for 0+ to 1+ trout between autumn and spring were estimated as:

$$Z = (\ln N_1 - \ln N_2) / (t_2 - t_1) \quad (1)$$

where N_1 and N_2 were density at time 1 (t_1) and time 2 (t_2), respectively.

Comparisons of density, biomass and instantaneous loss rate between seasons and years were made with one-way analysis of variance (ANOVA) and Fisher's LSD post hoc tests.

Population self-thinning

Population self-thinning is the process by which density adjusts for increasing mean size of fish over time when populations are close to carrying capacity (Begon et al. 1986; Elliott 1993a; Grant 1993). Self-thinning refers to the allometric relationship between density and body size generally expressed as:

$$\log(N) = a - b \cdot \log(W) \quad (2)$$

where N = density and W = mean body weight. The slope b is the self-thinning coefficient and is thought to be determined by competitive demands of space and food (Elliott 1993a; Grant 1993). The mechanism for the dependence of the self-thinning slope on food is the energetic equivalence hypothesis, which predicts that b is set by the allometry of metabolic requirements of food consumption, assuming constant food availability (Begon et al. 1986; Bohlin et al. 1994). As fish grow and require more energy, fewer individuals survive on the same amount of food. Over a range of species, resting metabolic rate is proportional to individual weight to the power of 0.75 (Kleiber 1961). Elliott (1975a) confirmed this for brown trout, but

Steingrímsson & Grant (1999) reported a mean of 0.87 from a review of studies on salmonids.

The space hypothesis for the self-thinning slope predicts that the allometry of territory size sets the maximum population density for each body size (Grant & Kramer 1990). As fish grow and defend larger territories, fewer individuals fit into a given area. Grant & Kramer (1990) reported a similar scaling of territory size to body mass (0.86) to that reported by Steingrímsson & Grant (1999) for metabolic rate (0.87).

We examined population self-thinning for the first year of life for six cohorts and used the departure of the estimated self-thinning coefficient from the expected coefficients for metabolic rate and territory allometry (0.75–0.87) to assess whether and when carrying capacity was exceeded. This analysis was useful for understanding compensatory survival in response to large-scale flow variation.

We fitted two-phase linear regressions to \log_{10} relationships between density and weight, estimating the break point (or threshold) between the phases by manual iteration until the regression lines converged.

Growth

Elliott et al.'s (1995) brown trout growth model was used to determine whether trout were experiencing food limitation and dependence of growth on density. The model was applied using Hayes's (2000) Excel Visual Basic© Cmax1995 computer programme.

Elliott et al.'s model predicts the wet weight of trout based on water temperature assuming maximum consumption of invertebrate prey (i.e. that the availability of invertebrate food is not limiting growth). The model (equation 5 in Elliott et al. 1995) is expressed as:

$$W_t = [W_0^b + bc(T - T_{LIM}) \bullet t\{100(T_M - T_{LIM})\}]^{1/b} \quad (3)$$

where W_0 is the initial weight of the trout, W_t is the weight after time t at $T^\circ\text{C}$, $b = 0.308$ and

$c = 2.803$. The parameter T_{LIM} is conditional on temperature falling within two ranges as follows: $T_{LIM} = T_L$ if $T \leq T_M$ or $T_{LIM} = T_U$ if $T > T_M$, where $T_M = 13.11$, $T_L = 3.56$ and $T_U = 19.48$.

Modelling was conducted for each of the growth periods between the spring and autumn sampling occasions for five cohorts, spanning the period 17 December 2003 to 30 March 2006. It included the two age-classes of juvenile fish: age 0 and 1. The model was run on a daily time-step with daily water temperature averaged from the 30–60-min water temperature records logged in the Rainy River. Because stream water temperature data were not available for the period from 30 March 2006–4 March 2008, a simulated water temperature time series was determined for this period using the following relationship between mean daily air temperature records for Nelson and mean daily water temperature in the Rainy River: Rainy water temperature = $0.8536 \times$ Nelson air temperature - 1.6906; $P < 0.001$, $R^2 = 0.87$, $n = 1322$.

Because the growth model factors out the effect of temperature on growth, food limitation can be identified by observed growth falling short of predicted growth. This convenient property of the model also allowed us to determine whether growth was density dependent, by examining the correlation between the weight residuals (observed–predicted) and mean cohort density and total biomass of all cohorts applying over each spring–autumn and autumn–spring period.

Results

Flow and water temperature

Flows in the Rainy River were highly correlated with flows in the Motupiko River at Christies Bridge (regression equation: Rainy = $0.5996 \times$ Motupiko - 0.2892; $P < 0.0001$, $R^2 = 0.843$, $n = 248$, flow range 0.33–25 m³/s), confirming that flows recorded at the Motupiko recorder could substitute for relative flow conditions in the Rainy River. Low flows were recorded in early

2003 (prior to the study beginning) and 2007 (Table 1) with estimated return intervals of 8.8 and 8.4 years, respectively. In 2003, flows in the Motupiko River were below MALF on a total of 72 days and below the 5-year 7-day low flow for 11 consecutive days, with most of these low flows occurring in February and March (Table 1). In late February–April 2007, flows in the Motupiko River were below MALF on a total of 46 days and below the 5-year 7-day low flow for 6 consecutive days (Table 1).

In late March 2005, an exceptionally large flood affected the Rainy and Motupiko Catchments. Its instantaneous peak flow was 166 m³/s in the Motupiko River (Table 1) and it had an estimated recurrence interval of more than 50 years. Peak discharge in the study reach was estimated at 70 m³/s and this event caused major changes to channel structure. Another large flood occurred in October 2007, and had a peak discharge of 65 m³/s in the Motupiko River (Table 1; estimated $Q_{max} = 27$ m³/s in Rainy) and an estimated recurrence interval of approximately 6 years.

The frequency of flows in excess of three times the median flow (3.3 m³/s for the Motupiko River), known as the FRE-3 (Clausen & Biggs 1997), was greatest in 2004 with 21 events of this magnitude or greater occurring within the year (Table 1). By contrast, the years with the lowest frequency of events of this magnitude were 2003, 2005 and 2007 (Table 1).

Water temperatures in the study sites ranged from 1.3 to 22.3°C (over 3 December 2002–18 July 2006), with a mean temperature of 9.7°C (over the period 3 December 2002–3 December 2005) (Fig. 2).

Density and biomass

Densities of trout fry in late spring over the years 2003 to 2006 were similar (Fig. 3a; one-way ANOVA: $F_{5,12} = 4.11$, $P = 0.021$, Fisher's LSD test). By contrast, initial densities of fry in 2007 were lower than those observed in

Table 1 Summary of hydrological variables for the Motupiko River (at Christies) for the period 2002–2009.

	Year						
	2003	2004	2005	2006	2007	2008	2009*
Mean flow, m ³ /s	1.48	2.20	1.24	1.79	2.01	2.18	0.66*
Median flow, m ³ /s	0.71	1.26	0.68	1.02	0.90	1.28	0.50*
Minimum flow (7-day average), m ³ /s	0.17	0.30	0.25	0.22	0.18	0.32	0.31*
Timing of minimum flows	28 Mar 03	28 Jan 04	4 Dec 05	2 Apr 06	30 Mar 07	22 Jun 08	12 Feb 09
Maximum flow (instantaneous), m ³ /s	37	33	166	39	65	37	4.94*
Timing of maximum flows	4 Oct 03	18 Jun 04	25 Mar 05	24 Apr 06	7 Oct 07	15 Feb 08	21 Feb 09
Number of records (96 × number of days)	35040	35136	35040	35040	35040	35136	9239*
Minimum flow (7-day)/MALF (7-day)	0.54	0.96	0.80	0.70	0.57	1.19	0.99
number days < 7day MALF	72	2	14	23	46	0	0*
number days < 5-year 7-day LF	11	0	0	0	6	0	0*
number days < 10-year 7-day LF	0	0	0	0	0	0	0*
FRE-3	9	21	9	16	10	15	na

FRE-3 is the frequency of flows exceeding three times the median flow (3.3 m³/s). *Only part of the 2009 record was analysed (1 January–31 March 2009), na, not applicable.

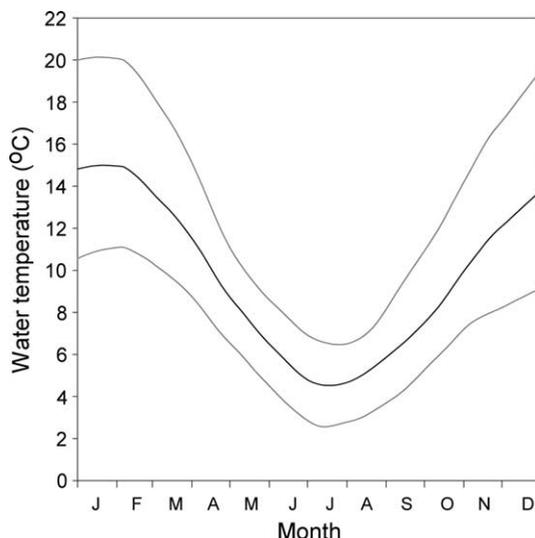


Fig. 2 Smoothed plots (Loess, tension = 0.2) of seasonal variation in mean, minimum and maximum water temperatures in the Rainy River study site. Based on temperature data collected over the periods: 3 December 2002–18 July 2006 and 4 March 2008–22 April 2009.

2004–2006, while initial densities of fry in 2008 were lower than those observed in 2004 and 2005 (Fisher's LSD test). Densities of 0+ fish in autumn were generally similar among years, with the exception of those in 2008, which were markedly lower than in other years (Fig. 3a; one-way ANOVA: $F_{5,12} = 3.82$, $P = 0.027$, Fisher's LSD test).

Total biomass (0+ and 1+ trout combined) was generally similar between seasons and between years during the period 2003–2006, with the exceptions to this being that total biomass estimates immediately after the March 2005 flood and in December 2006 were lower than the March 2006 estimate (Fig. 4; one-way ANOVA: $F_{11,24} = 6.71$, $P < 0.0001$, Fisher's LSD test). A single adult brown trout (550 mm, 1900 g) was captured in one of the pools sampled during the December 2006 survey. A large fish that was likely to be the same individual was also observed in September 2006 in a similar location. In addition, total biomass in March 2006 was significantly higher than that observed in December 2003, March 2004 and December 2004, and biomass in March 2007 was significantly higher

than biomass in December 2007 (Fig. 4). The density and biomass of the 2007 and 2008 cohorts were low relative to the cohorts of 2003–2006 (Fig. 3a, b) and consequently the total biomass of juvenile trout observed between December 2007 and December 2008 was markedly lower than in previous years (Fig. 4). Curiously, densities of 0+ fish in March 2009 were similar to densities observed in December 2008, in contrast to all previous years where the density of 0+ declined markedly between December and March (Fig. 3a).

Total biomass was much more variable after 2005 (post-March flood) than beforehand, related partly to fewer yearling fish present in December.

The March 2005 flood (a 1-in-50-year event) substantially reduced the abundance (by 66% relative to pre-flood densities) and biomass (by 73% relative to pre-flood) of the 2004 cohort, but this effect was relatively short-lived, with the biomass observed in December 2005 being similar to values observed in spring sampling occasions in previous years (Fig. 3a, b). Low flows observed in February–April 2007

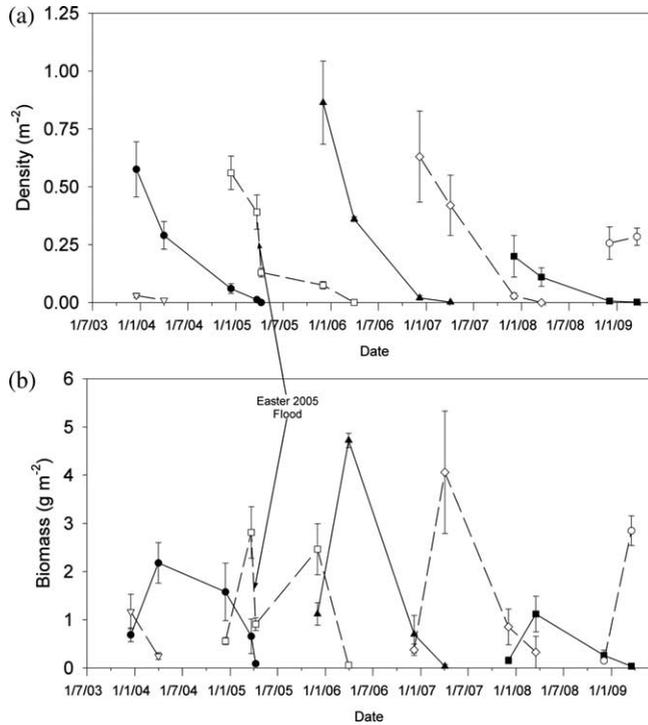


Fig. 3 (a) Density (number/m²) and (b) biomass (g/m²) estimates \pm SE for seven cohorts (year classes) of juvenile brown trout in the Rainy River based on biannual electrofishing surveys of three sites (each consisting of a riffle, run and pool) between 2003 and 2009.

did not appear to affected density or biomass in autumn or the following spring (Figs. 2 and 3).

Instantaneous loss rates of 0+ trout were similar between years over the autumn–spring period (one-way ANOVA, $F_{4,10} = 2.840$, $P = 0.082$) despite the March 2005 flood severely depressing densities of the 2004 cohort. Instantaneous loss rate of 0+ trout following this flood (from April–December 2005) was significantly lower than the autumn–spring loss rates in all other years except 2004 (one-way ANOVA, $F_{4,10} = 5.655$, $P = 0.0121$; Fishers LSD test $P < 0.01$). Instantaneous loss rates of 0+ trout over the spring–autumn period were similar between years for all except the 2008 cohort, with the latter being significantly lower than other years (one-way ANOVA, $F_{5,12} = 12.857$, $P < 0.001$, Fishers LSD test, $P < 0.001$).

Self-thinning

The compensatory survival following the March 2005 flood prompted us to examine evidence for population self-thinning. The relationship between \log_{10} density and \log_{10} weight exhibited a two-phase pattern (Fig. 5). The first phase extended for the first 4–5 months, over the fry to fingerling stage (i.e. December to April–May). During this phase, the density of survivors remained largely unchanged, despite increasing mean weight. The slope of the regression of \log_{10} density on \log_{10} weight during this first phase was not significantly different from zero ($F_{1,10} = 1.738$, $P = 0.216$, $R^2 = 0.15$), indicating that self-thinning did not take place. The second phase occurred between the fingerling and yearling stage (i.e. April–May–December). The break point between the phases occurred at a

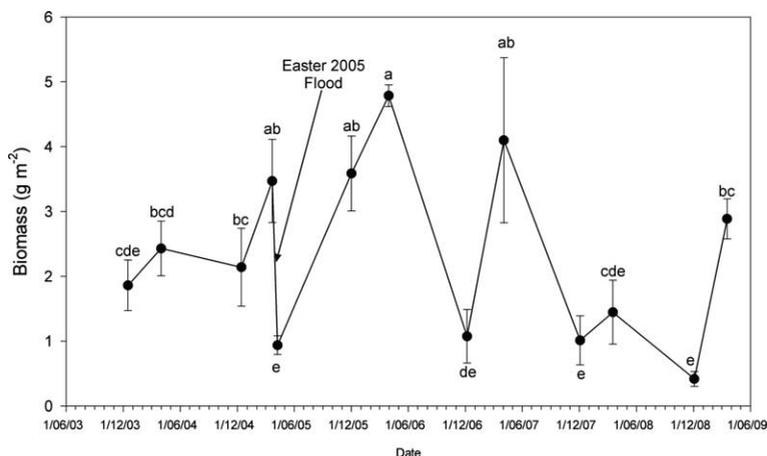


Fig. 4 Total biomass (g m^{-2}) estimates of juvenile brown trout (age 0 and age 1 combined) in spring and autumn in the Rainy River based on biannual electrofishing surveys of three sites (each consisting of a riffle, run and pool) between 2003 and 2009. Lowercase letters for each data point present the results of Fisher's LSD tests, with no statistical difference ($\alpha = 0.05$) between points that share the same letter.

weight of 22.08 g (length = 123.7 mm; \log_{10} weight = 1.334) and density of 0.31 fish/ m^2 (\log_{10} density = -0.585). The time taken from emergence to the threshold weight was about 150 days, assuming that mean time of emergence was about early November (about 45 days prior

to spring sampling). This second phase was characterised by a statistically significant, steep decline in \log_{10} density with increasing \log_{10} weight ($F_{1,4} = 9.509$, $P = 0.037$, $R^2 = 0.70$), providing evidence for self-thinning. The self-thinning slope over this second phase (-4.977) was substantially steeper than expected based on the allometry of metabolism to weight [-0.75 to -0.87 (Elliott 1975a; Steingrímsson & Grant 1999)] or allometry of territory size to weight [-0.86 (Grant & Kramer 1990)], suggesting severe food or space limitation.

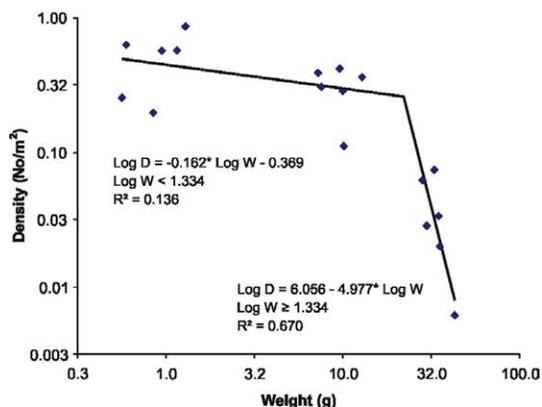


Fig. 5 Density versus weight relationships for juvenile brown trout from the Rainy River. Different regression lines are fitted to the two-phase self-thinning trajectories for fish < 22.08 g (including 0+ fish sampled in December (fry) and March fingerlings) and fish ≥ 22.08 g (yearlings sampled in December). Axes scales have been converted from \log_{10} to untransformed units to facilitate interpretation of actual densities and weights.

Growth

For most occasions, weight predicted by the growth model was either similar to or less than observed weight, which indicates that in the main food was not limiting growth (Fig. 5). Nevertheless, there were some discrepancies between predicted and observed growth. The model consistently under-predicted the weight of 0+ fish at the end of their first summer relative to observed weights (Fig. 6). However, the most notable deviation from the model's prediction was for the 2002 cohort in March 2004, when the observed mean weight (48.4 g)

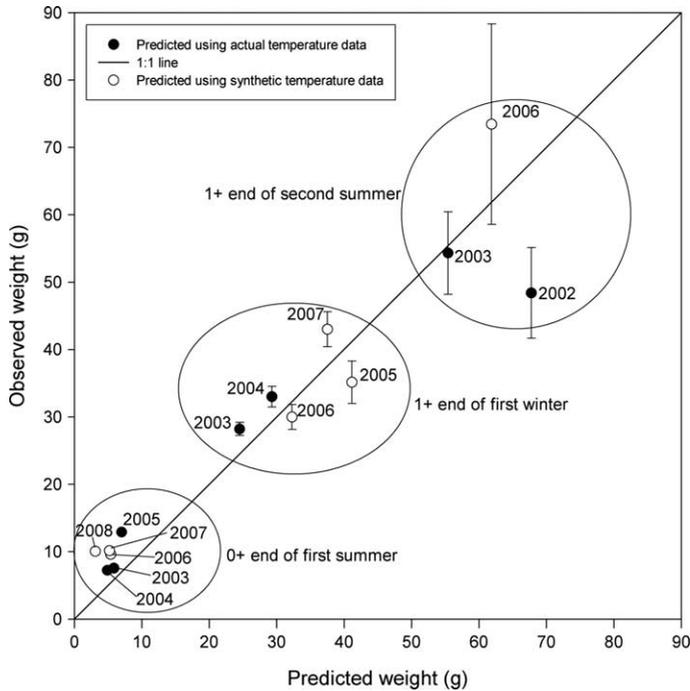


Fig. 6 Predicted weight of 0+ and 1+ brown trout from the Rainy River compared with observed weight for each sampling occasion. Data points are labelled by cohort, i.e. year hatched. Modelling was conducted using either actual mean daily water temperatures from temperature loggers (solid symbols) or mean daily water temperatures estimated from a correlation between water temperature in the Rainy River and air temperature at Nelson ($P < 0.001$, $R^2 = 0.87$, $n = 1322$). Error bars are one standard error on the mean observed weight.

was markedly lower than the weight predicted by the growth model (67.8 g).

A comparison of the weight residuals (observed–predicted weight) and mean cohort density and total biomass of all cohorts applying during the growth periods spring–autumn and autumn–spring, revealed no significant relationships; the regression coefficients were not significantly different from zero ($F_{1,12} = 1.985$, $P = 0.184$, $R^2 = 0.14$; $F_{1,12} = 1.298$, $P = 0.277$, $R^2 = 0.10$). This, and the previous result, indicates that growth was not density dependent and food was not limiting.

Discussion

Two significant floods and one significant low flow event occurred during our study,

presenting the opportunity to consider the effects of both high and low flow events on the juvenile trout population. Analysis of these effects has provided insights into the relative importance of density-independent (abiotic) and density-dependent controls on loss rates. We use the term loss because we could not distinguish between mortality and emigration. These insights are useful in assessing the likely sensitivity of juvenile trout populations to low flow management in the context of natural variability in population parameters.

Mortality of juvenile salmonids over the first year of life, particularly in the first 6 months, is high—in excess of 90% related to both biotic and abiotic causes (Allen 1951; Chapman 1962; LeCren 1965; Mortensen 1977). Much of the mortality in the first year

may take place over a critical period in the first few weeks following emergence. Elliott (1993b, 1994) found the critical period to vary between 30 and 70 days and to be density dependent; after the critical period, survival was proportionate. However, the existence of a critical period is not universal, as other studies have failed to find evidence for it (Elliott 1987, 1994). Our fry sampling, in early December (late spring), may have been too late to catch the critical period, if in fact it occurs in the Rainy River. We waited until fry had grown to about 40 mm in length before first sampling because smaller, recently emerged fry are not efficiently sampled with electric fishing equipment. Most fry probably had emerged about one month before our early December sampling.

Effects of floods

Abiotic factors, principally floods and droughts can also be agents for significant loss (mortality and displacement) of stream salmonids, and of juveniles in particular (Lobón-Cerviá 2009). Floods can have severe adverse effects at all stages of the life cycle but usually during late incubation and emergence of fry (Allen 1951; Elliott 1994; Jowett & Richardson 1989; Hayes 1995; Lobón-Cerviá 1996; Harvey et al. 1999; Jensen & Johnsen 1999; Nislow et al. 2002), significantly affecting year-class strength (Mortensen 1982; Elliott 1987; Nehring and Anderson 1993; Cattaneo et al. 2002; Lobón-Cerviá 2009). In addition to direct mortality caused by floods, associated high water velocity may also displace fry (Ottaway & Forrest 1983; Crisp & Hurley 1991) and reduce their suitable habitat (Nehring & Anderson 1993) and food availability (Elwood & Waters 1969).

The low initial density and biomass of the 2007 cohort recorded in the Rainy River in early December was preceded by a flood in early October with an estimated $Q_{\max} = 27 \text{ m}^3/\text{s}$ and return interval of ~ 6 years at the study site. However, low initial density and biomass was also observed in December 2008, but was not preceded by particularly high flows during

the incubation and emergence period. A debris dam, discovered downstream of our study sites in 2010, probably impaired upstream migration of spawners and is the most likely explanation for reduced recruitment observed in 2007 and 2008.

Of particular note was the March 2005 flood, which had a return interval of at least 50 years. This unusual event caused extensive changes to channel structure in the study reach and substantially reduced the abundance and biomass of the 2004 cohort, by 66% and 73%, respectively. However, by sampling immediately before and after this flood, and the following spring, we found that its effect was not long-lasting at the study sites; the density and biomass of yearling trout (the 2004 cohort) observed in December 2005 was similar to those observed in spring in other years. This came about because instantaneous loss rate following the flood to December 2005 was significantly lower than the autumn–spring loss rates in all other years except 2004. This observation provides evidence of density-dependent loss overtaking abiotic, density-independent loss over the longer term and is consistent with self-thinning (Begon et al. 1986; Grant 1993; Elliott 1994), whereby the density of a cohort of growing organisms that is close to carrying capacity declines because each individual needs a proportionately greater share of resources.

Self-thinning

When we examined the relationship between mean density and mean weight, we found evidence for severe self-thinning over the autumn–spring (March–December) period. The self-thinning slope (-4.977) was substantially steeper than those expected from the allometry of density to metabolism [-0.75 to -0.87 (Elliott 1975a; Steingrímsson & Grant 1999)] and territory size [-0.86 (Grant & Kramer 1990)]. The self-thinning slope was also markedly steeper and the length of the pre-thinning period was shorter than has

previously been reported in the literature (Steingrímsson & Grant 1999; Lobón-Cerviá 2008), whereas the threshold mass fell within the reported range [12.4–37.2 g (Lobón-Cerviá 2008)]. Elliott (1993a) reasoned that differences in self-thinning slopes could reflect variation in food supplies and therefore also indicate differences in carrying capacity. Gentle slopes indicate abundant food supplies, whereas steep slopes indicate low food supplies and decreasing food availability per capita (i.e. reduced carrying capacity). Following this argument, the steep self-thinning slope for trout in the Rainy River over autumn to spring (−4.977) would suggest that food or feeding space may be severely limited over this period in the Rainy River. Although metabolic demands of fish are lowest in winter (5–7°C mean temperature in winter in the Rainy; Fig. 2) and therefore food competition ought to be least likely then, food-limited growth has been reported for brown trout over winter elsewhere (Elliott 2009). However, a food limitation explanation is inconsistent with our growth modelling results, which indicated food was not limiting and growth was not density dependent in the Rainy trout population. Alternatively, winter hiding habitat may be limiting. Stream salmonids typically seek interstices among coarse substrate elements, or aquatic vegetation, for cover during winter, presumably for refuge from predators and floods while their swimming performance is compromised by cold temperature (Heggenes et al. 1993; Heggenes 2006). On the other hand, the Rainy trout population may be inherently migratory, independent of local environmental conditions, as has been suggested for juvenile brown trout in another New Zealand stream (Kristensen & Closs 2008). Nevertheless, it seems counter intuitive for all fish to vacate a stream (which they appear to do in the Rainy River by age 2+) if habitat and food conditions were sufficient to support residency. In our opinion, the most likely explanation is that the observed pattern of loss rate is a life history strategy that prompts fish to emigrate to deeper, more cover rich, and

possibly more productive habitats, downstream at an early age, driven by rapid growth rate (because of favourable temperature conditions), which anticipates fish out-growing suitable habitat and food conditions in shallow head-water streams before maturity at about age 4.

Water temperature in the Rainy River was reasonably favourable, although less than optimal for brown trout growth (mean annual water temperature = 9.7°C versus optimal temperature for growth = 13.9°C (Elliott et al. 1995) and the trout were growing at maximum rate for an invertebrate diet. Their fast growth induced by relatively favourable water temperatures, and unlimited by food, explains why the length of the pre-thinning period was shorter than reported by other studies.

By contrast to the autumn–spring period, we found no evidence for self-thinning over the late spring–early autumn period (December to April/May), indicating that the population remained below carrying capacity over that period. The two-phase density versus weight relationship that we found is similar in pattern to those reported for several streams in Spain by Lobón-Cerviá & Mortensen (2006) and Lobón-Cerviá (2008). The main difference in the two-phase relationships between sites in these studies and the Rainy River was in the length of the pre-thinning period. Lobón-Cerviá (2008) found that threshold density at the onset of the second phase, as a proxy for cohort strength, and mass, as a proxy for the growth experienced by individuals during the second phase, had strong effects on the second-phase self-thinning slopes. He concluded that mortality increased at a greater rate at sites where more abundant individuals grew faster, which is strongly consistent with the major assumption of self-thinning that intensity of intraspecific competition determines how quickly cohorts decline.

The energetic equivalence hypothesis (i.e. the allometry of density to metabolism) assumes that energy availability is constant over time (Bohlin et al. 1994). However, energy availability to stream salmonids over the first

summer of life is unlikely to be constant because as fish size, and mouth gape, increases, a larger range of prey sizes can be consumed and hence food availability increases (Elliott 1993a). By autumn the trout in the Rainy are large enough (10 g, 90 mm) to capture and ingest almost the full range of aquatic invertebrate prey sizes available. Assuming an aquatic invertebrate prey length:diameter ratio of 4.3 applied to the maximum prey size ingested (Hayes et al. 2000), a 90-mm trout could ingest prey in the size range 1.0–40.6 mm (Wankowski 1979).

As the population thins and individuals gain a greater per capita share of available food, total biomass might be expected to remain the same, i.e. total spring biomass ought to be similar to the previous autumn biomass in the Rainy. This was largely true except in 2006 and 2007 (Figs. 3 and 4). The large flood in October 2007 may explain the latter, through displacement and mortality of fish and invertebrate prey. No particularly large floods, or low flows, of a magnitude that might be expected to explain the former, occurred between autumn and spring in 2006. However, there were two reasonably large freshes just before this period (in mid-November), approximately 32 m³/s (cf. annual flood 49.8 m³/s). The streambed morphology and substrate in the study reaches appear to have been relatively unstable ever since the extreme flood that occurred in late March 2005, as evidenced by the need to frequently move our study sites following this event, because of ongoing channel changes. It is possible that, although these freshes were not particularly large, they may have been sufficient to cause substantial displacement or mortality of fry, particularly since the timing coincides with the early free swimming phase following emergence from the redds, when fry are known to be particularly susceptible to wash-out (Ottaway & Forrest 1983; Crisp & Hurley 1991).

Trout share the Rainy River with six other fish species, four of which are common, which raises the question whether these have any

competitive or predatory influence on trout population dynamics. The combined density of the four main native sympatric species (longfin and shortfin eel, upland bully and dwarf galaxias) usually did not exceed 0.5 fish/m² during our study. This compares with a mean trout density (combined cohorts) of 0.41 fish/m² (range = 0.12–0.94 fish/m²). So on some occasions the densities of native fish were on par with those of trout. Moreover, eels dominate the fish community biomass, with some individuals attaining or exceeding 3000 g. This contrasts with an average combined cohort trout biomass of only 2.32 g/m² (range = 0.42–4.79 g/m²). Therefore, given that most of the native fish have an invertebrate diet (as do juvenile trout) there is the potential for exploitative competition. Clearly though, the lack of evidence for self-thinning in the trout population over the spring–autumn period indicates that interspecific competition over the main seasonal growth period is not significant in the Rainy River. However, this does not preclude influence by native fishes on trout through interspecific predation. Large eels are the top aquatic piscine predator in New Zealand freshwater ecosystems so they could well be a major agent of trout (and smaller native fish) mortality, at least over the spring–autumn period. Interspecific predation by and competition with eels are unlikely to be major causes for the severe self-thinning occurring in the trout population over the spring–autumn period, because eels reduce their activity over winter and some even hibernate (McDowall 1990). Feeding activity by eels is substantially reduced when temperatures drop below 10°C (Todd 1982), which is the case over most of the autumn–spring period in the Rainy River (Fig. 2).

Effects of low flows

The period of low flows in February–April 2007 when 7-day low flows fell to 56% of the 7-day MALF and were less than the MALF for 46 days (Table 1) (recurrence interval ~8.4 years) did not appear to adversely affect juvenile trout

in the Rainy River. The loss rate of 0+ fish between December 2006 and March 2007 was similar to or less than that in the previous 3 years when low flows were higher (between 70% and 96% of the MALF) and were maintained for shorter durations (2–23 days) (Table 1). Furthermore, the observed average weight gain for the 2006 cohort exceeded predicted growth, and biomass increased at a similar (or greater) rate to that observed in previous years.

The lack of evidence for self-thinning over the spring–autumn period indicates that the population did not exceed carrying capacity over the period of record. This evidence, coupled with the fact that the period of record included the February–April 2007 low flow event indicates that the Rainy juvenile trout population is quite insensitive to low to moderate variation in summer low flows. In light of Lobón-Cervía's (2008) wide-scale Spanish stream study, it appears that it is not uncommon for brown trout cohorts to remain below carrying capacity over at least the first summer of life.

Further evidence of the resilience of the population to flow variation is provided by the recovery from the impact of the March 2005 flood. The observed loss rate (and therefore the self-thinning trajectory) adjusted to compensate for lower post flood densities, with the result that densities by spring of that year were similar to other years. Whether flow variation (high or low flow) can be considered to affect juvenile trout populations adversely depends on the contribution of juveniles to downstream parent populations. In this regard, an important information gap in our study is the relative contribution of mortality versus emigration to our loss estimates and the fate of migrants. The decline in density of stream salmonids related to self-thinning, resulting from competition for territories, is thought to be mediated through the movement of subordinates downstream to less saturated habitats (Chapman 1962; Elliott 1986; Nakano 1995). Emigration of juvenile trout, and their contribution to the

downstream populations, provides a potentially rich avenue for further investigation, which we are pursuing.

Lastly, these inferences pertaining to flow variation when self-thinning occurs relate only to juvenile populations upon which self-thinning operates. Adult trout populations composed of multiple age classes do not exhibit the dramatic annual cycle of decreasing abundance associated with increasing size characteristic of juvenile trout (Allen 1951; McFadden et al. 1967; Elliott 1994; Jowett 1995; Hayes 1995). Impacts from floods or low flows on adult trout populations, although less common, are therefore likely to be more lasting—with abundance and biomass remaining depressed until new year-classes are recruited into the population (Lobón-Cervía 2009).

Growth

Our approach to determining that trout in the Rainy River were not food limited and that growth was not density dependent was based on a comparison of observed with predicted growth; the assumption being that if observed growth matches predicted maximum growth then food must not be limiting. Comparison between residual weight (observed–predicted) and mean density and mean total biomass indicated that growth was not density dependent. The attraction with this approach is that the growth model accounts for the influence of temperature on growth, allowing the effect of food (and related density) to be isolated. This is different from the traditional approach to investigating density control on growth, which looks for correlation between density and mass, growth rate or per capita production (Jenkins et al. 1999; Lobón-Cervía 2007). A drawback with this traditional approach is that the effect of food (and density) is confounded with the effect of temperature. Elliott (2009) used the same growth model to assess food limitation and compensatory growth in juvenile anadromous brown trout in a small English stream, but he resorted to comparing mean mass with density

to determine that growth was not density dependent.

The observed weight of 0+ trout in the Rainy River was consistently greater than predicted based on our growth modelling, including in the year with the 1-in-8-year low flow (i.e. the 2006 cohort during the 2007 summer), whilst the observed weights of 1+ fish were consistent with modelled growth on all but one occasion. A small number of studies have found an earlier version of Elliott's growth model (Elliott 1975b) under-predicted observed growth, including one in New Zealand (Allen 1985; Jensen 1985). This model has been superseded by a better model based on more data and fewer parameters that are physiologically meaningful (Elliott et al. 1995), and this was the model used in our study. The only other published New Zealand study using this model demonstrated that, when coupled with a drift foraging model, it accurately predicted whole-life-time growth of brown trout in the Maruia River (Hayes et al. 2000). Furthermore, our experience in using this growth model on a wide range of New Zealand brown trout populations is that it has rarely under-predicted trout growth. Under-prediction is a sign of possible model failure, whereas over-prediction is not because this is expected owing to food limitation. A comprehensive study testing the Elliott et al. (1995) model in 42 populations covering a wide latitudinal variation in Europe showed that observed growth exceeded predicted growth in only eight Norwegian populations, all living in the coldest rivers with mean annual temperature below 5.1°C (Jensen et al. 2000). This study included a reanalysis of an earlier Spanish study that found that the Elliott et al. (1995) model under-predicted observed growth (Lobón-Cerviá & Rincón 1998). Another, recent, Spanish study supported Jensen et al.'s (2000) conclusion; the model underestimated the growth of brown trout in the coldest rivers (Nicola & Almodóvar 2004). The 5.1°C mean annual temperature threshold, mentioned above, excludes all New Zealand trout streams. Elliott (2009) reported another discrepancy in

the model's predictions. He found that 0+ sea-migratory brown trout demonstrated compensatory growth following periods of summer growth limitation in response to droughts (i.e. they grew faster than predicted by the model during the compensatory growth period). However, the overall result was that observed size of the corresponding 1+ trout matched that predicted by the model. Elliott concluded that although the documented discrepancies demonstrate that the Elliott et al. (1995) growth model is not comprehensive, it nevertheless performs well enough in most circumstances to provide a useful baseline from which changes in growth can be assessed.

The apparent under-prediction of growth of fish <15 g (Fig. 6) by the model in our study could simply be related to size selective mortality operating on small individuals. Recently emerged fry contribute to depressing the mean size estimates used for initial (spring) weight for growth modelling and these fish would have lower survival than larger fry. This hypothesis is consistent with the critical period concept, whereby density-dependent mortality operates over a short time window after emergence (e.g. 30–70 days; Elliott 1993b, 1994), and would explain why under-prediction of growth was found for 0+ but not 1+ fish.

The fact that observed growth of 0+ and 1+ fish was greater than, or similar to, predicted growth for the majority of occasions indicates that food was not limiting growth in the Rainy, and analysis of the weight residuals indicated that growth was not density dependent. An exception appeared to be 1+ fish in March 2004. On that sampling occasion, the observed weight of 1+ fish (2002 cohort) was markedly lower than the weight predicted by the growth model. It is difficult to determine the reason for this observation, as this was at the start of our study so we do not have previous information on this cohort. However, this sub-optimal growth rate does not appear to be attributable to low flows. The flow did briefly drop slightly below the MALF during the summer of 2004. However, similarly low

flows were recorded during the summer of 2008 and yet 1+ fish in that year (the 2006 cohort) achieved maximum weight gain as predicted by the growth model. The summer of 2003 was dry, with low flows reaching levels with a 1-in-8-year return period. However, it is difficult to conceive how the observed sub-optimal growth could be attributable to a lingering effect of these low flows. Again the 2006 cohort also experienced comparable very low flows in their first summer of life (\sim 1-in-8-year return period), but showed no sign of reduced growth rates the following summer.

Lack of evidence for food limitation and density-dependent growth in the Rainy is consistent with our self-thinning and biomass results indicating that the population remained below carrying capacity over summer and generally self-thinned sufficiently over winter for survivors to attain a greater per capita share of available food commensurate with their increasing size.

There has been some confusion in the literature over density-dependent growth in brown trout and other stream salmonids, but a consensus appears to be emerging from recent studies (Jenkins et al. 1999; Lobón-Cerviá 2005, 2007; Elliott 2009). Jenkins et al. (1999) demonstrated that density dependence of mass (and growth) is difficult to detect at high population density but is more apparent at lower density, and this was confirmed by others (Grant & Imre 2005; Lobón-Cerviá 2005, 2007). When sufficiently wide data ranges have been examined negative power trajectories between density and fish mass, per capita production or growth have become apparent (Lobón-Cerviá 2005, 2007). Density-dependent growth is usually most apparent at densities on the steepest, left hand extremes of these curves within the range 0.1–2 fish/m² (Lobón-Cerviá 2005). Mean density of juvenile trout in the Rainy River during our study was in the lower end of this range (<1 fish/m²) so density-dependent growth should have been apparent if it had occurred.

Conclusions and management implications

Our study emphasises the importance of long-term population monitoring to assemble data on population dynamics to inform assessment of effects of artificial flow change against the background of natural flow variation. The results on self-thinning in particular provide much needed empirical data on actual population response to inform flow decisions based on historical flow and habitat modelling methods. Our study is the first in New Zealand to demonstrate relationships between flow variability and fish population responses based on several years of record. Previous studies have been short term, lasting no longer than 3 years. Reassuringly, our study suggests that juvenile trout populations at the local scale should be relatively robust to even quite large-scale flow variation (floods and probably also temporary reductions in low flow) when they exceed carrying capacity and are subject to strong self-thinning. However, this will depend on the timing of flow variation, with negligible effects on final density expected when high or low flows occur at the beginning of a self-thinning period but adverse effects expected when they occur at the end of such a period. Another qualifier is that in terms of population impacts, it is important also to consider wider-scale effects on recruitment of migrants to downstream populations, and this is an issue that requires further research. Our study also provides evidence for excess summer carrying capacity, supported by research elsewhere (e.g. Spain), and related insensitivity of 0+ trout abundance and growth to summer low flow reductions. Such information is needed to understand whether fish populations are naturally limited by food and space in rivers and their capacity to cope with flow alteration.

A significant management implication arising from our study is that we have identified ecological redundancy, which could be exploited for flow allocation. Because carrying capacity was not exceeded over spring–summer, a not insubstantial portion of the

flow could be abstracted for short periods (weeks) for out-of-stream use without affecting the juvenile trout population. Moreover, a lesson from the autumn–spring period is that even when carrying capacity is exceeded, self-thinning trajectories may also offer opportunity for flow allocation. If juvenile trout populations can recover from such large flow variations as the March 2005 flood, then they ought to more easily recover from temporary reductions in carrying capacity resulting from seasonal flow abstraction such as occurs with irrigation demand (usually less than 30% reduction relative to MALF for durations in the order of 1–4 weeks). Abstraction demand traditionally occurs in summer with irrigation, although there is a growing interest in abstraction at other times for water storage schemes—and for hydropower generation. However, there is an important qualifier to the above assumption. The potential for lasting effects of artificial flow reduction will also depend on the duration of low flow. For example, if flow were artificially lowered year round, such as can occur with hydro-power diversions, then the carrying capacity would be reduced. In such circumstances, if self-thinning already occurs under the natural flow regime, then the final density and biomass, after self-thinning operates under the residual flow regime, will be reduced.

Of course, carrying capacity also varies over time and space (Lobón-Cerviá 2008), which complicates assessment of effects of artificial flow change. In our opinion, keys for dealing with this problem are first to reference density, mass and biomass against reported ranges over which density dependence appears to operate (e.g. Lobón-Cerviá 2005, 2007, 2008). Second, to assess carrying capacity metrics with respect to ecologically relevant flow statistics, a fruitful approach pioneered on fish habitat and periphyton community metrics by New Zealand researchers (e.g. Jowett 1992; Clausen & Biggs 1997; Biggs et al. 1998; Jowett & Biggs 2006).

Finally, our study demonstrates that juvenile trout populations can be resilient to low flows that fall below the MALF for quite considerable periods. This is a significant conclusion given that fish conservation advocates in New Zealand (e.g. Department of Conservation and Fish and Game New Zealand) sometimes demand that minimum flows be set no lower than the MALF, based largely on research by Jowett (1992), and related flow management decision precedents. This is a reasonable starting position when little is known about the fish populations, especially whether carrying capacity is exceeded, but our study cautions against generalisation. Of course, resilience will to some extent be site specific. Nevertheless, depending on how limiting food and space is, compensatory survival associated with self-thinning should impart resilience even when resources are limiting—notwithstanding our caution about the contribution of migrants to downstream fisheries.

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