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Food consumption rates of piscivorous brown trout (*Salmo trutta*) foraging on contrasting coregonid prey

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Abstract Knowledge of predator–prey dynamics is essential to understand ecosystem functioning. Quantification of such interactions is important for fisheries management, in particular in the case of stocking programmes. Here, food consumption rates (*FCR*) were quantified for wild and stocked piscivorous brown trout, *Salmo trutta* L., in three subarctic lakes with contrasting coregonid (*Coregonus* spp.) prey communities, using the Wisconsin and the Elliott–Hurley bioenergetic models. *FCR* was highest for stocked brown trout in lakes with the lowest predator densities, and lowest for wild brown trout. Although FCR estimate may vary somewhat depending on the specific model used, such tools are imperative for the proper impact assessment of brown trout stocking programmes and for the provision of advice on optimal stocking densities.

KEYWORDS: Elliott model, population dynamics, predator-prey dynamics, vendace, whitefish morphs, Wisconsin model.

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Introduction

Large piscivorous fish are highly valuable as human food resources and support important recreational fisheries around the globe. Piscivores are also essential top-down controllers of ecosystems as predation has decisive direct and indirect effects on the behaviour, life history, abundance and size structure of prey populations. The switch to a fish diet by piscivores permits energetic requirements to be maintained as individuals grow larger, and there has been an increasing interest in combining studies of predator diet and food consumption rates with population density estimates of both predator and prey (Svanbäck & Persson 2004; Scharf *et al.* 2009; Jensen 2009). Correspondingly, the selectivity of a predator is influenced by the relative species composition of the prey community (Stephens & Krebs 1986; Sih & Christensen 2001), and consumption rates influence prey abundance (Abrams & Ginzburg 2000), which in turn may affect overall ecosystem function (Allan *et al.* 2005; Belgrano *et al.* 2005). Thus, it is important to incorporate population densities of predator and prey into food consumption studies of piscivorous fish to understand the population dynamics and energy flow within food webs.

Bioenergetic models have been widely used as tools in fisheries management and research to estimate food consumption rates at the individual and population level to quantify the direct effects of predators on prey populations and ecosystems (Hewett & Johnson 1992; Elliott & Hurley 2000; Chipps & Wahl 2008). Although the application of bioenergetic modelling has increased, many models for important piscivores have not been adequately evaluated using independent field and/or laboratory data (Héroux & Magnan 1996; Chipps & Wahl 2008; Whitledge *et al.* 2010). Bioenergetic models may also be based on different input parameters (e.g. water temperature, feeding rates and growth efficiency) of species-specific characteristics, potentially making reliable estimates of food consumption rates difficult to achieve (Chipps & Wahl 2008). Although bioenergetic models are general in their framework, the typical situation is that no specific parameterised model has been experimentally calibrated to the particular population of interest for a field investigator or a fisheries manager. Hence, it may be informative to compare the output from different bioenergetics models to get a more realistic view of the model sensitivity and output differences.

The widely distributed brown trout, *Salmo trutta* L., typically turn to piscivory at lengths of 15–25 cm in lake and marine environments (L'Abée-Lund *et al.* 1992; Næsje *et al.* 1998; Rikardsen & Amundsen 2005), depending on sympatry with other fish species and the availability of prey fish of suitable size (Sánchez-Hernández & Amundsen 2015). Brown trout are commonly stocked into waters as it is a popular sport fish and due to conservation purposes. The subarctic Paatsjoki/Pasvik watercourse in northern Fennoscandia (Finland, Norway and Russia) provides an adequate set of different lake types for diet studies of brown trout foraging in lakes dominated by monomorphic whitefish, polymorphic whitefish, or polymorphic whitefish and vendace. In these systems, brown trout of both wild and stocked origin typically switch to piscivory from sizes ≥20 to 25 cm (Kahilainen & Lehtonen 2001, 2003; Jensen *et al.* 2004). The diet of these brown trout has previously been shown to be dominated by small and abundant prey fishes such as pelagic vendace, *Coregonus albula* (L.), or their congener, the European whitefish, *C. lavaretus* (L.) (Jensen *et al.* 2008). Whereas prey selection has been contrasted along the prey composition gradient of these lakes (Jensen *et al.* 2008), variation in consumption rates of brown trout has not been estimated. Furthermore, data for both predator and prey densities required for population-level bioenergetic calculations are available for these lakes (Jensen *et al.* 2006, 2008; Gjelland *et al.* 2009).

The main objective of this study was to quantify the prey consumption of piscivorous brown trout across three lakes with contrasting coregonid densities and species composition and to compare consumption rates between brown trout of wild and stocked origin. Consumption rates were expected to increase with prey fish densities, and to differ between the brown trout populations, with lower population density of predators facilitating faster growth conversion efficiency and higher individual food consumption rates. Secondly, food consumption estimates were derived from two different bioenergetics models: the Wisconsin (Hewett & Johnson 1992) and the Elliott–Hurley models, the latter specifically developed for calculating maximum energy intake in piscivorous brown trout (Elliott & Hurley 2000). As the assumption of maximum energy intake is likely to be broken over time for wild-living fish and that the water temperature seldom reaches the level for optimum growth and maximum consumption in these lakes, lower total consumption estimates were expected from the Wisconsin model than the Elliott–Hurley model.

Materials and methods

Study area and fish communities

Samples were collected from the subarctic Paatsjoki/Pasvik watercourse (68–69°N, 26–27°E). The upper part of the system is located in Finland and the lower part forms

Table 1. Basic data from the three study lakes. Lake type refers to the diversity of coregonid fish communities and brown trout populations. Coregonids and other fish species present in the study lakes are indicated with abbreviations

Parameter	L. Vuontis	L. Muddus	L. Vaggatem
Lake type	Monomorphic whitefish, stocked brown trout	Polymorphic whitefish, stocked and native brown trout	Polymorphic whitefish and vendace and predominantly stocked brown trout
Latitude (°N)	69°01′	69°00′	69°13′
Longitude (°E)	27°04′	26°50′	29°14′
Surface area (km^2)	11	48	15
Altitude (m.a.s.l.)	151	146	52
Max depth (m)	31	73	30
Mean depth (m)	6.5	8.5	4
Secchi depth (m)	8	3	4
Colour (mg Pt·L^{-1})	8	15	17
Tot P (μg L^{-1})	7	5	9
Tot N (μg L^{-1})	170	160	145
pH	7.2	7.2	6.8
Coregonid proportion (%)	90	86	78
Species/morphs present	b,f,g,h,i, j,k,l	a,b,c,e,f,g,h,i,j,k,l	a,b,c,d,f,g,i,j,k,l

a, DR whitefish; b, LSR whitefish; c, SSR whitefish; d, vendace; e, arctic charr (*Salvelinus alpinus* L.); f, grayling (*Thymallus thymallus* (L.); g, minnow (*Phoxinus phoxinus* (L.)); h, three-spined stickleback (*Gasterosteus aculeatus* L.); i, nine-spined stickleback *Pungitius pungitius* (L.)); j, perch (*Perca fluviatilis* L.); k, pike (*Esox lucius* L.); and l, burbot (*Lota lota* (L.)).

the border between Norway and Russia before draining into the Arctic Ocean. The study included three oligotrophic lakes in the system: in Finland, Vuontisjärvi (hereafter L. Vuontis) and Muddusjärvi (L. Muddus) and in Norway, Vaggatem (L. Vaggatem) (Table 1). In this region, the ice-free season lasts from May–June to October–November, during which there is also a two-month period of midnight sun (mid-May to mid-July). The lakes rarely experience water temperatures >20 °C, and most of the ice-free period experience temperatures <15 °C (Fig. 1).

Fish communities consist of 9–10 species, and coregonids dominate all lakes (Table 1). Lake Vuontis is inhabited by a monomorphic population of large sparsely rakered (LSR) whitefish, which is a generalist using both benthic and pelagic niches (Harrod *et al.* 2010). Lake Muddus has trimorphic whitefish populations: the small sparsely rakered (SSR) whitefish is a profundal benthivore, LSR whitefish a littoral benthivore and densely rakered (DR) whitefish a pelagic planktivore (Kahilainen *et al.* 2004; Harrod *et al.* 2010). The fish community of L. Vaggatem includes the same whitefish morphs as L. Muddus, as well as a dense population of introduced vendace, a pelagic specialist zooplanktivore (Amundsen *et al.* 1999; Kahilainen *et al.* 2011).

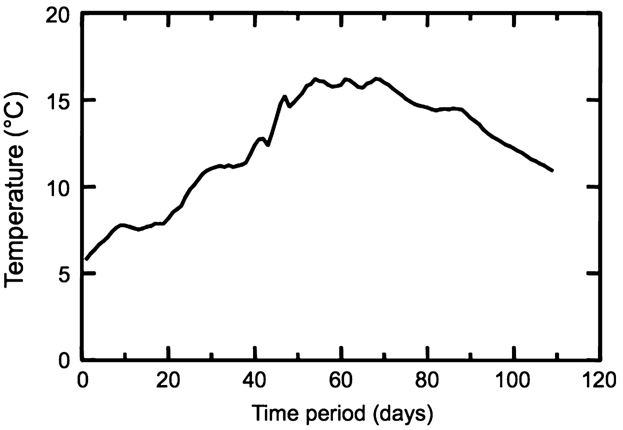

Figure 1. Water temperature profile in the Paatsjoki/Pasvik watercourse from day 1 (June 5th 2000) to day 113 (September 24th 2000).

Brown trout is the main pelagic piscivore in all lakes where it forages almost exclusively on small-sized (i.e. <15 cm in length) coregonids (Jensen *et al.* 2008). The origin of brown trout differs across the three study lakes: brown trout in L. Vuontis are of stocked origin, L. Muddus has approximately equal proportions of stocked and wild brown trout and L. Vaggatem is highly dominated by stocked brown trout (>82% of surveyed brown trout catches) (Jensen *et al.* 2008). Wild and stocked brown trout are approximately equal sized (±20 cm) at start of the first growing season in lake at early summer (Kahilainen & Lehtonen 2001; Jensen *et al.* 2008). In the present study, the wild and stocked brown trout have been pooled in the analyses as they have similar diet preferences and growth patterns (Kahilainen & Lehtonen 2001;. Jensen *et al.* 2004).

Field sampling

Brown trout and prey fish were sampled from June to September 2000 using gillnets (mesh sizes 10–60 mm) and by angling for brown trout, and additionally pelagic trawls for pelagic whitefish in the Finnish lakes (sampling details in Jensen *et al.* 2008). Gillnetting was performed in the main lake habitats (pelagic, littoral and profundal), and fish were removed from the nets after each 8- to 12-h fishing interval. After capture, a visual inspection was made of each fish to allow a field classification between stocked and wild brown trout according to adipose fin clipping and fin erosion of stocked fish (Kahilainen & Lehtonen 2001).

Prey fishes were identified to species, and whitefish to morph according to head and gillraker morphology (Amundsen *et al.* 2004; Kahilainen & Østbye 2006). SSR whitefish has the lowest number (<20 gill rakers) of very short and widely spaced gill rakers, large head, highly subterminal mouth, large eye and large fins. LSR whitefish has intermediate number of short gill rakers (20–30), subterminal mouth and normal silvery whitefish coloration. DR whitefish has a higher number of long and densely spaced gill rakers (30–40), slender body shape, terminal mouth and dark dorsal colouration. Vendace has the highest number of very long, fine and densely spaced gill rakers (40–50), a protruding superior lower jaw and a pointed head. The total length and wet mass of all fish were measured to the nearest millimetre and 0.1 g, respectively. The sample comprised 812 brown trout from all three lakes with a total length and mass range of 18–70 cm and 55–5600 g (mean length and mass range 35.2–40.1 cm and 508–747 g). Brown trout stomachs were removed and frozen at −20 °C for further analyses, and scale and otolith samples were taken for age determination.

Stomach contents and growth analyses

The prey fish in brown trout stomachs were identified whenever possible using the remaining external features for heavily digested specimens (bones, otoliths, spines, skin pigmentation), and whitefish to morph by gillraker examination whenever possible (Kahilainen & Lehtonen 2002; Amundsen *et al.* 2004). Fish prey other than coregonids (nine-spined stickleback, perch and minnow) were pooled as other fish, and invertebrates were pooled in a single group. The diet proportion (A_i, sum of all categories = 100%) was calculated as follows:

$A_\mathrm{i} = 100 \times \Sigma S_\mathrm{i}/\Sigma S_\mathrm{tot}$

where S_i is fullness for diet category i and S_tot is the total stomach fullness (Amundsen *et al.* 1996). The length of undigested fish prey in the brown trout stomachs was measured to the nearest millimetre, and the mass-length relationships were estimated by log–log linear regression (Jensen *et al.* 2006). These relationships were then used to estimate the mean dry mass of the brown trout fish prey to calculate the number of fish prey consumed from the estimated food consumption rates.

To determine growth increment of wild brown trout, fish were aged using otoliths and scales, and the mean values were determined for each age group. The data set consisted of four different lake-year classes (1 = first year in lake, 2 = second year in lake, etc.). This lake-year class approach was used instead of full age as stocked fish had been in the hatchery (3 years) and wild fish in the river (3–7 years) for their first years of life (Kahilainen & Lehtonen 2001; Amundsen *et al.* 2005). Winter conditions for salmonids are usually harsh with a loss of mass common and potentially even length (Post & Parkinson 2001; Huusko *et al.* 2011), and the mean initial mass at the beginning of the growing season (June) was calculated for each first lake-year class and the end mass (late September) for each first lake-year class was the mean mass of the second lake-year class in June. Similar calculations were carried out for all the lake-year classes to reach comparability for the different lakes.

Growth conversion efficiency (GCE) is a measure of the amount of ingested food that is converted into new tissue (Hanson *et al.* 1997) and was estimated as:

$GCE = 100\ \Delta G/\Delta I$

where ΔG is the grams of growth in total mass gain during the sampling period and ΔI is the wet mass (wm) of ingested prey consumed.

Bioenergetic models

The primary input of the Wisconsin model includes predator diet proportions and growth increment (see previous section), predator and prey energy contents and water temperature. The components of the Wisconsin model (Hanson *et al.* 1997) are those of the balanced energy equation:

$G = C - R - (F+U) - SDA$

where G is growth, C consumption, R respiration, F egestation, U excretion and SDA specific dynamic action. The Wisconsin model uses separate equations for C, R, F and U, which are not available for brown trout. Therefore, parameters from Pacific salmonids (Stewart & Ibarra 1991) were used in concert with parameter values taken from a previous study of brown trout bioenergetics in a Finnish lake (Vehanen *et al.* 1998). Brown trout energy content was expected to increase as a function of mass and condition, and energy content was estimated according to Elliott (1976) for each lake-age group. The different prey categories were divided into four categories with wet mass energetic values from the literature: vendace (5514 J g^{-1} wet mass; Vehanen *et al.* 1998), whitefish (4750 J g^{-1} wet mass; Pothoven *et al.* 2006), other fish (4000 J g^{-1} wet mass; Cummins & Wuycheck 1971) and invertebrates (3138 J g^{-1} wet mass; Hewett & Johnson 1992). Water temperature was measured in L. Vuontis and Muddus every two weeks through the whole water column, and daily in the lower Norwegian part of the watercourse using temperature loggers at a hydropower plant. As comparisons revealed a strong correlation in temperature data sets across the lakes, the high-resolution daily mean water temperature from the logger data was used (Fig. 1).

The Elliott model calculates the maximum food consumption of piscivorous brown trout (Elliott & Hurley 2000), using the values of maximum daily energy intake (C_{IN}, cal day^{-1}):

$C_{IN} = C_{max}\{(T\text{-}T_L)/(T_M\text{-}T_L)^b W^d\}$

where W is the wet mass of the brown trout in each lake (i.e. the end mass in lake age 1), d the mass exponent (=0.766), T the water temperature (°C), C_{max} the daily energy intake of a 1-g fish at the temperature T_M (=16 °C) for maximum energy intake (=403.62 cal), T_L the temperature at which energy intake was zero (=−7.48 °C) and b a constant with the value −3.002 (Elliott & Hurley 2000). The estimates of daily food consumption were converted and expressed in terms of dry mass using an energy value of 5.5 cal per mg dry mass (Winberg 1971).

Predator and prey population density and size estimates

Brown trout population density was estimated from mark–recapture data. All stocked fish were adipose fin-clipped in 1999, allowing their direct identification in survey catches and a comparison with stocking data. From previous years of stocking (1996–1998), data on the number of fish released and recaptured were collected by visual inspection of their appearance (e.g. fin condition) and later in the laboratory by the presence of large numbers of regenerated scales, as well as from fish age and growth patterns (Kahilainen & Lehtonen 2001). Subsequently, it was possible to divide stocked fish to lake-year classes from ageing results and use this proportion of stocked fish vs wild fish to calculate population sizes for each lake-year class with a mark–recapture method. Population densities were calculated using the modified Peterson model (Ricker 1975):

$N = (M_{BT} + 1)\ (C{+}1)\ (R{+}1)^{-1}$

where N is the estimated population size, M_{BT} is the total number of marked brown trout, C is the total catch of brown trout and R is the number of recaptured brown trout. Mortality (M) of brown trout was calculated from the catch curve (Ricker 1975):

$M = 1\text{-}e^{-Z}$

where M is the lake-specific annual mortality and Z is the lake-specific instantaneous mortality rate (the slope of linear regression between log$_e$-transformed number of fish captured in each lake-year classes). Total mortality was assumed to be constant for each year class in each year due to similar fishing pressure.

Pelagic prey densities were estimated using nocturnal hydroacoustic data collected from the study lakes in September using equidistantly placed transects in L. Vuontis (year 2004) and L. Muddus (2000) and zigzag transects in L. Vaggatem (2000) (for details, see Kahilainen *et al.* 2004; Jensen *et al.* 2008; Gjelland *et al.* 2009). The hydroacoustic surveys were performed in areas >6 m using a SIMRAD EY-500 echosounder equipped with downfacing split-beam transducers operating at 120 kHz frequency (ES120-7F in L. Vuontis and L. Muddus and ES120-4 × 10 in L. Vaggatem). Pelagic densities of coregonids were computed using EP500 (L. Vuontis and L. Muddus) and Sonar5 (L. Vaggatem) post-processing software. Fish abundance was estimated in the water column from three metres from surface to 0.5 m from the lake bed. The integration threshold was set to –60 dB. All targets were assumed to be coregonids with the exception of very small fish, which were likely to be nine-spined sticklebacks, according to trawl catches from L. Muddus and L. Vuontis. These were excluded from the coregonid density estimates by setting the target strength (TS) thresholds between −54 and −59 dB based on TS distributions. The pelagic coregonid density of each transect was computed using observed TS distributions (for details, see Kahilainen *et al.* 2004), and the hydroacoustic density estimates have been previously presented in Jensen *et al.* (2008).

Results

Diet selection

Stomach content analysis revealed that brown trout in all lakes mainly fed on coregonids. However, small-sized brown trout (i.e. lake-year 1) in L. Vuontis and L. Muddus (wild and stocked) also preyed upon invertebrates during June and July, but shifted almost exclusively to whitefish towards the autumn (Fig. 2). In L. Vuontis, LSR whitefish was the only coregonid prey present, whereas in L. Muddus the brown trout of both wild and stocked fish diet mainly consisted of DR whitefish. In L. Vaggatem, brown trout largely consumed vendace (80%) throughout the ice-free season, with DR whitefish forming 19% of the diet. In all lakes, the contribution of other prey fishes, for example nine-spined stickleback, perch, burbot and Arctic charr, was low throughout the whole sampling period (<5%).

Prey consumption and growth by individual brown trout

In L. Vuontis, prey consumption according to both the Wisconsin model and the Elliott–Hurley model increased in wet mass (wm) from 1.281 and 1.632 kg wm^{-1}, respectively, in lake-year 1 to 5.129 and 5.459 kg wm^{-1} in lake-year 4 (Fig. 3a). The lowest prey consumption rates were found in L. Muddus, with wild brown trout in lake-year 1 consuming on average only slightly over half

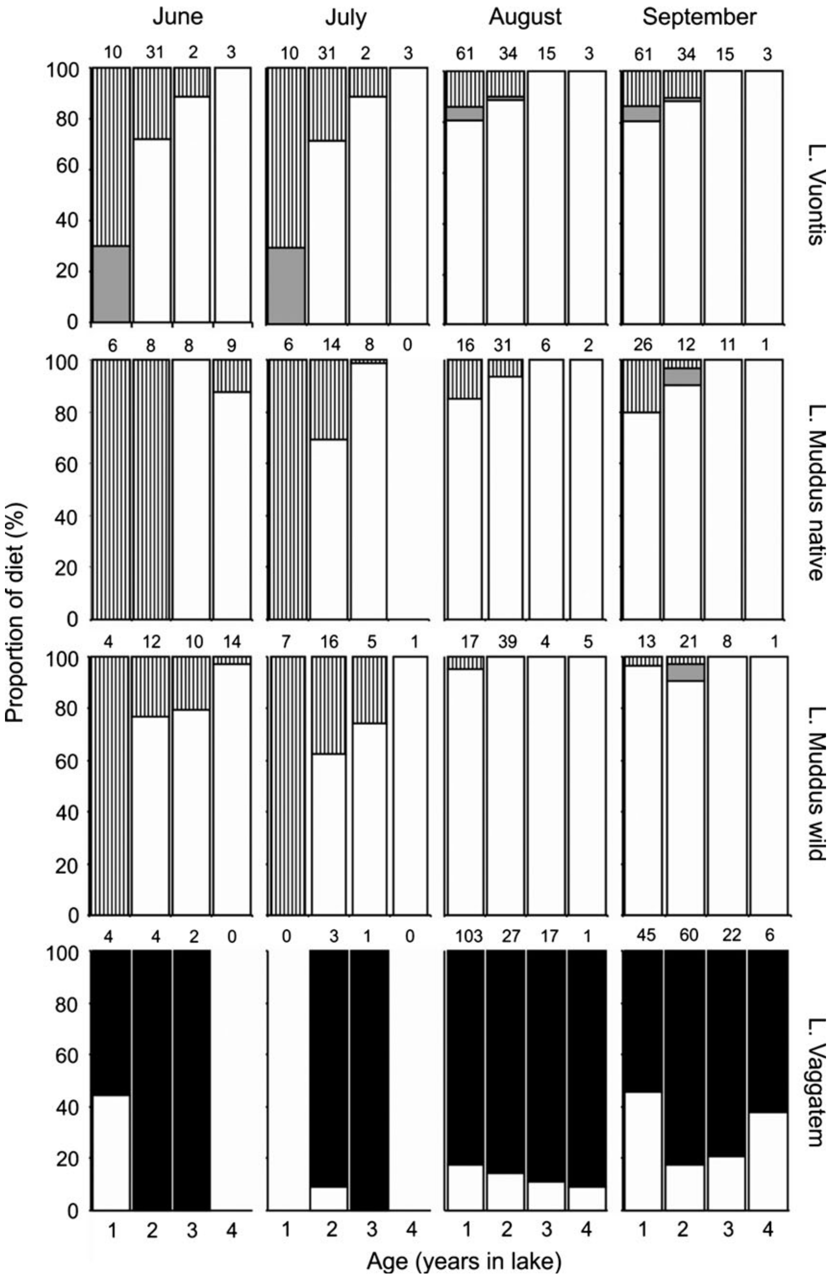

Figure 2. Brown trout diet in study lakes used for input data in bioenergetic modelling. Prey items are vendace (black), whitefish (white), other fish (grey) and invertebrates (vertical hatching). Number of studied stomach is indicated above the bars. Note that L. Vuontis data sets are lower and pooled for June–July and August–September.

that of stocked brown trout (0.658–0.927 kg wm^{-1} vs 1.075–1.482 kg wm^{-1}). The same trend was evident in lake-year 2 in L. Muddus, but thereafter wild brown trout grew faster and consumed more coregonids than stocked brown trout (Fig. 3a,b). Brown trout in the vendace-dominated L. Vaggatem had the highest individual consumption rates, rising from 1.373–1.978 kg wm^{-1} in lake-year 1 to 4.245–5.539 kg wm^{-1} in lake-year 4 (Fig. 3d). The lifetime prey consumption rates for brown trout estimated by the Wisconsin model were 11.245 (L. Vuontis), 6.954 (L. Muddus, stocked), 7.480 (L. Muddus, wild) and 10.809 kg wm^{-1} (L. Vaggatem). Overall, the Elliott–Hurley model provided higher estimates of consumption than the Wisconsin model, with average estimates being 32% larger (range 1.06–1.55; Fig. 3).

The growth increments of lake-year 1 and 2 fish ranged between 161–332 and 162–413 g season^{-1},

Table 2. Mean start wet mass (g), mass increment gained (growth g) and growth conversion efficiency (GCE) of different models for average L. Vuontis, L. Muddus and L. Vaggatem brown trout lake-year classes 1–4

Lake-year class	Start mass (g)	Growth (g)	GCE Wisconsin	GCE Elliott–Hurley
Lake Vuontis				
0	242.9			
1	494.8	251.9	19.7	15.4
2	827.0	332.2	17.9	13.7
3	1387.4	560.4	18.8	15.6
4	2392.4	1005.0	19.6	18.4
Lake Muddus stocked				
0	237.0			
1	436.1	199.1	18.5	13.4
2	598.5	162.4	13.4	8.6
3	995.8	397.3	18.7	14.2
4	1355.5	359.7	14.2	10.2
Lake Muddus wild				
0	75.4			
1	236.6	161.2	24.5	17.4
2	540.8	304.3	23.1	17.4
3	1100.4	559.6	22.9	18.6
4	1590.9	490.5	16.0	12.3
Lake Vaggatem				
0	303.1			
1	635.7	332.6	24.2	16.8
2	1049.0	413.3	20.5	14.2
3	1685.3	636.3	20.1	15.2
4	2438.0	752.7	17.7	13.6

respectively, being fastest in L. Vaggatem and slowest in L. Muddus (Table 2, Fig. 3). Among lake-year classes 3 and 4, growth of brown trout was faster in L. Vaggatem and Vuontis than in L. Muddus. Growth conversion efficiency (*GCE*) ranged between 8.6 and 24.5% (Table 2). In stocked brown trout, *GCE* was the highest in the lake with highest prey fish densities. *GCE* was also higher in wild brown trout than in stocked brown trout. In total, *GCE* gave significantly (*t*-test, $T = 12.46$, d.f. = 15, $P < 0.001$) higher values for the Wisconsin model (19.3%) than the Elliott–Hurley model (14.7%).

Prey availability and total consumption estimates

The availability of pelagic prey to potential predators was highly variable between the different lakes (Table 3). In L. Vuontis, where only LSR whitefish is present, pelagic prey density was very low (10 individuals ha^{-1}). In L. Muddus with polymorphic whitefish, pelagic DR whitefish prey was available in much higher densities (640 individuals ha^{-1}). Lake Vaggatem, which is inhabited by both the pelagic specialist vendace and the pelagic DR whitefish, showed the highest pelagic prey densities (2690 individuals ha^{-1}). In L. Vuontis, pelagic coregonids were LSR whitefish; in L. Muddus, predominantly DR whitefish; and in L. Vaggatem, approximately 90% was vendace and 10% DR whitefish according to pelagic catches. The average size of coregonids measured from brown trout stomachs were as follows: L. Vuontis – LSR whitefish 14.0 cm, 19.6 g; L. Muddus – DR whitefish 12.5 cm, 13.9 g; and L. Vaggatem – vendace 9.6 cm, 6.2 g and DR whitefish 10.3 cm, 8.1 g.

Table 3. Prey density and biomass estimates from vertical echosounding (Jensen *et al.* 2008) and brown trout population consumption estimates using the two bioenergetics models. Note that stocked and wild brown trouts are pooled in the population consumption estimates

Estimates	L. Vuontis	L. Muddus	L. Vaggatem
Pelagic prey densities in the lake			
Total number of prey/ha in lake (n ha^{-1})	10	640	2690
Total biomass of prey/ha in lake (g ha^{-1})	28	7211	21165
Consumption using Wisconsin model			
Total consumption (number prey ha^{-1})	148	433	630
Total consumption (g prey ha^{-1})	2903	6008	4054
Consumption using Elliott model			
Total consumption (number prey ha^{-1})	195	603	882
Total consumption (g prey ha^{-1})	3834	8357	5695

Brown trout annual mortality and population densities varied between the lakes (Table S1). The highest densities and the lowest mortality (0.49) were observed in the largest lake (L. Muddus), where stocked and wild brown trout estimated densities were 2.5 and 2.1 individuals ha^{-1}, respectively. Brown trout mortality was higher (0.64–0.77) and densities were much lower (1.9–2.1 individuals ha^{-1}) in L. Vuontis and L. Vaggatem, respectively (Table S1). Food consumption estimates combined with population density estimates of brown trout indicated that the Elliott–Hurley model gave 1.32–1.40 times higher population consumption estimates than the Wisconsin model with respect to both consumed prey individuals and prey biomass (Table 3, Fig. 3). In L. Vuontis, brown trout consumed much more LSR whitefish prey than were estimated to be available in the pelagic habitat, suggesting that brown trout may be largely consuming fish from benthic habitats. In L. Muddus, the food consumption of brown trout population was close to (Wisconsin) or higher (Elliott) than the

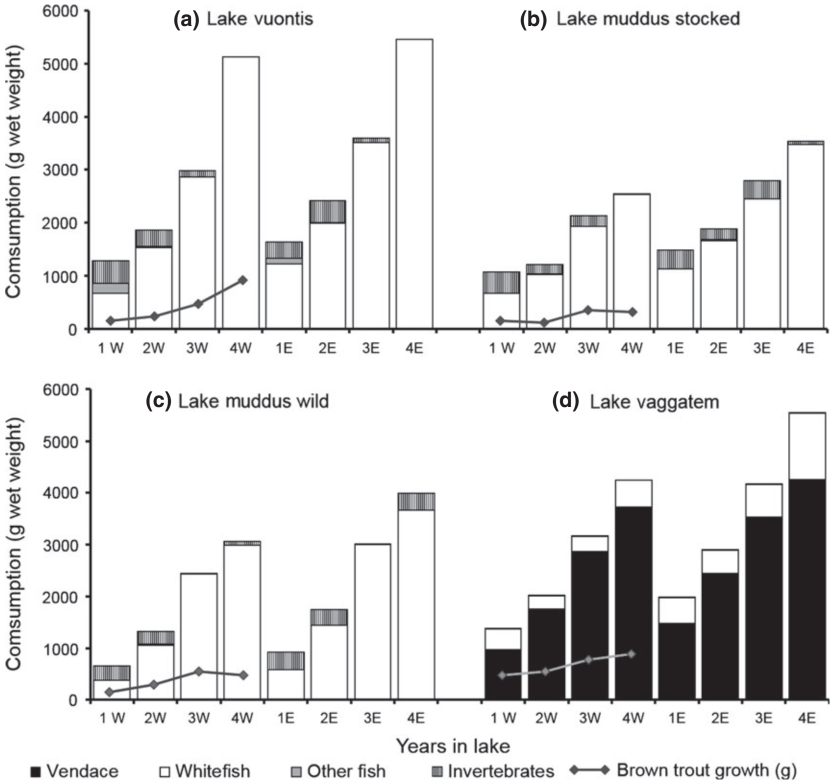

Figure 3. Consumption by individual brown trout (g wet mass) and growth from (a) Lake Vuontis, (b) stocked fish in Lake Muddus, (c) native fish in Lake Muddus and (d) Lake Vaggatem during lake-year 1–4. W = the Wisconsin model, E = the Elliott model. The grey lines indicate yearly growth increments of brown trout.

observed DR whitefish prey biomass in the lake. In L. Vaggatem, the population-level food consumption of vendace and DR whitefish by brown trout was lower than the estimated prey population density and biomass.

Discussion

The results of the present study show that brown trout largely consumed coregonid prey in the different lake types, and the bioenergetics modelling accomplished indicated that brown trout predation causes substantial mortality in the coregonid populations. As expected, consumption estimates were the highest in the lake with the most abundant prey fish communities. However, consumption rates were similar in the lakes with differing, but substantially lower prey densities, indicating a nonlinear relationship between prey densities and piscivore consumption rates. The Elliott–Hurley model gave significantly lower growth conversion efficiency (*GCE*) estimates than the Wisconsin model, indicating that the brown trout did not feed at maximum consumption rates.

The Elliott–Hurley model (2000) is based on feeding at maximum rations and reached higher consumption values in all calculations. The Elliott–Hurley consumption estimates resulted in substantially lower *GCE* estimates (8.6–18.6) than observed in the experiments the model was derived from (30–40, Elliott & Hurley 2000). The interpretation of this is that the brown trout in the study were not feeding at maximum rations. The higher growth conversion efficiency (13.4–23.5) obtained from the Wisconsin model also supports this view, indicating that the Wisconsin model likely represented more realistic consumption estimates in field studies. On the other hand, parameter inputs in the Wisconsin model largely rely on values estimated from Pacific salmonid (i.e. *Onchorynchus*) species, indicating a need to corroborate the model through targeted experimental work on brown trout.

GCE estimates in stocked brown trout were the highest in L. Vaggatem, which had the highest prey densities and the smallest mean prey fish size. The bioenergetics models used here take size dependence of respiration into account, but do not consider potential differences in respiration rates owing to activity differences. The lower *GCE* in the other lakes could therefore reflect that the brown trout in these lakes spend relatively more time and energy searching for prey, resulting in higher respiration rates and thereby lowering the *GCE* estimates. This interpretation could also explain why *GCE* increased with brown trout size for L. Vuontis, whereas it remained constant in L. Muddus and decreased in L. Vaggatem. Respiration increases with size, but if prey availability is constant, *GCE* will decrease with increasing size. Hence, in L. Vaggatem, almost all prey fish size categories are available to brown trout of all lake-year classes, and *GCE* can be expected to decrease with predator size. Conversely, in L. Vuontis, the mean length of prey fish is substantially larger, and the prey availability will increase with brown trout size, enabling an increased *GCE* with increasing predator size. Jensen *et al.* (2008) showed a positive relationship between predator size and prey size in all lakes, but the strength of the correlation was dependent on species composition, size structure and abundance of the prey. The steepest incline in prey size with increasing brown trout size was seen in Lake Vuontis, whereas the slope decreased to almost zero in Lake Vaggatem, which was dominated by the small-bodied but abundant vendace population (slope = 0.03). Respiration differences could also explain the observed differences in *GCE* estimates between wild and stocked brown trout, if stocked brown trout are less effective in prey search and capture than wild fish. The better growth in wild compared to stocked brown trout in L. Muddus supports this interpretation. Alternatively, *GCE* differences could have been caused by differences in behaviour mediated by differences in growth hormone expression as reported for other hatchery raised brown trout, but if this was the case, stocked brown trout should be the ones with the highest growth performance (Johnson *et al.* 2006).

The differences in individual consumption values estimated by the two models give similarly different results at the population level. Here, the higher food consumption values given by the Elliott–Hurley model led to estimates of prey consumption by brown trout exceeding that of estimates of prey availability in the pelagic zone. In this context, it should be noted that prey abundance and biomass estimates were from autumn season, following the period of highest water temperatures and the most important period of brown trout predation in L. Muddus and L. Vuontis, potentially explaining why prey consumption was higher than prey availability. For L. Vuontis, this mismatch was also apparent for estimates derived using the Wisconsin model. The total density estimates of brown trout were 1.9 fish ha^{-1} in L. Vuontis, 2.1 fish ha^{-1} in L. Vaggatem and 4.6 fish ha^{-1} in L. Muddus. Even the lowest density estimates are about four times higher than those reported from more southern Fennoscandian lakes (0.4 brown trout ha^{-1}; Vehanen *et al.* 1998). The elevated brown trout population density observed in L. Muddus is apparently due to a combination of natural reproduction (45% of brown trout population in 2000) and relatively high stocking rate between 1996 and 1999 (1 brown trout ha^{-1}), highlighting the importance of stocking management on the abundance of piscivorous brown trout.

The observed differences in brown trout densities also likely drove some of the differences recorded in individual food consumption rates, which were the highest for the lower density lakes Vuontis and Vaggatem. In L. Vaggatem, there were abundant pelagic vendace resources available for brown trout predation, whereas the high individual consumption rates of brown trout in L. Vuontis likely reflected consumption of LSR whitefish prey in benthic habitats. By contrast, L. Muddus, with both wild and stocked brown trout populations present in high density, displayed the lowest individual food consumption rates observed in this study. The high density of brown trout apparently induced high intraspecific resource competition as wild and stocked brown trout used the same prey, pelagic DR whitefish (this study, Kahilainen & Lehtonen 2001). In addition, the average size of DR whitefish prey in this system is larger than that preferred by brown trout (Jensen *et al.* 2008). Despite low individual consumption rates, it was observed that wild brown trout in L. Muddus had the highest growth conversion efficiency. This could be related to adaptations of wild brown trout to the feeding conditions in natural lake environment, which seldom provided excess feeding opportunities with high densities of prey. By contrast, stocked fish have been raised with excess feeding in fish farm for some generations, which is likely to lead hatchery selection, that is adaptation to excess feeding including high metabolic rates (e.g. Sundström *et al.* 2004; Araki *et al.* 2008).

In lakes Vuontis and Muddus, the estimated population-level consumption of prey by brown trout either exceeded or was close to that of the recorded densities of the pelagic coregonid prey, whereas in L. Vaggatem the consumption estimates constituted only 20–25% of the prey population density. In L. Vuontis, only a few LSR whitefish used pelagic habitats, resulting in extremely low pelagic prey density estimates at a time when catches from benthic gillnets were high (Malinen *et al.* 2014). Taken collectively, estimates of whitefish population densities should be considered as a minimum estimate, as a part of both LSR and DR populations use benthic and littoral habitats that are effectively hidden during echo-sounding surveys (Malinen *et al.* 2014). The brown trout growth and consumption rates observed in this lake cannot be supported by such a low pelagic prey density, suggesting that piscivorous brown trout actively fed in littoral habitats, as observed in other northern lakes (e.g.

L'Abée-Lund *et al.* 1992; Næsje *et al.* 1998; Jensen *et al.* 2012). Piscivorous brown trout could potentially also have an effect on the benthic fish community, in particular recruitment of benthivorous whitefish, but as density estimates for the benthic fish community were missing, brown trout consumption could not be estimated as a proportion of the population size.

The combination of bioenergetic models and estimates of predator and prey population densities is a potentially powerful tool for fisheries management. In lakes where monitoring of predator and prey stocks are continuous, these methods allow predator stocking densities and fishing regulations to be directly adjusted according to available pelagic prey density. The conversion efficiencies indicated that the brown trout fed at submaximal rations and that the Wisconsin bioenergetics model may be more realistic than the estimates obtained with the Elliott–Hurley model. However, it should be stressed that none of the models have been experimentally validated for the population or system in focus, and it cannot be known with certainty which of them is closest to the truth. Independent approaches, such as estimation of activity levels, could also give an indication of respiration levels and aid in the parameterisation of bioenergetics models. Moreover, even though the two bioenergetics models differ somewhat in the total consumption rate estimates, they may both give a good indication of the size of the predation impact on prey fish population sizes. One benefit of the approach taken here is that the comparison of the two models provides increased confidence as to what range the true consumption rates are likely to fall in. In this regard, Elliott–Hurley estimates indicate the upper limit to the potential consumption rates, whereas the Wisconsin model likely better reflects the true consumption rates. Both these aspects of bioenergetics modelling represent valuable information for those working towards sustainable fisheries management.

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References

Abrams P.A. & Ginzburg L.R. (2000) The nature of predation: prey dependent, ratio dependent or neither? *Trends in Ecology and Evolution* **15**, 337–341.

Allan J.D., Abell R., Hogan Z., Revenga C., Taylor B.W., Welcomme R.L., *et al.* (2005) Overfishing of inland waters. *BioScience* **12**, 1041–1051.

Amundsen P.-A., Gabler H.-M. & Staldvik F.J. (1996) A new approach to graphical analysis of feeding strategy from stomach contents data - modification of the Costello (1990) method. *Journal of Fish Biology* **48**, 607–614.

Amundsen P.-A., Staldvik F.J., Reshetnikov Y.S., Kashulin N., Lukin A., Bøhn T., *et al.* (1999) Invasion of vendace *Coregonus albula* in a subarctic watercourse. *Biological Conservation* **88**, 405–413.

Amundsen P.-A., Knudsen R., Klemetsen A. & Kristoffersen R. (2004) Resource competition and interactive segregation between sympatric whitefish morphs. *Annales Zoologici Fennici* **41**, 301–307.

Amundsen P.-A., Kashulin N.A., Gjelland K.Ø., Jensen H., Sandimirov S.S., Shirokov V., *et al.* (2005) *Brown Trout in the Pasvik Watercourse: Population Status, Potentials and Limitations for Recruitment, Productions and Management*. Tromso: University of Tromsø Report, 44 pp.

Araki H., Berejikian B.A., Ford M.J. & Blouin M.S. (2008) Fitness of hatchery-reared salmonids in the wild. *Evolutionary Applications* **1**, 342–355.

Belgrano A., Scharler U.M., Dunne J. & Ulanowicz R.E. (2005) *Aquatic Food Webs*. Oxford: Oxford University Press, 262 pp.

Chipps S.R. & Wahl D.H. (2008) Bioenergetics modeling in the 21st century: reviewing new insight and revisiting old constrains. *Transaction of the American Fisheries Society* **137**, 298–313.

Cummins K.W. & Wuycheck J.C. (1971) Caloric equivalents for investigations in ecological energetics. *Internationale Vereinigung für Theoretische und Angewandte Limnologie Mitteilung* **18**, 1–158.

Elliott J.M. (1976) Body composition of brown trout (*Salmo trutta* L.) in relation to temperature and ration size. *Journal of Animal Ecology* **45**, 273–289.

Elliott J.M. & Hurley M.A. (2000) Daily energy intake and growth of piscivorous brown trout, *Salmo trutta*. *Freshwater Biology* **44**, 237–245.

Gjelland K.Ø., Bøhn T., Horne J.K., Jensvoll I., Knudsen F.R. & Amundsen P.-A. (2009) Planktivore vertical migration and shoaling under a subarctic light regime. *Canadian Journal of Fisheries and Aquatic Sciences* **66**, 525–539.

Hanson P.C., Johnson T.B., Schindler D.E. & Kitchell F. (1997) *Fish Bionenegetics 3.0. Software for Windows*. Madison WI: University of Wisconsin Sea Grant Institute, 116 pp.

Harrod C., Mallela J. & Kahilainen K.K. (2010) Phenotype-environment correlations in a putative whitefish adaptive radiation. *Journal of Animal Ecology* **79**, 1057–1068.

Héroux D. & Magnan P. (1996) *In situ* determination of food daily ration in fish: review and field evaluation. *Environmental Biology of Fishes* **46**, 61–74.

Hewett S.W. & Johnson B.L. (1992) *A Fish Bioenergetics Model 2. An Upgrade of an Generalized Bioenergetics Model of Fish Growth for Microcomputers*. Wisconsin WI: University of Wisconsin Sea Grant Technical Report No. WIS-SG-92-250, 79 pp.

Huusko A., Mäki-Petäys A., Stickler M. & Mykrä H. (2011) Fish can shrink under harsh living conditions. *Functional Ecology* **25**, 628–633.

Jensen H. (2009) Ecological factors affecting piscivory of brown trout (*Salmo trutta* L.) in northern lakes. PhD Thesis, Tromsø: University of Tromsø, 99 pp.

Jensen H., Amundsen P.-A., Bøhn T. & Aspholm P.E. (2004) Feeding ecology of piscivorous brown trout (*Salmo trutta* L.) in a subarctic watercourse. *Annales Zoologici Fennici* **41**, 319–328.

Jensen H., Amundsen P.-A., Elliott J.M., Bøhn T. & Aspholm P.E. (2006) Prey consumption rates and growth of piscivorous brown trout in a subarctic watercourse. *Journal of Fish Biology* **688**, 838–848.

Jensen H., Kahilainen K.K., Amundsen P.-A., Gjelland K.Ø., Tuomaala A., Malinen T., *et al.* (2008) Predation by brown trout (*Salmo trutta*) along a diversifying prey community gradient. *Canadian Journal of Fisheries and Aquatic Sciences* **65**, 1831–1841.

Jensen H., Kiljunen M. & Amundsen P.-A. (2012) Dietary ontogeny and niche shift to piscivory in lacustrine brown trout *Salmo trutta* revealed by stomach content and stable isotope analyses. *Journal of Fish Biology* **80**, 2448–2462.

Johnsen R.L., Blumenshine S.C. & Coghlan S.M. (2006) A bioenergetic analysis of factors limiting growth in an Ozark tailwater river. *Environmental Biology of Fish* **77**, 121–132.

Kahilainen K. & Lehtonen H. (2001) Resource use by wild and stocked brown trout (*Salmo trutta* L.) in a subarctic lake. *Fisheries Management and Ecology* **8**, 83–94.

Kahilainen K. & Lehtonen H. (2002) Brown trout (*Salmo trutta* L.) and Arctic charr (*Salvelinus alpinus* (L.)) as predators on three sympatric whitefish (*Coregonus lavaretus* (L.)) forms in the subarctic Lake Muddusjärvi. *Ecology of Freshwater Fish* **11**, 158–167.

Kahilainen K. & Lehtonen H. (2003) Piscivory and prey selection of four predator species in a whitefish dominated subarctic lake. *Journal of Fish Biology* **63**, 659–672.

Kahilainen K. & Østbye K. (2006) Morphological differentiation and resource polymorphism in three sympatric whitefish *Coregonus lavaretus* (L.) forms in a subarctic lake. *Journal of Fish Biology* **68**, 63–79.

Kahilainen K., Malinen T., Tuomaala A. & Lehtonen H. (2004) Diel and seasonal habitat and food segregation of three sympatric *Coregonus lavaretus* forms in a subarctic lake. *Journal of Fish Biology* **64**, 418–434.

Kahilainen K., Siwertsson A., Gjelland K.Ø., Knudsen R., Bøhn T. & Amundsen P.A. (2011) The role of gill raker number variability in adaptive radiation of coregonid fish. *Evolutionary Ecology* **25**, 573–588.

L'Abée-Lund J.H., Langeland A. & Sægrov H. (1992) Piscivory by brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.) in Norwegian lakes. *Journal of Fish Biology* **41**, 91–101.

Malinen T., Tuomaala A., Lehtonen H. & Kahilainen K.K. (2014) Hydroacoustic assessment of mono- and polymorphic *Coregonus* density and biomass in subarctic lakes. *Ecology of Freshwater Fish* **23**, 424–437.

Næsje T.F., Sandlund O.T. & Saksgaard R. (1998) Selective predation of piscivorous brown trout (*Salmo trutta* L.) on polymorphic whitefish (*Coregonus lavaretus* L.). *Archiv für Hydrobiologie Special Issues in Advanced Limnology* **50**, 283–294.

Post J. & Parkinson E. (2001) Energy allocation strategy in young fish: allometry and survival. *Ecology* **84**, 1040–1051.

Pothoven S.A., Nalepa T.F., Madenjian C.P., Rediske R.R., Schneeberger P.J. & He J.X. (2006) Energy density of lake whitefish *Coregonus clupeaformis* in Lakes Huron and Michigan. *Environmental Biology of Fishes* **76**, 151–158.

Ricker W.E. (1975) Computation and interpretation of biological statistics of fish populations. *Bulletin of the Fisheries Research Board of Canada* **191**, 1–372.

Rikardsen A.H. & Amundsen P.-A. (2005) Pelagic marine feeding of Arctic charr *Salvelinus alpinus* and sea trout *Salmo trutta*. *Journal of Fish Biology* **66**, 1163–1166.

Sánchez-Hernández J. & Amundsen P.-A. (2015) Trophic ecology of brown trout (*Salmo trutta*) in lakes. *Ecology of Freshwater Fish* **24**, 148–161.

Scharf F.S., Buckel J.A. & Juanes F. (2009) Contrasting patterns of resource utilization between juvenile estuarine predators: the influence of relative prey size and foraging ability on the ontogeny of piscivory. *Canadian Journal of Fisheries and Aquatic Sciences* **66**, 790–801.

Sih A. & Christensen B. (2001) Optimal diet theory: when does it work and when does it fail? *Animal Behaviour* **61**, 379–390.

Stephens D.W. & Krebs C.J. (1986) *Foraging Theory*. Princeton: Princeton University Press, 246 pp.

Stewart D.J. & Ibarra M. (1991) Predation and production by salmonine fishes in Lake Michigan. *Canadian Journal of Fisheries and Aquatic Sciences* **110**, 909–922.

Sundström L.F., Bohlin T. & Johnsson J.I. (2004) Density-dependent growth in hatchery-reared brown trout released into a natural stream. *Journal of Fish Biology* **65**, 1385–1391.

Svanbäck R. & Persson L. (2004) Individual diet specialization, niche width and population dynamics: implications for trophic polymorphisms. *Journal of Animal Ecology* **73**, 973–982.

Vehanen T., Hyvärinen P. & Huusko A. (1998) Food consumption and prey orientation of piscivorous brown trout (*Salmo trutta*) and pikeperch (*Stizostedion lucioperca*) in a large regulated lake. *Journal of Applied Ichthyology* **14**, 15–22.

Whitledge G.W., Bajer P.G. & Hayward R.S. (2010) Laboratory evaluation of two bioenergetics models for brown trout. *Transactions of the American Fisheries Society* **139**, 929–936.

Winberg G.G. (1971) *Methods for the Estimation of Production of Aquatic Animals*. London: Academic Press, 175 pp.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1 Brown trout data used for population density estimation in three study lakes