

Phenotype flexibility in wild fish: Dolly Varden regulate assimilative capacity to capitalize on annual pulsed subsidies

Jonathan B. Armstrong*† and Morgan H. Bond†

School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, WA 98195, USA

Summary

1. Large digestive organs increase rates of energy gain when food is plentiful but are costly to maintain and increase rates of energy loss when food is scarce. The physiological adaptations to this trade-off differ depending on the scale and predictability of variation in food abundance.

2. Currently, there is little understanding of how animals balance trade-offs between the cost and capacity of the digestive system in response to resource pulses: rare, ephemeral periods of resource superabundance. We investigated the physiological and behavioural tactics of the fish Dolly Varden (*Salvelinus malma*) that rear in watersheds with low *in situ* productivity, but experience annual resource pulses from the spawning migrations of Pacific salmon. The eggs of Pacific salmon provide high-energy food for Dolly Varden.

3. Dolly Varden sampled 6 weeks prior to the resource pulse exhibited atrophy of the stomach, pyloric caeca, intestine and liver. Throughout the portion of the growing season prior to the resource pulse, fish exhibited empty stomachs, low indices of energy condition and muscle isotope signatures reflecting the previous resource pulse.

4. During the resource pulse, Dolly Varden exhibited large digestive machinery, gorged on salmon eggs and rapidly stored energy in fat reserves, somatic growth and gonad development. Dolly Varden appeared to achieve nearly their entire annual energy surplus during the ~5-week period when sockeye salmon spawn.

5. Digestive flexibility provides Dolly Varden the energy efficiency required to survive and reproduce when resource abundance is concentrated into an annual pulse that is predictable, yet highly ephemeral. Although fish are known to incur extremely variable energy budgets, our study is one of the first to document digestive flexibility in wild fish. Our study emphasizes that fish can rely heavily on rare, high-magnitude foraging opportunities. Human actions that attenuate spikes in food abundance may have stronger than anticipated effects on consumer energy budgets.

Key-words: adaptive plasticity, bioenergetics, digestive capacity, foraging, freshwater, physiological ecology, streams and rivers

Introduction

Many ecosystems exhibit resource pulses: rare, high-magnitude events that offer ephemeral feasts for consumers (Yang *et al.* 2008). These bottom-up perturbations can transmit through food webs and generate lasting effects on species abundance, community structure and other ecosystem attributes (Ostfeld & Keesing 2000; Yang *et al.*

2008). The degree of these broader ecological effects may ultimately depend on the ability of consumers to acquire and store energy during the pulse. Some consumers, especially small birds and mammals, hoard food and continue to feed on pulsed food items long after the pulse itself has subsided (Humphries *et al.* 2002; Brodin & Clark 2007). Alternatively, many consumers convert food into internal energy stores such as fat reserves (Brodin & Clark 2007), a process that requires digestion and absorption by the gut (i.e. assimilation). To rapidly store energy in the body (as is needed to capitalize on a resource pulse), animals

*Correspondence author. E-mail: jonny5armstrong@gmail.com

†Both the authors contributed equally to this project

require high assimilative capacity, which is metabolically costly to maintain (Cant, McBride & Croom 1996; Armstrong & Schindler 2011; Piersma & van Gils 2011). This generates a potentially crippling trade-off, as the traits that increase energy gain during the resource pulse also increase energy losses after the pulse. There are two general strategies for balancing trade-offs between the cost and capacity of the digestive system. If variation in food abundance is unpredictable, animals should exhibit excess assimilative capacity (Gans 1979; Diamond 2002; Armstrong & Schindler 2011), maintaining large guts that are wasteful under average conditions, but compensate by providing large energy gains during spikes in food abundance. In contrast, if variation in food abundance is predictable, there is the potential to adaptively regulate digestive capacity to match ambient levels of demand, such that individuals would exhibit large expensive guts during periods of food abundance and small economic guts during periods of resource scarcity [i.e. phenotype flexibility (Piersma & van Gils 2011)].

Phenotype flexibility is well documented in the digestive systems of reptiles (Secor, Stein & Diamond 1994), birds (McWilliams & Karasov 2001), and mammals (Naya, Karasov & Bozinovic 2007), yet has received relatively little study in fishes. Laboratory experiments have shown that fish can indeed regulate digestive capacity. For example, Atlantic cod reduced gut size during 68 days of starvation and increased gut size to prestarvation levels following just 2 weeks of feeding (Blier *et al.* 2007). However, study of digestive flexibility in wild fish is extremely rare. Wild fish have been shown to exhibit seasonal changes in organ size (Kent, Prosser & Graham 1992; Jobling *et al.* 1998), but we know of no studies that have empirically linked temporal changes in digestive organ size with changes in feeding rate [except terminal changes in semelparous fish, (Rutter 1902)]. Past research has largely considered changes in organ size to be a response to lipid storage and depletion in organ tissues (Htunhan 1978; Jobling *et al.* 1998), rather than adaptive manipulation of the cost and capacity of the digestive system (Piersma & van Gils 2011). Here we report one of the first studies exploring the role of digestive flexibility in the foraging ecology and energy budget of a wild fish. Specifically we monitored the diet, energy status and organ size of high-latitude fish that experience annual pulsed subsidies.

As latitude increases, freshwater systems generally become less productive, while marine systems increase in productivity. This counter-gradient is likely responsible for the prevalence of anadromy in high-latitude fishes (Gross 1987). Pacific salmon are the numerically dominant anadromous fish across much of the Northern hemisphere, and their spawning migrations generate resource pulses when fish spawn and die in streams and lakes (Gende *et al.* 2002; Schindler *et al.* 2003). Salmon eggs are energy-rich (Armstrong 2010) and provide high-quality foraging opportunities for resident fishes during the period when salmon are spawning (Scheuerell *et al.*

2007; Denton, Rich & Quinn 2009; Armstrong *et al.* 2010). Single populations of salmon typically spawn for 3–6 weeks (Schindler *et al.* 2010), so resident fishes require high levels of digestive capacity to capitalize on eggs before they are gone. However, once salmon spawning subsides, foraging opportunities may be sparse, making large guts especially taxing on energy budgets. There is currently limited understanding of how fish, or consumers in general, balance the physiological trade-offs associated with maximizing energy gain during resource pulses and minimizing energy loss during interpulse periods (Yang *et al.* 2008). We addressed this dearth of knowledge by studying the foraging ecology and digestive physiology of adult Dolly Varden (*Salvelinus malma*) that reside in high-latitude streams and exploit annual pulsed subsidies from sockeye salmon (*Oncorhynchus nerka*) (Wipfli *et al.* 2003; Denton, Rich & Quinn 2009). Our specific objectives were to: (i) characterize seasonal variation in the diet composition, ration size and energy condition of Dolly Varden to explore the extent to which they capitalize on sockeye salmon subsidies, (ii) measure changes in organ size before and after the subsidy to test for phenotype flexibility in the digestive system, and (iii) explore the contribution of digestive flexibility to the annual energy budgets of Dolly Varden.

Materials and methods

STUDY SYSTEM

We conducted our study in the Chignik Lakes on the Alaska Peninsula, consisting of two interconnected lakes (Chignik Lake and Black Lake) and tributaries that form a 1536 km² watershed. Our study focused on Dolly Varden in the Alec River, the largest tributary of Black Lake, where Dolly Varden are present year round. The Chignik watershed supports the largest run of sockeye salmon in the region with annual commercial harvests of 1–3 million fish, and spawning escapements of 600 000–1.2 million. More than half of the escaped sockeye in the system form a single distinct population that spawns in the main stem and tributaries of the Alec River (Templin *et al.* 1999). Single populations of sockeye salmon rarely spawn for longer than a month (Schindler *et al.* 2010). In the Alec River, spawning commences at the end of July and is nearly complete by the end of August (M. Bond unpublished data). To characterize seasonal variation in water temperature (i.e. identify the growing season), we recorded temperature in the main stem of the Alec River from September 2009–September 2010 using Intech brand loggers (Intech Instruments LTD, Auckland, New Zealand) which recorded temperature with ± 0.3 °C accuracy at 1-h time intervals.

DOLLY VARDEN FORAGING ECOLOGY

To determine how Dolly Varden diet, body condition and isotopic signature change throughout the growing season, we angled Dolly Varden in the Alec River in 2009 (26 June, 18 August), 2010 (17 June, 14 July, 5 August, 26 August) and 2011 (14 June and 22 August). During each sampling event, 20 angled fish were euthanized in a buffered MS-222 (tricaine methane sulfonate)

solution (250 mg L⁻¹) and immediately placed on ice. For each individual, we measured the fork length, mass, diet composition and removed otoliths for age analysis. In addition, we froze a plug of dorsal muscle as well as diet items from each stomach of the four most common orders of invertebrate prey (Tricoptera, Ephemeroptera, Plecoptera, Diptera) for stable isotope analysis. For each individual, we calculated condition factor (K) as:

$$K_i = ((w_i/l_i^3) \times 100,000) \quad \text{eqn 1}$$

where w_i is the mass of the fish (g) and l_i is the fork length (mm). In addition, we calculated the ration size as the mass of the stomach contents (mg) divided by the mass of the fish (g).

Fish and invertebrate tissues were freeze-dried in a lyophilizer for 36 h, then ground to a fine powder and packed into tin capsules. Stable isotope analyses were conducted at the University of Washington Isolab with a Costech elemental analyzer (Analytical Technologies Inc, Valencia, CA, USA) coupled to a Finnigan MAT-253 stable isotope-ratio mass spectrometer (Thermal Electron Corporation, Bremen, Germany). The isotopic ratio of nitrogen ($\delta^{15}\text{N}$) was expressed in standard notation of per mil differences from the standard atmospheric nitrogen gas (Fry 2006). As an additional measure of body condition, we also measured the ratio of carbon to nitrogen (C/N) in muscle tissue as a proxy for lipid content (Post *et al.* 2007). We used ANOVA and post hoc Tukey's tests where appropriate, to evaluate changes in each of the indices for samples collected in June, July and August.

CHANGES IN ORGAN SIZE

To assess the physiological response of Dolly Varden to the salmon subsidy, we performed additional analyses with the 2011 collection. An initial sample was taken on 14 June, approximately 1.5 months prior to the onset of salmon spawning. We performed a second, identical round of angling on 22 August, after nearly 1 month of salmon spawning and the senescence of much of the salmon run. In the laboratory, we wrapped each fish in plastic (to prevent dessication) and froze them to -20 °C within 6 h of initial collection. In September, fish were moved to a -40 °C shipping container and transported to our laboratory in Seattle. In the laboratory, we thawed each fish slowly on ice, measured total mass, fork length and performed a dissection to assess each of the major organs in the peritoneal cavity. We removed and measured the wet weight of the spleen, heart, liver and a plug of dorsal muscle tissue to the nearest 0.01 g. We removed the entire digestive tract of each fish and computed the full gut weight, then separated the stomach, pyloric caeca and intestine at natural constrictions to maintain repeatability. We removed food contents/digesta from the gut components and weighed each prey type separately (e.g. stream invertebrates, eggs and salmon flesh). The total mass of gut contents was subtracted from the full gut mass to calculate total gut wet mass. Each gut component was weighed for wet mass after removing the digesta. We placed all organs and muscle samples into plastic or glass vials, dried them in a lyophilizer for 36 h and re-weighed them. We used linear mixed effects models to analyse changes in organ dry mass before and after the salmon subsidy, implemented via the *nlme* library in R (R Core Development Team 2012). We modelled each organ mass separately. Our response variable, M , was the natural logarithm of organ dry mass, m :

$$M = \ln(m) \quad \text{eqn 2}$$

Our candidate models included time period and the natural logarithm of fork length as fixed effects. The full model, shown below, included sex as a random effect.

$$M_i = \beta_0 + \tau_0 + \beta_1 X_i + n_i + \tau_1 X_i + \varepsilon_i \quad \text{eqn 3}$$

where M_i is the natural logarithm of organ mass for an individual i , β_0 is the intercept, τ_0 is an adjustment to the intercept due to the fixed effect of time period on organ mass, β_1 is a coefficient (i.e. slope) describing the fixed effect of fork length, X_i , on organ mass, n_i is the random effect of sex, τ_1 is the adjustment to slope due to time period, and ε_i is error. Following standard methods (Zuur *et al.* 2009), we assessed the random effect of sex by comparing how its inclusion affected the AICc scores (Burnham & Anderson 2002) of the full models. Accounting for sex did not improve model fits, so we proceeded to fit models with only fixed effects. We compared five candidate models nested within each full model by setting different parameters (τ_0 , τ_1) to zero and selecting the best model using Akaike Information Criterion adjusted for small samples size [AICc: (Burnham & Anderson 2002)].

Including an interaction term between time period and fork length (τ_1), worsened model fit for every organ we considered. This suggested that the magnitude of temporal changes in the natural logarithm of organ mass were consistent across the range of fish lengths we sampled, so we expressed our results graphically as organ mass divided by fish length. We did not standardize by body mass (e.g. somatic indices) because our fish show large seasonal oscillations in body mass, but relatively constant length, as they have nearly reached the saturation of their age-length relationship (i.e. 1-infinity, Fig. S1, Supporting information). Thus, temporal changes in length-standardized organ mass are similar to the actual changes in organ size exhibited by an individual fish. To assess whether changes in organ mass outpaced changes in somatic mass, we compared changes in length-standardized organ mass to changes in length-standardized somatic mass (the total mass of the fish minus stomach contents and gametes).

Otoliths from each individual were mounted in resin and polished until annuli from the core to the otolith edge were exposed. Each otolith was examined by an experienced otolith reader to determine the total age of each individual. We used these data to estimate the parameters of a Von Bertalanffy growth function (Von Bertalanffy 1938; Essington, Kitchell & Walters 2001):

$$L_t = L_{\text{inf}}(1 - e^{-K(t-t_0)}) \quad \text{eqn 4}$$

Where L_t is the fork length at time t , L_{inf} is the asymptotic mean length of the population, K is the growth coefficient, and t_0 is the age at which the fish has zero length.

To determine whether individuals collected in 2011 as part of the organ size analysis had recently returned from sea, possibly confounding our results, we performed otolith microchemical analysis (Campana 1999). Otoliths were analysed using laser ablation inductively coupled plasma mass spectrometry (LA-ICPMS) at the Oregon State University Keck Collaboratory for Plasma Spectrometry, to determine the migratory status of each individ-

ual after the winter 2010–11 annular otolith band. Previous research indicates that individuals residing within the freshwater portion of the Chignik Lakes watershed maintain an otolith strontium to calcium ratio of ≤ 1.5 mmol/mol (M. Bond unpublished data). In this study, all individuals were resident in freshwater habitats prior to the winter 2010–11 annulus, and therefore, all changes in organ mass are assumed to have occurred within the confines of the freshwater habitat.

ENERGETICS SIMULATION

We compared the energy gains accrued by Dolly Varden during the sockeye salmon subsidy to the energy losses predicted to occur during the period prior to the next salmon subsidy (1 September–1 August) without cost reductions from organ atrophy. We considered these gains and losses for a fish of roughly the median size in our August sample (889 g). Energy gains during the subsidy were calculated as the sum of changes in energy content observed in the liver, gut, heart, spleen, gonads and carcass (entire body excluding the gonads and organs under study). We calculated the changes in energy content for each tissue type by comparing the average mass and energy density of organs before and after the resource pulse.

For organs and soma, we calculated energy density based on the observed per cent dry mass of each tissue using an existing model (Breck 2008):

$$E = 37.89 - 42.94 * (1 - DW) \quad \text{eqn 5}$$

Where E is energy density in $\text{kJ} \cdot \text{gram wet mass}^{-1}$, and DW is the per cent dry mass of tissue. The change in energy content for a given tissue was calculated as follows:

$$\Delta kJ = W_f * E_f - W_i * E_i \quad \text{eqn 6}$$

Where W_f and E_f are the wet mass and energy density, respectively, of each tissue in late August, following the salmon subsidy, and W_i and E_i are the corresponding values in late June, prior to the subsidy. The energy density of gametes was estimated as $9 \text{ kJ} \cdot \text{g}^{-1}$ based on the empirical estimates compiled in (Armstrong 2010). We considered energy losses to include basal metabolism and the cost of spawning. We assumed males and females exhibited similar energy investment in spawning, males primarily through activity, and females through gamete production (Jonsson, Jonsson & Hansen 1991; Jobling *et al.* 1998). We estimated that females achieved a gonadosomatic index (GSI: gonad mass/body mass) of 17.1%, the midpoint of female GSI values reported for closely related Arctic charr (Fleming 1998). Thus, the cost of spawning, S , was estimated as

$$S = 0.171 * W_f * E_g \quad \text{eqn 7}$$

Where E_g is the energy density of eggs, and W_f is mass in August from eqn (4).

We estimated the cost of basal metabolism for a Dolly Varden with nonatrophied organs using the Wisconsin Bioenergetics model (Hanson *et al.* 1997) parameterized for actively feeding bull trout (*S. confluentus*) by Mesa *et al.* (2013). Bull trout are a closely related congener of Dolly Varden, and the two are sympatric across much of their range (Taylor *et al.* 2001). The Wisconsin model estimates basal metabolism as a function of

temperature and body mass, using empirically derived models (Hanson *et al.* 1997). We simulated accrued costs of basal metabolism from 1 September to 1 August the following year (i.e. the interpulse period), using the observed temperature regime and an initial body mass equal to the median mass from our late August sampling event (889 g). Body mass dropped by 17.1% in October to simulate reduced mass following spawning. We assumed Dolly Varden selected over-wintering habitat (e.g. deep pools) that remained at 1°C when our temperature logger indicated freezing temperatures, although including this ecological realism changed total energy expenditure by less than 1.5%. Our estimate of accrued metabolic cost is conservative, assuming no activity and no inefficiency in utilizing energy stores to support basal metabolism. We also estimated the maintenance ration during the period of the growing season prior to the subsidy, so that we could assess whether the observed rations (i.e. stomach contents) from June–July would be likely to meet basal energy demands. We defined maintenance ration as the mass of food needed to equal the daily cost of basal metabolism. We calculated maintenance ration for the minimum and maximum sized fish (370 and 987 g, resp.) in the June and July samples given the average observed temperature during that period (8.3°C). We assumed benthic invertebrate prey had an energy density of 3.5 kJ g^{-1} (Armstrong *et al.* 2010) and that 27% of consumption was lost to waste [egestion, excretion and specific dynamic action: (Brett & Groves 1979)].

Results

DOLLY VARDEN FORAGING ECOLOGY

The Alec River experiences a long winter, spanning from October through May, where monthly mean temperatures never exceed 5°C and 75% of days are below 3.5°C (Fig. 1). A shorter growing season occurs from June through September, in which temperatures average 8.2°C and range from 4.1 – 12.3°C (Fig. 1). ANOVA indicated significant differences among summer months (June, July and August) in Dolly Varden ration [$F(2,117) = 40.99$, $P < 0.001$], condition factor [$F(2,168) = 76.96$, $P < 0.001$] and C/N ratio [$F(2, 64) = 31.9$, $P < 0.001$]. Tukey's pairwise comparisons demonstrated that the changes in feeding level and energy status were associated with the occurrence of the salmon resource pulse in August and that these indices did not differ between the prepulse months of June and July (P -values reported below). During June and July, Dolly Varden diets were comprised of benthic invertebrates (100% of total mass recorded across all individuals) and indices of feeding level and energy status were low (Fig. 2). Instantaneous rations were negligible prior to the resource pulse [June: $0.65 (\pm 1.16) \text{ mg}_{\text{prey}} \cdot \text{g}_{\text{fish}}^{-1}$, July: $2.2 (\pm 1.8) \text{ mg}_{\text{prey}} \cdot \text{g}_{\text{fish}}^{-1}$, $P = 0.88$, all values are monthly means ± 1 standard deviation], below the daily maintenance ration of 1.7 – 3.9 g of prey (4.0 – $4.6 \text{ mg}_{\text{prey}} \cdot \text{g}_{\text{fish}}^{-1}$) (Fig. 2a). The C/N ratio of muscle tissue, an index of lipid content, was $3.34 (\pm 0.10)$ in June and $3.28 (\pm 0.08)$ in July, $P = 0.94$, (Fig. 2c). The condition factor was $0.85 (\pm 0.08) \text{ g mm}^{-3}$ in June and $0.85 (\pm 0.08) \text{ g mm}^{-3}$ in July, $P = 0.98$, (Fig. 2b). In the second half of the growing season, following the resource pulse,

ration and energy status increased substantially. The stomach contents of fish were comprised virtually entirely of salmon eggs and ration size increased by over an order of magnitude to $18.9 (\pm 14.2) \text{ mg}_{\text{prey}} \text{ g}_{\text{fish}}^{-1}$, June–August $P < 0.001$, July–August $P < 0.001$, (Fig. 2a). The C/N ratio increased to $3.63 (\pm 0.19)$, June–August $P < 0.001$, July–August $P = 0.010$ and condition factor increased to $1.07 (\pm 0.11) \text{ g} \cdot \text{mm}^{-3}$ June–August $P < 0.001$, July–August $P < 0.001$, (Fig. 2b,c). The $\delta^{15}\text{N}$ of tissue samples during the resource pulse matched that of salmon eggs (after accounting for trophic fractionation) (Fig. 2d). We observed no monthly change in $\delta^{15}\text{N}$ throughout the sampling season [$F(2,66) = 0.49$, $P = 0.61$]. The $\delta^{15}\text{N}$ of tissue samples collected throughout the interpulse phase of the growing season continued to reflect the isotopic signature of salmon eggs, despite the absence of eggs and the occurrence of isotopically dissimilar prey in stomach contents (Fig. 2d). This suggests Dolly Varden did not achieve the energy surplus required to build new somatic tissue during the ~11-month interpulse period.

ORGAN SIZES

For each organ under study, the best model structure included fork length and time period as fixed effects, with no interaction between these effects (Table S1, Supporting information). Including time period greatly improved the

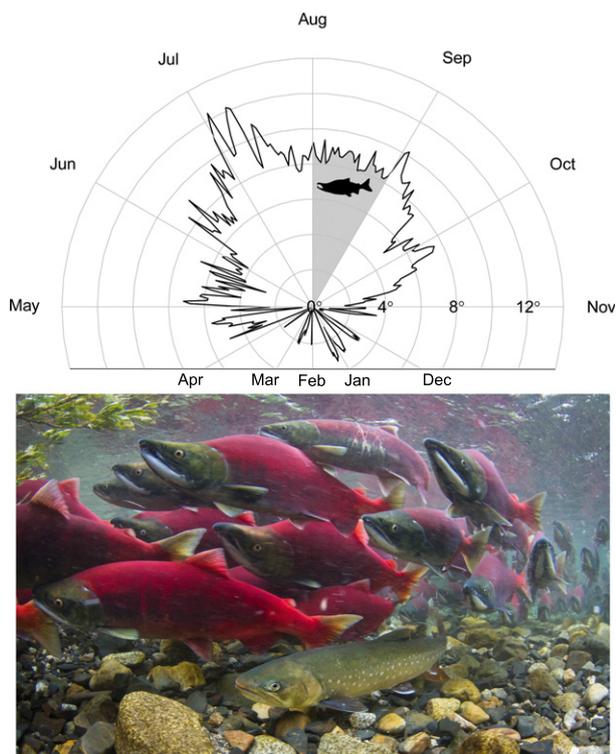


Fig. 1. Top: Radial plot showing seasonal variation in water temperature at our study site, the Alec River, Alaska, USA. The shaded portion of the graph indicates when sockeye salmon spawn and their eggs provide a resource pulse for Dolly Varden. Bottom: Image of a Dolly Varden and spawning sockeye salmon.

AICc scores for models of the stomach, pyloric caeca, intestine and liver (Table S1, Supporting information), reflecting significant changes in masses of digestive organs between the two sampling periods. The increase in digestive organ mass far exceeded the corresponding increase in body mass. For example, the mean length-specific wet mass of the carcass (body with gametes and organs removed) increased by 1.4-fold from June to August, whereas the mean length-specific wet mass of the gut (with food and digesta subtracted) increased by 2.6-fold. The length-specific dry masses of digestive organs differed before and after the resource pulse as follows (mean \pm standard deviation): liver before: $5.52 \pm 1.35 \text{ mg mm}^{-1}$, liver after: $19.52 \pm 4.71 \text{ mg mm}^{-1}$, stomach before: $4.84 \pm 0.98 \text{ mg mm}^{-1}$, stomach after: $12.00 \pm 3.62 \text{ mg mm}^{-1}$, pyloric caecae before: $3.89 \pm 1.28 \text{ mg mm}^{-1}$, pyloric caecae after: $8.21 \pm 2.45 \text{ mg mm}^{-1}$, intestine before: $0.87 \pm 0.29 \text{ mg mm}^{-1}$ and intestine after: $1.98 \pm 0.63 \text{ mg mm}^{-1}$ (Fig. 3). The heart exhibited a small increase in length-specific mass after the resource pulse; before: $0.40 \pm 0.13 \text{ mg mm}^{-1}$ and after: $0.54 \pm 0.13 \text{ mg mm}^{-1}$ (Fig. 3), which paralleled increases in somatic mass, causing the mass-specific heart mass to remain unchanged; before: $0.30 \pm 0.088 \text{ mg g}^{-1}$ after: $0.29 \pm 0.051 \text{ mg g}^{-1}$. In contrast to the heart and digestive organs, spleen mass was higher prior to the resource pulse: before: $0.83 \pm 0.58 \text{ mg mm}^{-1}$, after: $0.57 \pm 0.37 \text{ mg mm}^{-1}$ (Fig. 3).

ENERGETICS ANALYSIS

The median sized fish from our sample was estimated to have increased in energy content by 2067 kJ following the resource pulse. This increase occurred mostly in the soma and gonads (change in energy content: soma: +1428 kJ, liver: +161 kJ, pyloric caecae: +115 kJ, stomach: +64 kJ, intestine: +13 kJ, heart: +1 kJ, gonads: +298 kJ, spleen: -2 kJ). During the interpulse period, the predicted energy loss for a median sized fish with an active gut was 2933 kJ: 1565 kJ due to basal metabolism and 1368 kJ due to spawning. This suggests Dolly Varden would not be able to survive the interpulse period without either feeding substantially or cutting the costs of basal metabolism through mechanisms such as the observed atrophy of digestive organs.

Discussion

Here, we document physiological adaptation that enables a high-latitude fish to survive in environments with extreme, but predictable variation in foraging opportunity. Adult Dolly Varden in our focal system acquired the vast majority of their annual energy gain while gorging on sockeye salmon eggs for roughly 5 weeks. During this resource pulse, Dolly Varden exhibited large guts (Fig. 3), which enabled them to rapidly store energy in somatic growth, fat reserves and gonads (Fig. 2). During the inter-

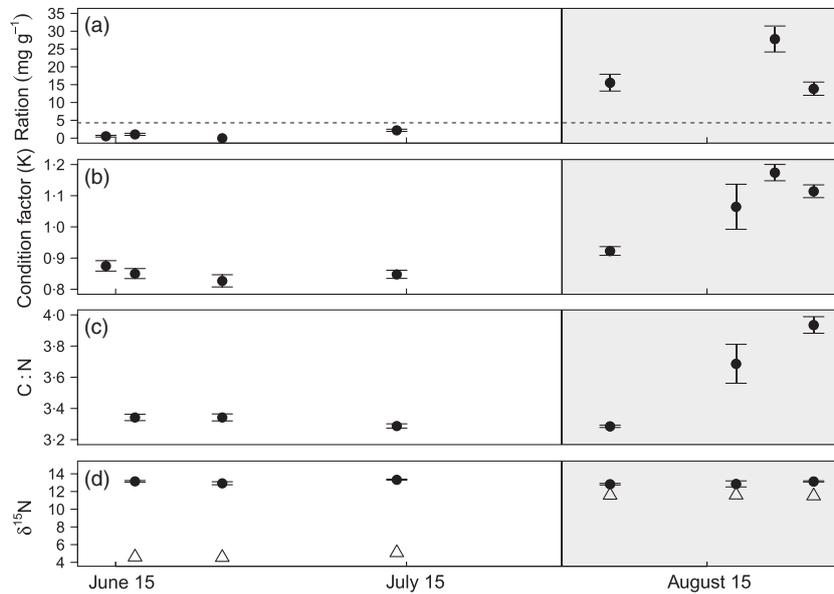


Fig. 2. The temporal pattern of foraging level and energy condition in Dolly Varden during the summer growing season. The portion of the growing season when spawning sockeye salmon are present is shaded in grey. Panels show (a) instantaneous ration (dashed line indicates maintenance ration), (b) condition factor, (c) C/N ratio of muscle tissue (a proxy of lipid content), and (d) the $\delta^{15}\text{N}$ isotopic signatures of both Dolly Varden muscle tissue (dots) and their diet contents (triangles) (pooled across all diets in each sampling interval). Diets were comprised of benthic invertebrates during the inter-pulse period and salmon eggs during the resource pulse. In all panels, error bars show ± 1 SE.

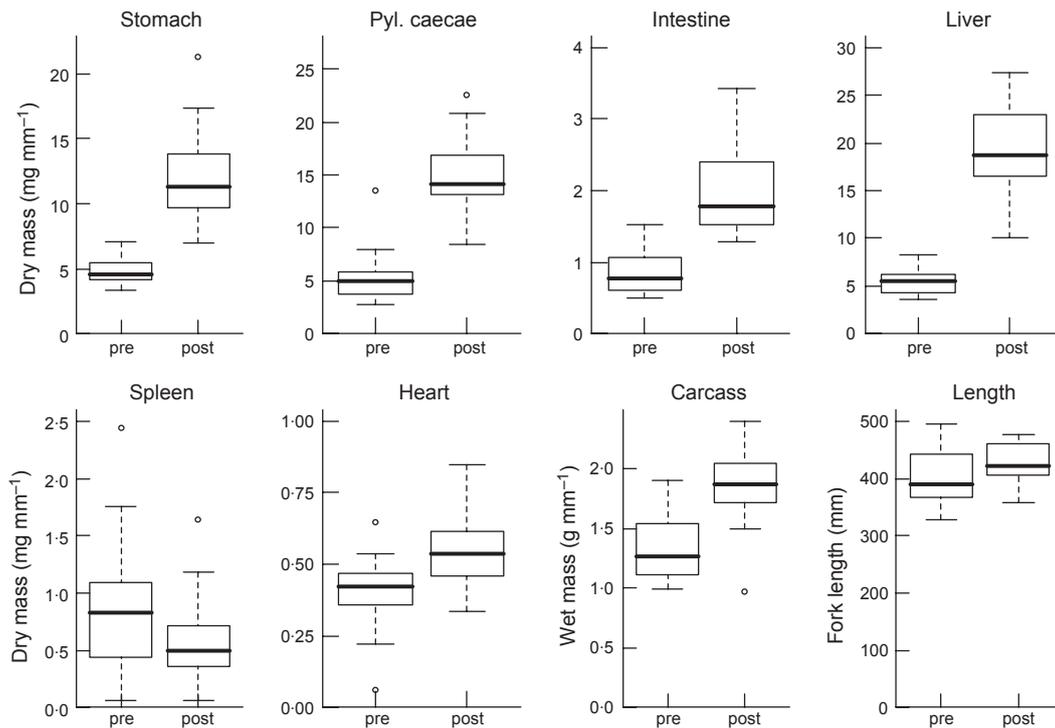


Fig. 3. Boxplots depicting the organ mass, carcass mass and body length of Dolly Varden sampled prior to the annual salmon resource pulse ('pre': 16 June) and near the terminus of the resource pulse ('post': 22 August). Organ and carcass masses are standardized by body length (mg mm^{-1} and g mm^{-1} , respectively). Body Length is expressed as fork length in millimetres (distance from nose to tail fork). Description of boxplots: each rectangle spans the interquartile range (IQR), showing the median as a bold line. Whiskers encompass data within $1.5 \times \text{IQR}$ of each quartile, beyond which outliers are represented as circles.

pulse period, Dolly Varden showed no signs of significant feeding (Fig. 2), yet incurred far less energy loss than predicted by a bioenergetics model parameterized for actively

feeding fish. These energy savings appears to derive from down-regulation of the digestive system through atrophy of the gut and liver. Our results provide one of the first

examples of both digestive flexibility in wild fish and physiological adaptation of consumers to resource pulses.

Like most high-latitude residents, Dolly Varden in the Alec River endure a long winter followed by a relatively short growing season (Conover 1992). It is widely documented that temperate fishes lose energy during winter (Conover 1992; Biro *et al.* 2004) and Dolly Varden were no exception. Fish in our system showed greatly reduced condition factor and C/N ratio (a proxy of lipid content) between late August and the following June. When considering the seasonal constraints on energy budgets, researchers have assumed that fish regain energy stores (somatic growth or lipids) throughout the nonwinter months (i.e. growing season) (Conover 1992). In contrast, Dolly Varden in the Alec River showed no signs of positive energy balance during the first half of the 'growing' season. Fish sampled in June and July had virtually no food in their stomachs and the isotopic signature of their muscle tissue never equilibrated to available prey items, suggesting fish did not achieve energy surplus from *in situ* trophic pathways. Indeed, indices of energy status (condition factor and C/N) remained low until the sockeye salmon run in August. Following the onset of the sockeye salmon subsidy, ration size increased by more than an order of magnitude and energy indices greatly increased. Combined these field data suggest Dolly Varden achieve nearly all of their annual energy profits during the roughly 1 month that they gorge on sockeye salmon eggs.

Alternating periods of feast and famine generate trade-offs between phenotypes that maximize energy gain during resource abundance, and those that conserve energy during resource scarcity. Instead of expressing fixed traits that compromised between cost and capacity, Dolly Varden exhibited flexible organ size, showing a 2-6-fold increase in gut mass between mid-June, during the beginning of the growing season and August, during the sockeye salmon subsidy. As Dolly Varden exhibited no signs of energy surplus prior to the subsidy, it is likely that their guts remained atrophied until they could acquire energy from salmon eggs, but further study is needed to characterize the finer-scale timing of digestive flexibility and the cues that trigger it. Adaptive regulation of assimilative capacity enabled Dolly Varden to increase rates of energy storage during the resource pulse and reduce rates of energy loss during the remainder of the year. Without a flexible gut, it is unlikely that Dolly Varden could survive the long period between sockeye salmon runs. The median sized Dolly Varden in our study gained ~2050 KJ in energy stores during the resource pulse, whereas the combined costs of spawning and basal metabolism during the interpulse period were conservatively predicted to be ~2950 KJ for a charr with an active gut. To close this apparent energy deficit, Dolly Varden would need to feed throughout the year (increase revenue) or incur less energy costs than predicted by existing models (cut spending). Multiple lines of evidence suggest that Dolly Varden are not acquiring significant energy surplus

by feeding during the interpulse period (Fig. 2). This implies that Dolly Varden close much of the apparent annual energy deficit by cutting the costs of basal metabolism. Our results suggest the primary cost-cutting mechanism is the down-regulation of organ systems providing assimilative capacity, specifically the gut and liver.

Among the organs we sampled, the liver exhibited the largest change in mass. This probably results from the dual function of the liver, which supports not only assimilation, but also the storage of lipids. Indeed, the dry weight/wet weight ratio of the liver increased by 22% following the resource pulse, indicating increased lipid content. We observed relatively similar increases in mass across the components of the gut: 148% in the stomach, 193% in the pyloric caecae and 129% in the intestine. This suggests the absence of a single bottleneck to food processing along the components of the fish gut. In contrast, wading birds that consume hard-shelled prey are limited by the rate at which the muscular stomach (i.e. gizzard) can crush food, and may exhibit large changes in the mass of the gizzard without corresponding increases in the mass of the intestine or liver (Piersma & van Gils 2011). The mass of the heart increased somewhat per unit of fish length (35%), but not per unit of somatic mass. Animals generally exhibit less plasticity in heart mass than gut or liver mass (Piersma & van Gils 2011), perhaps because heart cells have extremely slow turnover rates (Bergmann *et al.* 2009). However, components of heart cells can change rapidly (Hoppeler & Fluck 2002) and increased heart mass and beat rate accompany up-regulation of digestive capacity in other poikilotherms [pythons:(Secor 2008)]. A nonatrophied gut consumes a substantial proportion of cardiac output, even when empty (Farrell *et al.* 2001), so it is unclear why the observed increase in gut size was not accompanied by a greater increase in heart size. In contrast to the other organs measured, the spleen actually decreased in size and energy density in concert with up-regulation of digestive capacity. The spleen functions to filter blood and support immune response (Press, Dannevig & Landsverk 1994; Agius & Roberts 2003). The mass of the spleen has been positively associated with disease resistance in salmonids (Hadidi *et al.* 2008). If increased spleen size does represent up-regulation of the immune system, it is unclear whether it functions to mitigate the physiological stress of negative energy balance, or if actually results in an increased level of immune function compared with levels during the resource pulse.

Yang *et al.* (2008) suggest that consumers exploiting resource pulses fall into two general categories: 'mobile specialists', which move to track multiple resource pulses as they shift through space and time (Ruff *et al.* 2011), and 'opportunistic residents', which switch to pulsed items when they become available but rely primarily on alternative food sources. This classification implies that animals cannot rely on a single resource pulse for energy gain and instead require behavioural adaptation to stabilize seasonal variation in energy intake. Our study provides an

alternative view, in which a third type of consumer, the 'specialist resident' can rely exclusively on annual resource pulses through physiological adaptation that maximizes energy gain during the pulse and minimizes energy expenditure during the interpulse period. This is analogous to physiological adaptations in desert plants to rare, high-magnitude precipitation events (Noy-Meir 1973).

Our study site, the Alec River, is a component of the hydrologically diverse Chignik Watershed, which flows into productive marine environments. Dolly Varden are capable of impressive migrations (Decicco 1992) and could likely find alternative food sources across this physically and biologically diverse waterscape (Templin *et al.* 1999). Why then, do adult fish in our focal population incur energy losses by remaining in unproductive habitat? We suggest this is a form of asset-protection (Clark 1994) that maximizes fitness rather than energy gain. After capitalizing on the sockeye salmon subsidy, Dolly Varden could maintain their digestive machinery and search for food across the Chignik watershed or Gulf of Alaska. Given the high scope for energy profit in fishes (Brett & Groves 1979; Hanson *et al.* 1997; Armstrong & Schindler 2011) and the diversity of prey resources across the region, the expected energy profit from this migratory strategy would likely be higher than resident strategies. However, maintaining digestive capacity could increase the risk of dying from starvation while searching for patchy prey resources, and the activities of foraging and migration would likely increase predation risk (Stoks, McPeck & Mitchell 2003), especially in the most productive marine environments. Instead, adult Dolly Varden in the Alec River exhibit a risk-averse behavioural strategy made possible by phenotype flexibility. Adaptive regulation of assimilative capacity enables Dolly Varden to live off the energy savings they accrue from salmon subsidies with minimal feeding during the months in between, a strategy that foregoes opportunity for supplemental energy gain in exchange for reduced predation risk. The profitability of this strategy depends on the magnitude of the resource pulse, and therefore the health of Pacific Salmon stocks. Charr species exhibit tremendous resource polymorphism and can occur in high-latitude watersheds which lack salmon subsidies by exhibiting life-history strategies that exploit alternative trophic pathways (e.g. anadromous or lake-resident phenotypes) or are specialized for resource scarcity [e.g. stunted phenotypes (Griffiths 1994)]. However, salmon subsidies are likely essential to the persistence of large-bodied stream-resident phenotypes, which are prized by anglers and contribute to a commercially important recreational fishery in Southwest Alaska.

Charr species have suffered population declines and extirpation across the southern extent of their range in North America, where humans have had a larger footprint on aquatic ecosystems. The plight of southern charr (e.g. *S. confluentus*) has been largely blamed on habitat degradation (Rieman, Lee & Thurow 1997), negative interactions with invasive species (Leary, Allendorf & Forbes 1993; Baxter *et al.* 2007) and overharvest (Post *et al.* 2002). Our

study suggests that the functional extirpation of salmon subsidies (Moore, Schindler & Ruff 2008) may also play a substantial role in the decline of charrs. The adult Dolly Varden in our focal system appear to acquire virtually all of their annual energy surplus from salmon subsidies, as their isotopic signatures never equilibrate to *in situ* food sources. This heavy reliance on salmon subsidies is not unique to our focal system; salmonid fishes in other systems have been shown to acquire the majority of their annual growth by exploiting salmon eggs (Scheuerell *et al.* 2007; Denton, Rich & Quinn 2009; Armstrong *et al.* 2010) or other life stages of salmon (Denton, Rich & Quinn 2009; Lowery 2009). Indeed, charr species have declined or extirpated in watersheds with relatively pristine habitat following the loss of salmon subsidies (Rode 1988), whereas healthy charr populations occur in heavily altered watersheds where salmon subsidies remain intact (Lowery 2009) or anadromous populations have been replaced with landlocked populations (Beauchamp & Van Tassell 2001). Efforts to conserve charr populations may benefit by expanding their current emphasis on the physical restoration of habitat to more explicitly consider the restoration of food webs and resource fluxes among ecosystems.

Our results emphasize the importance of ephemeral food sources to the conservation of fish in general. The Dolly Varden in our study system appear to achieve nearly all their annual energy surplus from a ~5-week, long resource pulse. This is encouraging because it demonstrates that the natural growth efficiency of fish (Brett & Groves 1979), combined with their plastic physiology and behaviour, can enable them to survive long periods of food scarcity as long as they can periodically capitalize on high-quality foraging opportunities. Thus, fishes are resilient to resource scarcity and can recoup energy losses over short periods, as long as ecosystems provide intermittent periods of resource abundance. On the other hand, our study demonstrates how fishes may rely heavily on ephemeral resources that are not produced *in situ* (Nakano & Murakami 2001; Wipfli & Baxter 2010). This suggests that harvest policies that attenuate resource pulses (Moore, Schindler & Ruff 2008; Levi *et al.* 2012) or land use actions that interrupt subsidies (Wipfli & Baxter 2010) may have unexpectedly severe consequences.

Acknowledgements

This is a contribution of the Alaska Salmon Program, funded by the National Science Foundation, The Gordon and Betty Moore Foundation, the Alaska salmon processors and the University of Washington School of Aquatic and Fishery Sciences. Jennifer Griffiths and Conrad Gowell assisted with fieldwork; Kale Bentley, Daniel Schindler and Loveday Conquest contributed to data analysis. Two anonymous reviewers provided helpful comments that improved the manuscript.

References

- Agius, C. & Roberts, R.J. (2003) Melano-macrophage centres and their role in fish pathology. *Journal of Fish Diseases*, **26**, 499–509.

- Armstrong, J.B. (2010) Comment on Egg consumption in mature Pacific salmon (*Oncorhynchus* spp.). *Canadian Journal of Fisheries and Aquatic Sciences*, **67**, 2052–2054.
- Armstrong, J.B. & Schindler, D.E. (2011) Excess digestive capacity in predators reflects a life of feast and famine. *Nature*, **476**, 84–89.
- Armstrong, J.B., Schindler, D.E., Omori, K.L., Ruff, C.P. & Quinn, T.P. (2010) Thermal heterogeneity mediates the effects of pulsed subsidies across a landscape. *Ecology*, **91**, 1445–1454.
- Baxter, C., Fausch, K., Murakami, M. & Chapman, P. (2007) Invading rainbow trout usurp a terrestrial prey subsidy from native charr and reduce their growth and abundance. *Oecologia*, **153**, 461–470.
- Beauchamp, D.A. & Van Tassell, J.J. (2001) Modeling seasonal trophic interactions of adfluvial bull trout in Lake Billy Chinook, Oregon. *Transactions of the American Fisheries Society*, **130**, 204–216.
- Bergmann, O., Bhardwaj, R.D., Bernard, S., Zdunek, S., Barnabé-Heider, F., Walsh, S., Zupicich, J., Alkass, K., Buchholz, B.A., Druid, H., Jovinge, S. & Frisan, J. (2009) Evidence for cardiomyocyte renewal in humans. *Science*, **324**, 98–102.
- Biro, P.A., Morton, A.E., Post, J.R. & Parkinson, E.A. (2004) Over-winter lipid depletion and mortality of age-0 rainbow trout (*Oncorhynchus mykiss*). *Canadian Journal of Fisheries and Aquatic Sciences*, **61**, 1513–1519.
- Blier, P.U., Dutil, J.D., Lemieux, H., Balanger, F. & Bitetera, L. (2007) Phenotypic flexibility of digestive system in Atlantic cod (*Gadus morhua*). *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, **146**, 174–179.
- Breck, J.E. (2008) Enhancing bioenergetics models to account for dynamic changes in fish body composition and energy density. *Transactions of the American Fisheries Society*, **137**, 340–356.
- Brett, J.R. & Groves, T.D.D. (1979) Physiological energetics. *Fish Physiology*, (eds W.S. Hoar, D.J. Randall & J.R. Brett), pp. 279–352. Academic Press, New York.
- Brodin, A. & Clark, C.W. (2007) Energy storage and expenditure. *Foraging: Behavior and Ecology*, (eds D.W. Stephens, J.S. Brown & R.C. Ydenberg), pp. 221–269. University of Chicago Press, Chicago.
- Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer Verlag, New York.
- Campana, S.E. (1999) Chemistry and composition of fish otoliths: pathways, mechanisms and applications. *Marine Ecology-Progress Series*, **188**, 263–297.
- Cant, J.P., McBride, B.W. & Croom, W.J. (1996) The regulation of intestinal metabolism and its impact on whole animal energetics. *Journal of Animal Science*, **74**, 2541–2553.
- Clark, C.W. (1994) Antipredator behavior and the asset-protection principle. *Behavioral Ecology*, **5**, 159–170.
- Conover, D.O. (1992) Seasonality and the scheduling of life history at different latitudes. *Journal of Fish Biology*, **41**, 161–178.
- Decicco, A.L. (1992) Long-distance movements of anadromous Dolly Varden between Alaska and the USSR. *Arctic*, **45**, 120–123.
- Denton, K.P., Rich, H.B. & Quinn, T.P. (2009) Diet, movement, and growth of Dolly Varden in response to sockeye salmon subsidies. *Transactions of the American Fisheries Society*, **138**, 1207–1219.
- Diamond, J. (2002) Quantitative evolutionary design. *Journal of Physiology-London*, **542**, 337–345.
- Essington, T.E., Kitchell, J.F. & Walters, C.J. (2001) The von Bertalanffy growth function, bioenergetics, and the consumption rates of fish. *Canadian Journal of Fisheries and Aquatic Sciences*, **58**, 2129–2138.
- Farrell, A.P., Thorarensen, H., Axelsson, M., Crocker, C.E., Gamperl, A.K. & Cech, J.J. (2001) Gut blood flow in fish during exercise and severe hypercapnia. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, **128**, 551–563.
- Fleming, I.A. (1998) Pattern and variability in the breeding system of Atlantic salmon (*Salmo salar*), with comparisons to other salmonids. *Canadian Journal of Fisheries and Aquatic Sciences*, **55**, 59–76.
- Fry, B. (2006) *Stable Isotope Ecology*. Springer, New York.
- Gans, C. (1979) Momentarily excessive construction as the basis for protoadaptation. *Evolution*, **33**, 227–233.
- Gende, S.M., Edwards, R.T., Willson, M.F. & Wipfli, M.S. (2002) Pacific salmon in aquatic and terrestrial ecosystems. *BioScience*, **52**, 917–928.
- Griffiths, D. (1994) The size structure of lacustrine Arctic charr (*Pisces: Salmonidae*) populations. *Biological Journal of the Linnean Society*, **51**, 337–357.
- Gross, M.R. (1987) Evolution of diadromy in fishes. *American Fisheries Society Symposium*, **1**, 14–25.
- Hadidi, S., Glenney, G.W., Welch, T.J., Silverstein, J.T. & Wiens, G.D. (2008) Spleen size predicts resistance of rainbow trout to *Flavobacterium psychrophilum* challenge. *The Journal of Immunology*, **180**, 4156–4165.
- Hanson, P.C., Johnson, T.B., Schindler, D.E. & Kitchell, J.F. (1997) *Fish Bioenergetics 3.0*. University of Wisconsin Sea Grant Institute, Madison.
- Hoppeler, H. & Fluck, M. (2002) Normal mammalian skeletal muscle and its phenotypic plasticity. *Journal of Experimental Biology*, **205**, 2143–2152.
- Htunhan, M. (1978) Reproductive biology of dab (*Limnada limnada*) in the North Sea: gonadosomatic index, hepatosomatic index, and condition factor. *Journal of Fish Biology*, **13**, 369–378.
- Humphries, M.M., Thomas, D.W., Hall, C.L., Speakman, J.R. & Kramer, D.L. (2002) The energetics of autumn mast hoarding in eastern chipmunks. *Oecologia*, **133**, 30–37.
- Jobling, M., Johansen, S.J.S., Foshaug, H., Burkow, I.C. & Jørgensen, E.H. (1998) Lipid dynamics in anadromous Arctic charr, *Salvelinus alpinus* (L.): seasonal variations in lipid storage depots and lipid class composition. *Fish Physiology and Biochemistry*, **18**, 225–240.
- Jonsson, N., Jonsson, B. & Hansen, L.P. (1991) Energetic cost of spawning in male and female Atlantic salmon (*Salmo salar* L.). *Journal of Fish Biology*, **39**, 739–744.
- Kent, J., Prosser, C.L. & Graham, G. (1992) Alterations in liver composition of channel catfish (*Ictalurus punctatus*) during seasonal acclimatization. *Physiological Zoology*, **65**, 867–884.
- Leary, R.F., Allendorf, F.W. & Forbes, S.H. (1993) Conservation genetics of bull trout in the Columbia and Klamath River Drainages. *Conservation Biology*, **7**, 856–865.
- Levi, T., Darimont, C.T., MacDuffee, M., Mangel, H., Paquet, P. & Wilmers, C.C. (2012) Using grizzly bears to assess harvest-ecosystem trade-offs in salmon fisheries. *PLoS Biology*, **10**, e1001303.
- Lowery, E.D. (2009) Trophic relations and seasonal effects of predation on Pacific salmon by fluvial bull trout in a riverine food web. MS thesis, School of Aquatic and Fishery Sciences, University of Washington, Seattle.
- McWilliams, S.R. & Karasov, W.H. (2001) Phenotypic flexibility in digestive system structure and function in migratory birds and its ecological significance. *Comparative Biochemistry and Physiology A: Molecular & Integrative Physiology*, **128**, 579–593.
- Mesa, M., Weiland, L., Sauter, S. & Beauchamp, D. (2013) Development and evaluation of a bioenergetics model for bull trout. *Transactions of the American Fisheries Society*, **142**, 41–49.
- Moore, J.W., Schindler, D.E. & Ruff, C.P. (2008) Habitat saturation drives thresholds in stream subsidies. *Ecology*, **89**, 306–312.
- Nakano, S. & Murakami, M. (2001) Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. *Proceedings of the National Academy of Sciences of the United States of America*, **98**, 166–170.
- Naya, D.E., Karasov, W.H. & Bozinovic, F. (2007) Phenotypic plasticity in laboratory mice and rats: a meta-analysis of current ideas on gut size flexibility. *Evolutionary Ecology Research*, **9**, 1363–1374.
- Noy-Meir, I. (1973) Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics*, **4**, 25–51.
- Ostfeld, R.S. & Keesing, F. (2000) Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *Trends in Ecology & Evolution*, **15**, 232–237.
- Piersma, T. & van Gils, J.A. (2011) *The Flexible Phenotype: A Body-Centred Integration of Ecology, Physiology, and Behaviour*. Oxford University Press, Oxford and New York.
- Post, J.R., Sullivan, M., Cox, S., Lester, N.P., Walters, C.J., Parkinson, E.A., Paul, A.J., Jackson, L. & Shuter, B.J. (2002) Canada's recreational fisheries: the invisible collapse? *Fisheries*, **27**, 6–17.
- Post, D., Layman, C., Arrington, D., Takimoto, G., Quattrochi, J. & Montaña, C. (2007) Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia*, **152**, 179–189.
- Press, C.M., Dannevig, B.H. & Landsverk, T. (1994) Immune and enzyme-histochemical phenotypes of lymphoid and nonlymphoid cells within the spleen and head kidney of Atlantic salmon (*Salmo salar*). *Fish & Shellfish Immunology*, **4**, 79–93.
- R Core Development Team. (2012) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rieman, B.E., Lee, D.C. & Thurow, R.F. (1997) Distribution, status, and likely future trends of bull trout within the Columbia River and Klamath River Basins. *North American Journal of Fisheries Management*, **17**, 1111–1125.

- Rode, M. (1988) *Bull trout, Salvelinus Confluentus* (Suckley), in the McCloud River, Status and Recovery Recommendations. Inland Fisheries Administrative Report No. 1988. Department of Fish and Game, California.
- Ruff, C.P., Schindler, D.E., Armstrong, J.B., Bentley, K.T., Brooks, G.T., Holtgrieve, G.W., McGlauffin, M.T., Torgersen, C.E. & Seeb, J.E. (2011) Temperature-associated population diversity in salmon confers benefits to mobile consumers. *Ecology*, **92**, 2073–2084.
- Rutter, C. (1902) Natural history of the Quinnet salmon. *United States Fish Commission Bulletin*, **22**, 66–141.
- Scheuerell, M.D., Moore, J.W., Schindler, D.E. & Harvey, C.J. (2007) Varying effects of anadromous sockeye salmon on the trophic ecology of two species of resident salmonids in southwest Alaska. *Freshwater Biology*, **52**, 1944–1956.
- Schindler, D.E., Scheuerell, M.D., Moore, J.W., Gende, S.M., Francis, T.B. & Palen, W.J. (2003) Pacific salmon and the ecology of coastal ecosystems. *Frontiers in Ecology and the Environment*, **1**, 31–37.
- Schindler, D.E., Hilborn, R., Chasco, B., Boatright, C.P., Quinn, T.P., Rogers, L.A. & Webster, M.S. (2010) Population diversity and the portfolio effect in an exploited species. *Nature*, **465**, 609–612.
- Secor, S.M. (2008) Digestive physiology of the Burmese python: broad regulation of integrated performance. *Journal of Experimental Biology*, **211**, 3767–3774.
- Secor, S.M., Stein, E.D. & Diamond, J. (1994) Rapid up-regulation of snake intestine in response to feeding - a new model of intestinal adaptation. *American Journal of Physiology*, **266**, G695–G705.
- Stoks, R., McPeck, M.A. & Mitchell, J.L. (2003) Evolution of prey behavior in response to changes in predation regime: Damselflies in fish and dragonfly lakes. *Evolution*, **57**, 574–585.
- Taylor, E.B., Redenbach, Z.A., Costello, A.B., Pollard, S.J. & Pacas, C.J. (2001) Nested analysis of genetic diversity in northwestern North American char, Dolly Varden (*Salvelinus malma*) and bull trout (*Salvelinus confluentus*). *Canadian Journal of Fisheries and Aquatic Sciences*, **58**, 406–420.
- Templin, W., Seeb, L., Crane, P. & Seeb, J. (1999) *Genetic Analysis of Sockeye Salmon Populations from the Chignik Watershed*. Regional Information Report No. 5J99-08. Alaska Department of Fish and Game, Anchorage, AK.
- Von Bertalanffy, L. (1938) A quantitative theory of organic growth (inquires on growth laws II). *Human Biology*, **10**, 2129–2138.
- Wipfli, M.S. & Baxter, C.V. (2010) Linking ecosystems, food webs, and fish production: subsidies in salmonid watersheds. *Fisheries*, **35**, 373–387.
- Wipfli, M.S., Hudson, J.P., Caouette, J.P. & Chaloner, D.T. (2003) Marine subsidies in freshwater ecosystems: salmon carcasses increase the growth rates of stream-resident salmonids. *Transactions of the American Fisheries Society*, **132**, 371–381.
- Yang, L.H., Bastow, J.L., Spence, K.O. & Wright, A.N. (2008) What can we learn from resource pulses? *Ecology*, **89**, 621–634.
- Zuur, A., Ieno, E., Walker, N., Saveliev, A. & Smith, G. (2009) *Mixed Effects Models and Extensions in R*. Springer, New York.

Received 22 September 2012; accepted 11 February 2013

Handling Editor: Martin Genner

Supporting Information

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

Fig. S1. Length at age plot for all Dolly Varden sampled in the Alec River, 2009–2011 (age 3–11). Age 1 and 2 individuals added from collections in Chignik Lake to improve the model fit. Solid line is fitted von Bertalanffy curve ($L_{\text{inf}} = 458$ mm, $K = 0.46$).

Table S1. Candidate linear models of Dolly Varden organ mass as a function of fish length (L) and time period (P) relative to the salmon resource pulse. K denotes total parameters, LL denotes log-likelihood.