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Integrative measures of consumption rates in salmon: expansion and application of a trace element approach

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Summary

1. Establishing reliable estimates of consumption is necessary for understanding the physiology, bioenergetics and trophic relationships of organisms. For fish, the inability to measure consumption directly prevents a mechanistic understanding of habitat–foraging relationships. Building upon established models for ^{137}caesium (Cs) mass balance in fish, we used natural abundances of a stable geologically derived isotope of Cs to estimate consumption rates over the first growing season for Atlantic salmon *Salmo salar* and to derive a general model that provides integrative estimates of consumption rates for individuals of all sizes.

2. To test the reliability of the trace metal approach we (i) performed a sensitivity analysis of model parameters and (ii) parameterized the model with site-specific data, including gut contents, Cs concentrations of invertebrate prey and assimilation rates.

3. We applied the method in two sites to make the first *in situ* determinations of consumption rates of individual age-0 salmon at post-larval and fry stages, for fish as small as 0·1 g. Consumption estimates were most responsive to changes in three parameters: Cs body burdens, Cs concentration in prey items and assimilation efficiency, all of which could be measured with high precision using inductively coupled plasma mass spectrometry.

4. The assimilation efficiency of Cs measured on field-caught age-0 salmon was approximately 60%. Consumption rates at 2 weeks post-stocking were highly variable in both sites, ranging from no detectable consumption to 8·5% fresh weight (fw) day^{-1}. By the end of the growing season, consumption rates were less variable (2–4% fw day^{-1}).

5. *Synthesis and applications.* This study is the first to demonstrate that background levels of geologically derived Cs can be used to estimate consumption rates of fish. Our results show that extremely low consumption rates during the first 6 weeks of life correspond closely with the critical survival period in other fish populations, and suggest a mechanism for a hypothesized survival bottleneck at this time. The results implicate the importance of early season habitat availability when considering management priorities of fish. Additionally, our use of stable Cs at natural abundance concentrations permits the global application of this trace element approach for estimating consumption rates of fish as well as other organisms. This general approach can be adopted for conservation and management settings in which it is necessary to identify suitable foraging habitat of a species or to quantify the relationship between consumption and growth.

Key-words: assimilation, bioenergetics, caesium (Cs), critical period, Atlantic salmon

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Introduction

Establishing reliable field-based estimates for fish consumption has long been an obstacle to the study of fish physiology, bioenergetics and ecology (Brandt & Hartman 1993). A major challenge has been extrapolating from individual-based or population-level measures at a single point in time to truly integrative measures of consumption, given the considerable temporal and spatial variability that an individual fish experiences over time. Common techniques for estimating consumption do not incorporate this variability into individual estimates of consumption because they rely upon (i) averaged measurements of habitat conditions, (ii) interpolation between time points or (iii) combined samples of stomach contents. Bioenergetic models, for example, can be used to predict consumption rates for individuals based upon habitat measurements for the specific location in which the fish was caught. However, these measurements necessarily simplify the spatial heterogeneity in habitat or food availability that a mobile fish may experience. Alternatively, field-based techniques, such as gastric evacuation, require the aggregation of samples from many fish to determine a single average food weight (Eggers 1977; Elliott & Persson 1978). Finally, for all methods that require repeated measures, events between sampling periods can have a large effect on estimates of consumption, as the food conditions or physiological state of fish may change rapidly (Whitledge & Hayward 2000). Consequently, none of these methods produces an integrative estimate of consumption by individuals while preserving the day-to-day variations in environmental and physical conditions experienced by all small fish.

Despite the methodological challenges, consumption rates are a fundamental component of many aspects of fisheries sciences. Estimates of consumption have been used extensively to develop growth and population models (Stewart *et al*. 1983; Boisclair & Leggett 1988), to study predator–prey relationships (La Bar 1993; Olson 1996) and to explain pollutant accumulation in fish populations (Post, Vandenbos & McQueen 1996; Trudel & Rasmussen 2001). Predictions of consumption based upon bioenergetic models suggest that a strong relationship exists between consumption, growth and survival of young fish (Nislow, Folt & Parrish 1999). However, the inability to measure consumption rates independently *in situ* makes it difficult to test these predictions directly and has therefore limited our understanding of the ways in which habitat availability regulates fish populations. Instead, consumption rates of juvenile salmonids are frequently estimated as a function of prey abundance and hydrological conditions (Hill & Grossman 1993) or calculated from the sum of growth and metabolic costs. However, because calculations for consumption are based upon model parameters (i.e. they are not independent), it is impossible to test how different variables such as food availability, metabolic costs and temperature separately influence consumption rates or how consumption rates influence growth and metabolism. To circumvent these interdependencies, researchers have used fluxes of non-essential and physiologically inert trace elements as an integrative and independent measure of consumption rates over the lifetime of the fish (Kolehmainen 1974; Forseth *et al*. 1992; Trudel & Rasmussen 2001).

For years, scientists have exploited the widespread distribution of radionuclides to measure fish foraging and trophic relations (Davis & Foster 1958; Kevern 1966). One radioisotope of caesium (^{137}Cs, half-life 30·1 years) is elevated in the aquatic environment as a result of globally dispersed nuclear fallout. This radioisotope, as well as the stable isotope of caesium (^{133}Cs), is dilute in streams and lakes but is bioconcentrated by primary producers by a factor of 100–1000-fold (Rowan & Rasmussen 1994). Cs is taken in by fish primarily in diet items, with only a minor contribution of Cs from aqueous phases through gills and body surfaces (Kolehmainen, Häsänen & Miettinen 1967; Hewett & Jefferies 1976). Additionally, Cs is not required metabolically, thereby eliminating the complex non-linear relationships between growth, respiration and elemental turnover that can occur with essential nutrients, such as nitrogen (N) and phosphorus (P). Consequently, the change of Cs body burdens in an individual fish is directly proportional to the amount of food ingested by a fish (Ugedal *et al*. 1995).

There has been renewed interest in the use of radionuclides to estimate food consumption after the Chernobyl nuclear accident in 1986. This work has led to several elegant tests of the Cs radioisotope approach as well as novel applications of the method (Forseth *et al*. 1992; Forseth, Ugedal & Jonsson 1994; Rowan & Rasmussen 1996). However, the use of radionuclides to estimate consumption has some limitations: (i) the dispersal of radionuclides is spatially heterogeneous (Aarkrog *et al*. 1997; Tucker *et al*. 1999) and cannot be easily quantified world-wide; (ii) gamma radiation can be difficult to measure in very small organisms (B. P. Kennedy, personal observation), sometimes making it necessary to pool many individuals (Rowan & Rasmussen 1996); and (iii) radioactive Cs is released to the environment in pulses (Jonsson, Forseth & Ugedal 1999; Sundbom *et al*. 2003), which can complicate year-to-year comparisons. We have developed and applied an alternative method for estimating consumption based upon the accumulation of stable geologically derived ^{133}Cs at natural abundance levels. Measurements of the naturally occurring isotope of Cs using inductively coupled plasma mass spectrometry (ICP-MS) can be made at concentrations as low as one part per trillion with relative SD of 1–2%, permitting the measurement of Cs and estimation of consumption rates for very small fish (< 1 g). Additionally, the occurrence of stable Cs in aquatic systems is controlled by bedrock geology and thus should not change appreciably with time, facilitating comparisons among years and across broad geographical areas.

Despite its potential advantages, few studies have studied the fate of stable Cs in the environment or its transfers in biological systems, because of its extremely low background concentrations. Three studies that have used stable Cs to estimate consumption rates have relied upon ^{133}Cs-enriched compounds (Hakonson, Gallegos & Whicker 1975; Forseth *et al*. 1999, 2001). In these studies, stable Cs behaved similarly to radiocaesium, as would be expected because organisms cannot differentiate between isotopes of heavy metals. However, pulsed additions of a tracer over short intervals requires the incorporation of two-component elimination curves and can complicate the approach by introducing time lags in trophic transfers. In contrast, the equilibrial conditions of a geologically derived tracer permit simplifying steady-state assumptions.

This study is the first to demonstrate that background levels of geologically derived Cs can be used to estimate consumption rates of fish. The goals were to develop a method for estimating integrative consumption rates using naturally occurring levels of stable Cs and to use this method to compare *in situ* consumption rates of age-0 Atlantic salmon *Salmo salar* L. fry at two sites across 3 years. In the process of expanding this trace element approach for estimating consumption rates, we parameterized several components of the Cs-based model and conducted a sensitivity analysis on all parameters. We compared our estimated consumption rates with those of other methods. Lastly, our individual estimates of consumption allowed us to address whether food limitation could serve as one possible mechanism for a critical period of survival in age-0 salmon.

Methods

STUDY SITES AND SAMPLING

Atlantic salmon are stocked annually into tributaries of the Connecticut River, USA, as unfed fry. We sampled age-0 salmon from two third-order tributaries of the West River, Flood and Utley Brooks, in southern Vermont, USA (Fig. 1) in the years, 1991, 1992 and 1998. Flood and Utley Brooks are within 7 km of each other (Fig. 1) and have similar temperature profiles, hydrographs and underlying geology. In 1992, fish were sampled using a backpack electroshocker and small nets in the early season, 15 and 17 days after stocking in Utley and Flood Brooks, respectively. Mid-season samples (approximately 40–45 days after stocking) were collected in 1991 and late-season samples (approximately 90 days after stocking) were collected from both sites in 1991 and 1998 (Table 1). Invertebrate diet items were sampled using a Surber sampler and drift nets in Flood and Utley Brooks in August 1998, at the same time as fish samples were taken. Collected fish and invertebrates were stored on ice while in the field and frozen immediately upon return to the laboratory (2–6 h after collection).

EXPANSION OF THE MODEL

Integrative consumption rates of juvenile Atlantic salmon were measured using a kinetic model that describes the turnover and accumulation of non-essential trace elements in tissues. The model was developed for estimating consumption rates with fluxes of radiocaesium (^{137}Cs) and is based upon mass balances for growth and ^{137}Cs body burdens (Forseth *et al*. 1992; Rowan & Rasmussen 1996). Between any two sampling periods, Cs body burdens (Q) change as a function of dietary uptake, fish growth and excretory loses, such that the body burden of Cs at time t (Q_t) is related to the initial body burden (Q_0) by the equation:

$$Q_t = \frac{C\alpha(^{137}\mathrm{Cs}_{\mathrm{food}})w_0(e^{Gt} - e^{-(E+D)t})}{(G + E + D)} + Q_0 e^{-(E+D)t} - Q_{\mathrm{gonad}} \quad \text{eqn 1}$$

where C is the specific consumption rate [g food$_{\text{wet weight}}$ g fresh (or wet) weight^{-1} day^{-1}], α is the proportion of ^{137}Cs assimilated from food, $^{137}\mathrm{Cs}_{\mathrm{food}}$ is the concentration of Cs in food (ng g^{-1}), w_0 is the initial body mass (g),

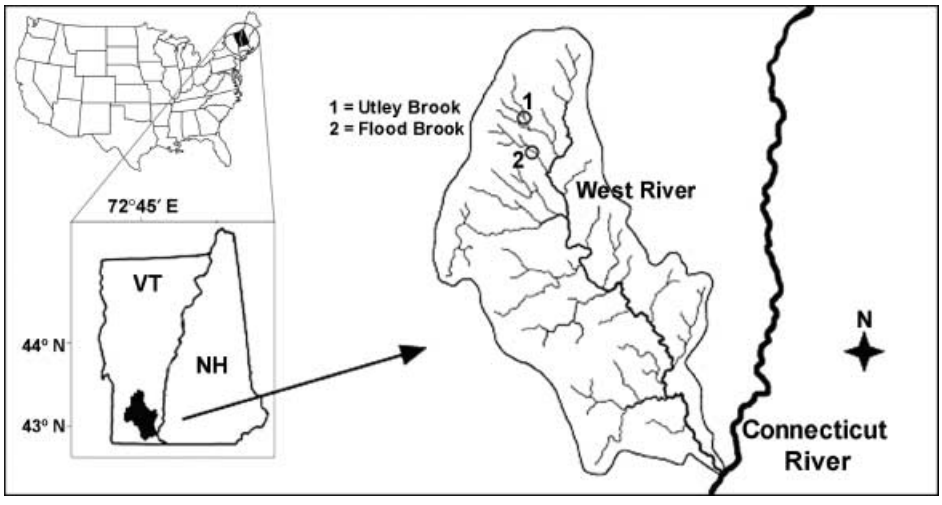

Fig. 1. Map of study sites in West River watersheds, Vermont, USA.

Table 1. Summary of collection information, fish sizes, Cs concentrations and average consumption values (± SD) for all fish included in this study. $Late_1$ and $Late_2$ are collections made at the end of the growing period in 1991 and 1998, respectively

	Flood Brook				Utley Brook			
Growing season	Early	Middle	$Late_1$	$Late_2$	Early	Middle	$Late_1$	$Late_2$
Year	1992	1991	1991	1998	1992	1991	1991	1998
Age (days)	17	40	85	107	15	45	91	107
n	10	4	9	28	10	8	10	22
Fresh weight (g) ± SD	0·24 ± 0·06	1·48 ± 0·33	3·07 ± 0·34	4·88 ± 1·05	0·23 ± 0·03	1·48 ± 0·09	2·81 ± 0·59	3·32 ± 0·61
Concentration Cs (ng g^{-1}) ± SD	1·22 ± 1·78	2·42 ± 0·49	3·83 ± 1·23	3·51 ± 0·76	0·99 ± 0·42	2·85 ± 1·66	2·34 ± 0·87	2·89 ± 0·74
Consumption rate (% day^{-1}) ± SD	1·64 ± 2·46	3·05 ± 0·86	3·17 ± 1·03	2·64 ± 0·59	0·62 ± 0·80	3·25 ± 1·98	1·77 ± 0·71	1·99 ± 0·56

G is the specific growth rate (g g^{-1} day^{-1}), E is the elimination rate of ^{137}Cs (g g^{-1} day^{-1}), D is the radioactive decay of ^{137}Cs in (Bq Bq^{-1} day^{-1}) and Q_{gonad} is the gonadal ^{137}Cs burden lost at reproduction. Solving this equation for C produces an equation based upon the accumulation of ^{137}Cs. Our approach differs from previous applications because we use fluxes of naturally occurring stable Cs in immature fish and we can therefore eliminate two parameters from the radiocaesium model: (i) the loss of radiocaesium due to radioactive decay and (ii) the Cs lost in reproductive tissue during reproduction. This results in the final model form:

$$C = \frac{(Q_t - Q_0 e^{-E \cdot t})(G + E)}{\alpha(^{133}Cs_{food}) w_0 (e^{G \cdot t} - e^{-E \cdot t})} \quad \text{eqn 2}$$

STABLE CS CONCENTRATION MEASUREMENTS

Sample preparation was performed in class-100 clean room facilities. Cs concentrations were measured on whole fish minus stomachs. Sample fish were rinsed well with deionized water and placed into trace metal-clean Teflon® beakers. Samples were dried at 60 °C overnight, weighed and digested in a high-pressure microwave accelerated digestion apparatus (MLS1200, CEM Corp., Matthews, NC) using quartz-distilled concentrated Seastar™ HNO_3 (Sidney, BC, Canada). Elemental concentrations were determined using a magnetic sector inductively coupled plasma mass spectrometer (ELEMENT I, Finnigan/MAT, Bremen, Germany) equipped with a guard electrode for enhanced sensitivity. Detection limits for Cs were approximately 0·1 ng Cs kg^{-1} (approximately 10 fentograms (fg) absolute). Procedural blanks were performed for each batch of sample digestions and were below detection limits. A National Institute of Standards and Technology standard reference material (1643d, Trace Elements in Water) was analysed with each sample batch and yielded 100 ± 2% recovery for all elements examined [potassium (K), rubidium (Rb) and Cs]. Recovery rates of digestion techniques were tested using a prawn standard reference material (number GBW 08572, Institute of Food Detection, Ministry of Commerce, Beijing, China) with a certified K concentration. The mean measured concentration for 11 digestion runs was 0·575 ± 0·012% K (certified 0·597 ± 0·012%, i.e. a procedural recovery of > 96%). The mean Cs concentration of 11 replicates of a laboratory standard (Cs = 0·0251 μg kg^{-1}) over the course of all analyses was 0·0251 μg kg^{-1}, with SD = 0·0004. We estimated that our overall relative SD for fish samples was approximately 1–2% at part per trillion concentration levels.

PARAMETERIZATION OF THE MODEL

Initial conditions: fry sizes and Cs body burdens

Initial sizes of stocked fry were similar in all sites. Wet weights of fry from three different stocking dates in 1998 ranged from 0·14 to 0·24 g (mean = 0·196, SD = 0·027). For mid- and late-season fish collected in 1991 and 1998, we used a single initial size that was the average of more than 601 998 fry on their respective days of stocking. Final weights of age-0 fish were measured at the time of capture to the nearest 0·1 g in 1991 and 1992 and to the nearest 0·01 g in 1998. Daily growth rates were determined using the standard equation: specific growth rate = $\ln(W_t/W_{t=0})/t_{days}$. Because of the extremely small sizes of early season 1992 fish caught 2 weeks after stocking, changes in mass were difficult to estimate precisely in the field and weights were estimated using length-weight regressions. The length–weight regression for these fish corresponded closely with all successive years for hatchery and early season fish (no difference in mean weights or the interaction between length and year tested by the homogeneity of covariate slopes; P = 0·14). Fry from 1992 were on average 2·6 mm smaller than those stocked in 1998 (22·2 mm vs. 24·8 mm standard length). Therefore our initial size for early season 1992 fry was 0·152 g, compared with 0·196 g for 1991 and 1998 fish. Importantly, consumption estimates are driven by the measured change in body burden between two time points. Therefore, the calculated daily ration for any individual over these short intervals is relatively constant regardless of the estimated mass change over the time period. Also, for mid- to late-season fish, estimates of consumption are not affected by variability in initial weights because the variability of weights during this time is less than 1% of the final weight.

To quantify the impacts of different growth functions on our estimates of consumption for individual

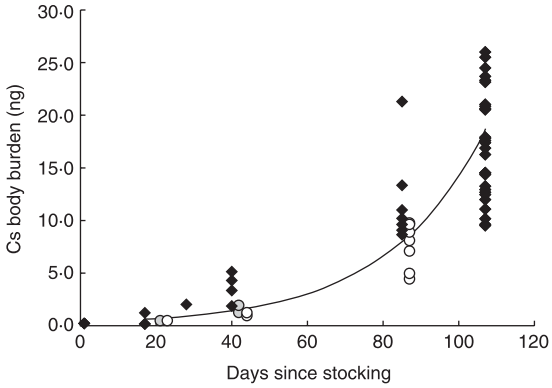

Fig. 2. Measured (black triangles) and back-calculated (circles) Cs body burdens in Flood Brook across all study years. Solid symbols represent the actual measured values from this study. Back-calculated values at each time point are based upon exponential fits to measured values at later time points. For example, the dashed line represents back-calculated body burdens for the individual with the mean body burden at day 107. Open circles represent the estimated retrospective values on three previous dates for a range of individuals, including the highest and lowest body burdens sampled at day 107. Grey circles represent those values back calculated for all individuals sampled on day 85.

fish, we also calculated average daily consumption rates using the incremental approach of Forseth *et al*. (1992). This approach is based upon the same general equations as those above (equations 1 and 2) except that the model calculates the consumption rate on each individual day required to achieve the final Cs body burden. By quantifying the consumption rates on a daily basis, we can manipulate the specific growth and Cs accumulation functions (e.g. exponential vs. linear) for each individual fish over the studied time interval and compare the model consumption rates under these different scenarios. Additionally and most importantly, based upon our modelled curves for Cs accumulation in later season fish, we can estimate the Cs body burdens of fish at earlier time points and thereby compare burdens directly with fish sampled from the population at that time (Fig. 2). This allows us not only to confirm that our body burden trajectories are consistent through time, but also to estimate what critical body burdens may have been for fish that survive through a particular time period. Our model comparisons confirmed that both approaches give nearly identical results when an exponential model of Cs accumulation is used. Our consumption estimates were robust for a broad range of growth functions, including zero growth in 2-week-old fry. In other words, given accurately measured changes in the Cs body burden of small fish over time, small errors in the growth trajectory for any given fish had little effect on its consumption rate.

Initial Cs concentrations of salmon fry were measured on hatchery individuals taken from three different stocking populations in May 1998. Four individual fry were combined in each of 11 replicates (44 hatchery fry total). From these data a single mean initial Cs concentration was used to characterize the initial concentration ($1{\cdot}297 \pm 0{\cdot}12$ ng g^{-1}). In most cases, the body burden increased throughout the 2–15-week periods, suggesting that fish were accumulating Cs through the ingestion of diet items. In the few cases where body burdens decline through the first 2 weeks it can be directly attributed to loss of Cs at a rate that approaches the steady-state elimination rate.

Concentration of Cs in prey

We calculated the average Cs concentration in salmon diets by (i) measuring the concentration of Cs in different invertebrate taxa and (ii) weighting each taxa-specific concentration by its relative representation in fish gut contents (Table 2). Based upon their prevalence in the diets of juvenile salmon in these streams, we measured the Cs concentrations of six insect families (Chironomidae, Heptageniidae, Tipulidae, Hydropsychidae, Brachycentridae and Perlidae). Detection limits required about 5–10 mg dry weight of insect material, so multiple individuals of most taxa were combined for each analysis. Drift samples and gut content analysis of more than 400 age-0 individuals from these streams and other streams in southern Vermont suggest that there are no differences in the relative availability or preference of different prey taxa for salmon fry across sites. This allowed us to construct an average for juvenile salmon, for example chironomids and grazing

Table 2. Cs concentration (ng $g^{-1}_{\text{wet weight}}$) of six representative families of benthic macroinvertebrates from Flood and Utley Brooks. Relative proportions of these (and related families) are from stomach analyses (C.L. Folt & D. Parrish, 1994 and unpublished data). This Cs mass balance model uses a single value for prey Cs concentration estimated as the average concentrations of these six common families weighted by their representation in age-0 stomachs

	Cs concentration (ng $g^{-1}_{\text{wet weight}}$)				
Taxa	Flood Brook	Utley Brook	Average (± SE)	% in diet	Weighted contribution
Chironomidae	11·38	8·22	9·80 ± 1·58	60·0	5·88
Heptageniidae	5·80	5·89	5·84 ± 0·05	20·0	1·17
Tipulidae	1·59	0·47	1·03 ± 0·46	10·0	0·10
Brachycentridae	8·27	4·32	6·29 ± 1·97	3·3	0·21
Hydropsychidae	5·90	2·50	4·20 ± 1·70	3·3	0·14
Perlidae	2·16	1·66	1·91 ± 0·20	3·3	0·06
Weighted average	8·69	6·44			7·56

mayflies collectively comprised approximately 80% of the age-0 salmon diets in each site by weight (Folt & Parrish 1994; Newbrough, Parrish & Folt 1995). We applied a single value for prey Cs concentration based upon the similarities of Cs concentrations between streams and the consistent differences in Cs concentrations among taxa (Table 2). We believe that the pooling and weighting of different prey items averages the variability in diet experienced by salmon over time and space.

Assimilation efficiency

Increased suspended clays generally decrease assimilation efficiency of Cs in fish diet because of adsorption of metals onto clay particles and low digestibility of this mineral fraction (Kolehmainen 1974; Eyman & Kitchings 1975). Our study sites were headwater streams with very low suspended clay content and very similar thermal regimes, chemical patterns and invertebrate assemblages. Therefore, we assumed that a single assimilation efficiency could be used that describes an average realized assimilation over the consumption interval.

To estimate assimilation efficiency of salmon in the study streams, we tracked the Cs concentrations in invertebrate prey as the metals pass from benthos to salmon fore-gut to hind-gut. We compared the elemental concentrations at each stage with that of acid insoluble ash, which serves as an unassimilable marker (Tucker & Rasmussen 1999). The amount of Cs assimilated equals:

$$\alpha = 1 - \frac{(AIA_{fg})(^{133}Cs_{hg})}{(AIA_{hg})(^{133}Cs_{fg})} \qquad \text{eqn 3}$$

where *AIA* is the proportion of stomach wet weight composed of acid insoluble ash and [^{133}Cs] is the concentration of Cs in both fore-gut (fg) and hind-gut (hg). The fore-gut was defined as the combined oesophagus and stomach. The hind-gut was defined as the portion of the gastrointestinal tract between the duodenum and the anus. Each sample was randomly divided, half of which was analysed for metals and half for ash. Each of the matched replicates contained the gut contents from five to six individual fish. All samples were dried at 60 °C overnight and weighed. The stomach contents that were analysed for metals were treated for analysis as described for fish tissue above. The AIA fractions were ashed at 550 °C for 8 h, rinsed three times with trace pure 1 N HNO_3 then deionized water, redried at 60 °C and weighed.

This approach allowed us to estimate the mean and variability of metal assimilation for field-caught fish over daily intervals. Our estimates for assimilation efficiency were derived from the same late-season 1998 fish (standard length 55·0–78·0 mm) on which consumption estimates were made. As an independent test of this method we compared our assimilation estimates with estimates of assimilation of two related alkali metals, K and Rb, which were analysed simultaneously on the same individuals.

Elimination rates

We used the equation from Rowan & Rasmussen (1995) for calculating elimination rates (E) of Cs at steady state:

$$\ln E = -6{\cdot}583 - 0{\cdot}111(\ln W) + 0{\cdot}093T \qquad \text{eqn 4}$$

where W is fish wet weight (g) and T is the interval average temperature (°C). As in the case of other model parameters, we did not expect quantitative differences among streams or among individuals when averaged over a growing season. Our study streams drain similarly sized catchments with similar geology and nearly identical temperature regimes. Fish were similarly sized throughout the entire study, thereby eliminating confounding metabolic factors due to temperature or fish size.

Temperatures were measured at 15-min intervals in both streams in 1998. Average temperatures at both sites were very similar for each sampling interval [3–20 May, temperature (T) = 12·43 °C; 3 May–25 June, T = 13·50 °C; and 3 May–28 August, T = 15·25 °C].

SENSITIVITY ANALYSIS

A sensitivity analysis was performed to evaluate the relative contribution of model parameters to the uncertainty of our consumption estimates. We used individual parameter perturbations, in which parameter values were drawn randomly from a normal distribution, while remaining parameters were fixed at their nominal values (Bartell *et al.* 1986; Ugedal, Forseth & Jonsson 1997). Means and SD of perturbed parameters, as well as nominal values, were based upon data from this study as well as literature values when appropriate. Coefficients of variation of parameter values ranged between 10% and 30%. The relative changes in predictions for consumption rates were used to assess parameter sensitivities. The impact from each parameter perturbation was ranked with respect to its contribution to the variance of the consumption estimate.

STATISTICS

We used a two-way analysis of variance (ANOVA) (SAS Institute Inc. 2000) to test for variation in consumption rates across the two study sites and the three collection seasons. Sites and seasons were treated as fixed effects. A Tukey–Kramer honestly significant difference multiple comparison test was applied when significant differences in treatment effects were found (Tukey 1953). In some cases, unequal variances violated the assumption of an ANOVA. This was a particular problem when comparing consumption rates across seasons because consumption rates in the early season were generally lower and more variable. Significant differences in variances (Levene's test) across treatments were an ecologically meaningful outcome for which we were explicitly

testing. When variances were significantly different, we conducted additional non-parametric tests to compare the significance of statistical results, and we used a Welch ANOVA to test for treatment effects despite unequal variances (Welch 1951).

Results

PARAMETERIZATION OF THE MODEL

Initial conditions and Cs body burdens

At the time of stocking, hatchery fish were similarly sized and had similar Cs concentrations (Fig. 3a). Low variance in initial conditions allowed us confidently to apply a single value for Cs body burdens of stocked salmon fry. This is in contrast to the large variability for both weight and Cs concentration within 40 days of stocking. By this time fry had increased their average weight sevenfold (0·2 g to 1·5 g) and Cs concentrations were, on average, twice as high as initial conditions (Fig. 3a). There was no difference in the mean size of fish from either stream (Table 1). However, variability in fish size coupled with variability in Cs concentrations led to large differences in Cs body burdens among individuals 6 weeks after stocking, which ultimately resulted in estimates for consumption that varied widely during this period (Fig. 3b).

Concentration of Cs in diet

The concentrations of Cs in benthic invertebrates were similar across sites. Invertebrate taxa at both sites had a range of Cs concentrations from about 1 ng $ng^{-1}_{wet\ weight}$ to about 10 $ng^{-1}_{wet\ weight}$. Relative differences in Cs concentration among the six taxa measured were consistent across sites (Table 2). Chironomid larvae had the highest concentrations of Cs in both sites (11·4 ng g^{-1} in Flood Brook and 8·2 ng g^{-1} in Utley Brook). Larval tipulids had the lowest Cs concentrations (1·6 ± 0·5 ng g^{-1} in Flood Brook, 0·5 ± 0·05 ng g^{-1} in Utley Brook).

Cs assimilation efficiency by age-0 salmon

Field-based estimates for assimilation of Cs by age-0 salmon were approximately 60%, with no significant differences between Flood and Utley Brooks ($P = 0·716$; Table 3). Assimilation efficiencies for all three alkali metals (Cs, K and Rb) were similar, with K having slightly higher assimilation (67%) than Rb (63%) or Cs (60%) (Table 3). Our estimates of assimilation efficiency were within the range of those measured previously for Cs and representative of relatively high assimilation efficiencies experienced by fish in streams with low levels of suspended clays (Fig. 4) (Rowan & Rasmussen 1996; Tucker & Rasmussen 1999).

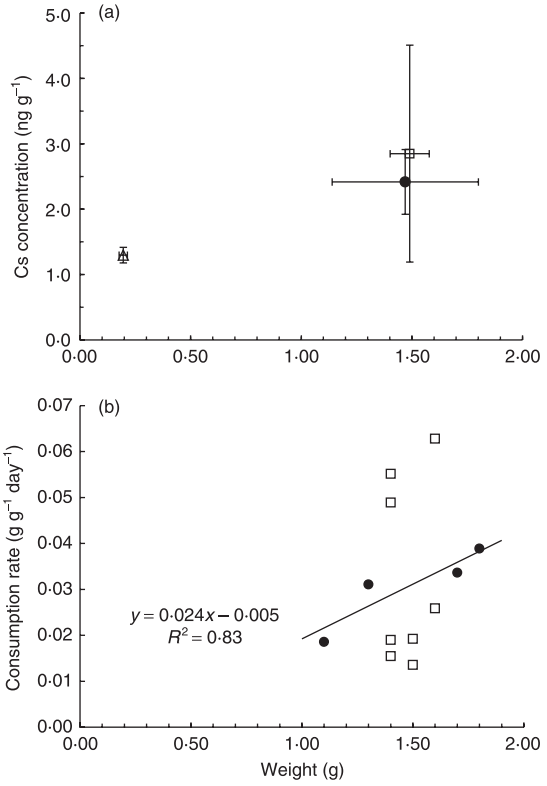

Fig. 3. (a) Means and SD of weights and Cs concentrations for hatchery fry and under-yearling Atlantic salmon in Flood Brook (solid circles) and Utley Brook (open squares) at 40–45 days after stocking (June sampling) in 1991. Mean weights at 40–45 days are identical (1·48 g) but are offset for clarity. (b) The same individuals as in (a) with consumption rates plotted as a function of size. Each point represents a single fish. The line describes the relationship between size and consumption for Flood Brook.

Table 3. *In situ* assimilation efficiencies (± SE) of three alkali metals (Cs, Rb and K) from an analysis of diet items in the fore-guts and hind-guts of age-0 Atlantic salmon in two sites approximately 100 days after stocking. Each replicate is the combination of stomach contents from five to six fish. The negative value for the fourth replicate of Cs assimilation in Utley Brook is a result of an anomalously high Cs value in the hind-gut of that sample. This value was excluded from analysis and not included in the parameterization of the Cs model

	Cs assimilation efficiency (%)		Rb assimilation efficiency (%)		K assimilation efficiency (%)	
Replicate	Flood Brook	Utley Brook	Flood Brook	Utley Brook	Flood Brook	Utley Brook
1	65·6	61·9	60·5	66·2	64·3	67·7
2	49·1	47·4	64·0	64·7	68·5	66·9
3	50·1	72·7	59·2	68·7	65·8	69·9
4	64·3	–11·7	57·7	63·4	63·8	66·1
Average (± SD)	57·3 (± 8·9)	60·7 (± 12·7)	60·4 (± 2·7)	65·7 (± 2·3)	65·7 (± 2·1)	67·7 (± 1·7)

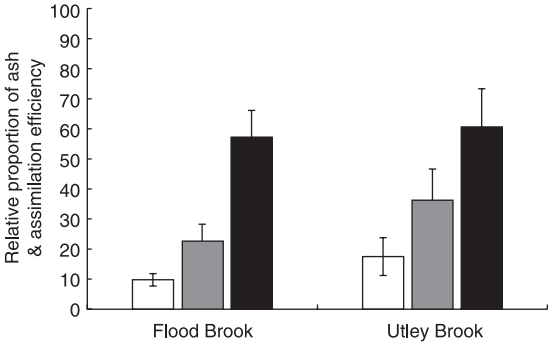

Fig. 4. Means and standard errors of the relative proportion of ash in the stomach contents of the fore-gut (open bars) and hind-gut (grey bars) of more than 40 age-0 Atlantic salmon from Flood and Utley Brooks from the August 1998 sampling. Solid bars represent the average Cs assimilation (± SE) on the same individuals.

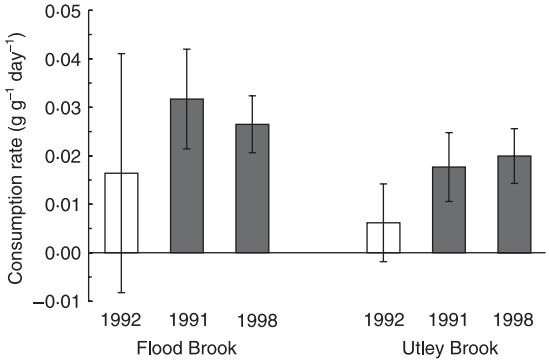

Fig. 5. Consumption rates with SD of age-0 Atlantic salmon in Utley and Flood Brooks at 2 weeks post-stocking (open bars) and over the entire growing season in two different years, August 1991 and 1998 (grey bars).

SENSITIVITY ANALYSIS

The Cs mass balance model was most sensitive to changes in (i) the Cs body burden of salmon parr between time points, (ii) the Cs concentration of prey items, and (iii) the assimilation efficiency of Cs from the diet (Table 4). Changes in the variance of these parameters led to commensurate changes in the variance of the consumption estimate when standardized to the mean, i.e. $CV_{model} = CV_{perturbation}$. In contrast, relatively large perturbations to the elimination rates of Cs and to initial conditions (weight and Cs concentration at time of stocking) had little influence on estimated consumption rates (Table 4).

FIELD ESTIMATES OF CONSUMPTION

Consumption rates of age-0 Atlantic salmon ranged between 0 and 0·085 g g fresh weight (fw)$^{-1}$ day^{-1} throughout the summer growing season. There were no significant differences in mean consumption rates between Flood and Utley Brooks in the May (n = 20, P = 0·228) or June (n = 12, P = 0·856) sampling periods. High variability in the Cs body burdens of individuals at 40–45 days led to estimates for consumption that varied widely (0·0136–0·0629 $g_{wet\ weight}$ g^{-1} day^{-1}; Fig. 3b). Although sample sizes were low for this period, there was a suggestion of site differences in the allocation of consumed food to growth at this time (Fig. 3b). In Flood Brook, there was larger variability in size (range = 1·1–1·8 g) and a marginally significant positive relationship between growth and consumption despite a low sample size (n = 4, P = 0·07). In Utley Brook there were large differences in consumption rates among individuals that were not related to size, as all eight individuals were similarly sized at 40 days (range 1·4–1·6 g).

By August, consumption was significantly higher in Flood Brook than in Utley Brook in both 1991 (0·032 g vs. 0·017 g g fw^{-1} day^{-1}; n = 19, t = 3·483, P = 0·003) and 1998 (0·026 g vs. 0·020 g g fw^{-1} day^{-1}; n = 50, t = 3·988, P < 0·0001) (Table 1 and Fig. 5). Within both sites, there was a strong seasonal component, with consumption rates in the early and mid-season being on average lower (P = 0·091) but much more variable than consumption rates in the late season (Levene's test for homogeneity of variance, P < 0·0001; Fig. 5). For example, 2 weeks after stocking in May, salmon fry consumed between 0 g and 0·084 g g fw^{-1} day^{-1}. In

Table 4. Results of a sensitivity analysis for the five parameters of the Cs mass balance model. Nominal parameter values (± SD) are based on results from this study and literature values. Parameters for each iteration were randomly selected from a normal distribution using the expected values for means and SD. Two-hundred iterations of the model produced a range of consumption values. The coefficient of variation (CV) index is the ratio of the CV of model output to the CV of the perturbed parameter ($CV_{model}/CV_{perturbation}$) and is a relative measure of the sensitivity of model output to perturbations in a single parameter. Consumption measurements based upon Cs mass balance are particularly sensitive to changes in parameter values marked with *

Parameter	Mean ± SD of simulations	Source	Consumption range (mean = 2·34% day^{-1})	CV index
Concentration of Cs of prey items	7·56 ± 1·19 ng g^{-1}	This study	1·7–4·1% day^{-1}	1·13*
Assimilation efficiency	60 ± 10%	This study	1·7–3·5% day^{-1}	1·05*
Concentration of Cs of salmon parr	3·18 ± 0·95 ng g^{-1}	This study	0·7–3·8% day^{-1}	1·01*
Initial weight	0·196 ± 0·019 g	This study	2·2–2·4% day^{-1}	0·26
Elimination rate	0·4 ± 0·1%	Rowan & Rasmussen (1995)	2·1–2·4% day^{-1}	0·11
Initial concentration of Cs of fry	1·30 ± 0·12 ng g^{-1}	This study	2·31–2·35% day^{-1}	0·01

Table 5. Average wet weights of entire gastrointestinal tract contents on the day of sampling. Each replicate is the combination of four individuals chosen at random. Consumption measurements for each replicate are the average of the same four individuals

	Flood Brook		Utley Brook	
Replicate	Stomach contents (g g fw^{-1})	Consumption (g g^{-1} day^{-1})	Stomach contents (g g fw^{-1})	Consumption (g g^{-1} day^{-1})
1	0·0128	0·0255	0·0157	0·0181
2	0·0187	0·0260	0·0159	0·0161
3	0·0135	0·0261	0·0104	0·0242
4	0·0143	0·0294	0·0118	0·0204
Average	0·0148	0·0268	0·0134	0·0197
Stomach contents (% of consumption)		55·4		68·2

June, consumption rates ranged between 0·013 g and 0·063 g g fw^{-1} day^{-1}, and by the end of the growing season consumption rates averaged over the entire season were between 0·016 and 0·042 g g fw^{-1} day^{-1}. There were no annual differences (1991 vs. 1998) in consumption rates over the entire growing season in either site (Flood Brook, $n = 37$, $P = 0{\cdot}070$; Utley Brook, $n = 32$, $P = 0{\cdot}342$). Estimated consumption rates of late-season fish were consistent with the weight of their stomach contents at the time of capture, which occurred in late morning after dawn feeding only. The weights of total stomach and intestine contents of fish averaged 55% and 68% of daily consumption rates in Flood and Utley Brooks, respectively (Table 5), which is what one would expect if the stomach contents at that single time represented a fraction of the daily ration.

Discussion

EXPANSION AND PARAMETERIZATION OF THE CS MODEL

This study represents the first attempt to use natural abundances of stable Cs to estimate consumption rates of individual fish. Several previous studies have exploited the unique qualities of radiocaesium to measure consumption rates of fish under field conditions (Forseth *et al*. 1992; Rowan & Rasmussen 1995; Tucker & Rasmussen 1999). Researchers have not used the geologically derived stable form of Cs because it is found only at trace levels in the environment (low part per trillion in surface waters) and historically has been difficult to measure (Forseth *et al*. 1998). However, because it originates in geological material, it has two distinct advantages over radiocaesium as an inert tracer of consumption rates: (i) stable Cs is present at trace levels world-wide which makes this method universally applicable, and (ii) Cs concentrations in nature are likely to be stable over time, which eliminates potential complications when consumers are not in equilibrium with their prey.

We used the relatively new and highly sensitive method of magnetic sector ICP-MS to measure quantitatively Cs concentrations as low as 1 part per trillion in fish as small as 0·1 g fw. Two previous studies have used stable ^{133}Cs to estimate consumption. However, in both of these cases Cs was pulsed into the system to achieve elevated levels of Cs (Hakonson, Gallegos & Whicker 1975; Forseth *et al*. 1999). A significant advantage of a method based upon geologically derived stable ^{133}Cs, which is more uniformly distributed than a radioisotope tracer, is the minimization of temporal fluctuations across seasons and years. With the exception of minor fluctuations during storm events or snowmelt, background concentrations of alkali metals, such as Cs, in aquatic systems are not likely to vary widely. The concentrations of Cs in prey and predators should remain relatively constant. In our study, concentrations of Cs in stocked salmon fry began at approximately 1·2 ng g^{-1}. After stocking, the average Cs concentration of fish quickly increased to approximately 3·0 ng g^{-1} after 40 days and remained at approximately 3·2 ng g^{-1} through August.

Relatively large differences in the Cs concentrations of different prey taxa were consistent across sites. In both sites chironomids had the highest Cs concentrations (8·2–11·4 ng g^{-1}) while perlid stoneflies and tipulids had the lowest Cs concentrations (0·5–2·2 ng g^{-1}). Because the Cs mass balance model relies upon a single value for Cs prey concentration, these differences stress the importance of quantifying fish diet composition before applying the Cs model. A common oversimplification of trace metal approaches for estimating bioenergetic parameters is assuming that the metal concentrations of all prey taxa are equal (but see Rowan & Rasmussen 1996). However, our study suggests that using numbers that are not derived from taxa-specific Cs concentrations or that misrepresent the occurrence of some taxa in the diet can have significant impacts on model predictions. Interestingly, the differences in Cs concentration among taxa suggest that Cs is not bioconcentrated with increasing trophic levels, but rather that, among all the macroinvertebrate taxa, predators (e.g. perlids and tipulids) have the lowest Cs tissue concentrations. There is even some suggestion of biodilution in higher trophic levels, with invertebrate and fish predators having among the lowest Cs concentrations. Chironomidae, heptageniidae and brachycentridae are all primarily grazers and collectors, yet they have concentrations of Cs two to three

times as high as the predatory insects and fish. This is supported by the comparison between Cs in fish tissue and Cs in a generalized salmon diet, which shows a 50% decrease in Cs concentration from prey to diet (7·78 ng g^{-1} in prey to 3·18 ng g^{-1} in fish). These findings are consistent with those of previous researchers that have found lower radiocaesium concentrations in fish than in food (Kolehmainen 1972; Mailhot, Peters & Cornett 1988; but for examples of biomagnification see Rowan, Chant & Rasmussen 1998; Sundbom *et al*. 2003). The absence of biomagnification for fish in this study may be partially explained by the high specific growth rates of age-0 salmon through their first growing season. Regardless, consistent differences in the Cs concentrations of common prey taxa across trophic levels underscored the need to quantify fish diet composition before applying this technique.

FIELD ESTIMATES OF CONSUMPTION

Consumption rates of fry at approximately 16 days ranged from nearly 0 to about 0·08 g g^{-1} day^{-1}. These estimates of consumption for fish 2 weeks after stocking represent some of the first estimates for consumption rates of such young fish. In addition, only one other study has measured consumption rates of Atlantic salmon in the field (Tucker & Rasmussen 1999). Our results suggest that the period immediately after yolk sac completion is an energetically challenging time for juvenile salmon, as many individuals have no measurable consumption. There are also likely to be differences among fish between sites as the two streams in this study had different relationships between growth and consumption throughout the first growing season. It is likely that heterogeneity in habitat and food conditions in the early season contributed to the lower overall consumption at both sites but increased variability in consumption soon after stocking (Nislow, Folt & Parrish 2000; B. P. Kennedy, unpublished data). For example, in Utley Brook in the mid-season, there are large differences in consumption rates despite very similar sizes among all individuals. These patterns are suggestive of habitat trade-offs occurring among fish, in which fish that occupy areas with high potential consumption rates are also negatively impacted by high energetic demands.

The stable Cs methodology compares favourably with established radionuclide methods and provides realistic estimates of consumption (Forseth *et al*. 1992; Rowan & Rasmussen 1996). Recent models have been developed that estimate maximum consumption rates for Atlantic salmon based upon fish size and ambient temperature conditions (Forseth *et al*. 2001). In comparison with this study, only a subset of fish with the highest consumption rates slightly surpassed the predicted maximum consumption rates for each season. However, the proportion of fish that consumed maximally was quite low (< 10%; Fig. 6). In the early season, very few fish were consuming even 50% of the maximum daily ration for moderately fast growing fish (Forseth *et al*. 2001).

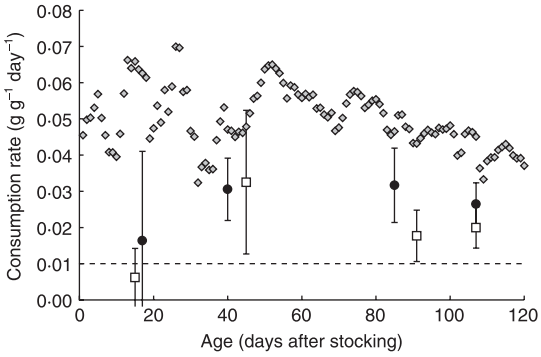

Fig. 6. Consumption rates (± SD) of all fish in this study (solid circles, Flood Brook; open squares, Utley Brook) plotted as a function of age since stocking and compared with the estimated maximum consumption for fish based upon the age-specific size and temperature of the average Atlantic salmon fry throughout an average growing season (diamonds) (Forseth *et al*. 2001). Maintenance ration (dashed line) represents the theoretical level at which consumption exactly matches the energy required to maintain body size (Tucker & Rasmussen 1999).

Our estimates of consumption deviate from expectations for consumption rates for juvenile fish. Our most compelling result is that salmon fry survive over an extended period of time (approximately 4 weeks) at an apparent energetic deficit. However, there is evidence that salmon fry can survive under laboratory conditions for extended periods of time without food. In one laboratory experiment (Letcher & Terrick 2001), greater than 50% of the starved salmon fry (at the same developmental index as the fry used in this experiment) were still alive 30 days after their 'stocking date'. In a more recent experiment (B. H. Letcher, unpublished data), temperatures were manipulated to more closely reflect that of Vermont streams in May and survival was found to be even longer. Again at 15 °C, 50% of the population was still alive 4 weeks after their stocking date, while at 10 °C 50% of the population survived as long as 6 weeks without eating. We feel that these results substantiate the finding that stocked fish can survive for extended periods in the field with no measured consumption.

By the late season, the proportion of fish with consumption rates that exceeded 50% of the predicted maximum daily ration was much greater (78% in Flood Brook and 30% in Utley Brook). Observed consumption rates of late-season fish (0·024 g g^{-1} day^{-1}) were 1·7 times the amount of food in their entire gastrointestinal tract (0·014 g g^{-1}). It is important to note that the stomach samples were taken only once daily, which prohibits a proper analysis of daily ration based on gut contents. Despite this limitation, one-time stomach content samples were collected from individuals that were captured between the hours of 09:00 and 14:00, a time during which significant feeding is likely to have taken place and approximately 50–75% of the daily ration would be

present in the stomach. Fish in the two study streams had on average 55% and 68% of the estimated daily consumption in their guts at this time. Although we realize that this is only a partial analysis of stomach contents and a suboptimal comparison with gastric evacuation techniques, we feel that it provides the most direct *in situ* corroboration of our Cs method possible because it compares rations of the same individuals which have not experienced repeated and invasive sampling. For comparison, a study of several hundred salmon diets in the same streams found wet weights of stomach contents to range from 0·004–0·013 g g^{-1} (Raffenberg 1998). However, in this study stomach contents were sampled using a gastric lavage technique, which samples only the most recently eaten items and would therefore be expected to produce a significantly lower estimate than one based upon the quantity of food in the entire gastrointestinal tract.

Typically, consumption rates are the most difficult parameter to measure in bioenergetic models and yet differences in consumption rates may play a critical role in establishing survival patterns across many fish species. A spatially explicit bioenergetics model developed for Atlantic salmon (Nislow, Folt & Parrish 1999, 2000) suggests that foraging habitat and food availability in the earliest stages of the salmon life cycle are essential for juvenile survival, and may provide a mechanistic basis for the critical period evident in other salmonid populations (Elliott 1989). However, exactly how these factors interact to determine prey consumption, growth and survival under a range of habitat conditions is often complex and difficult to ascertain without reliable field-based techniques for measuring consumption rates.

Novel applications for radionuclides, like Cs, came at a time when the conventional methods of measuring fish consumption were re-evaluated and critiqued (Boisclair & Leggett 1988; Boisclair & Marchand 1993). Biases and errors in the often-used gastric evacuation methods (Eggers 1977; Elliott & Persson 1978) have been attributed to inconsistencies in the sampling date intervals and sampling gear, as well as the complexities of model parameters and statistical methods (Hayward *et al*. 1989; Whitledge & Hayward 2000). Approaches based upon radionuclide mass balance, as well as the trace element methodology detailed herein, circumvent these problems by measuring consumption rates integratively over the lifetime of an individual fish. These elemental approaches are appealing because they are computationally simple and use only biologically interpretable variables that are relatively easy to parameterize. The new approach using stable Cs represents a major improvement over conventional radionuclide methods because it is geologically derived and therefore not limited in its application to particular geographical areas. Therefore, the use of stable caesium at natural abundance concentrations permits the global application of this trace element approach for estimating consumption rates of all size classes of fishes, as well as many different aquatic and terrestrial organisms. For purposes of fisheries management, these results not only implicate the importance of early season habitat availability for young fish, but also provide a method for testing explicitly how habitat availability affects foraging and growth.

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