

Seasonal shift in the effects of predators on juvenile Atlantic salmon (*Salmo salar*) energetics

Darren M. Ward, Keith H. Nislow, and Carol L. Folt

Abstract: Predator effects on prey populations are determined by the number of prey consumed and effects on the traits of surviving prey. Yet the effects of predators on prey traits are rarely evaluated in field studies. We measured the effects of predators on energetic traits (consumption and growth rates) of juvenile Atlantic salmon (*Salmo salar*) in a large-scale field study. Salmon fry were released at 18 sites that encompassed a wide range of predatory slimy sculpin (*Cottus cognatus*) abundance. We sampled salmon after 21 and 140 days to measure salmon growth and estimate consumption using a mass-balance model of methylmercury accumulation. Salmon population density was reduced fivefold at sites with abundant sculpin. Over the early season, salmon consumed less where sculpin were abundant, suggesting that reduced foraging under predation risk contributed to predator-caused mortality. In contrast, over the late season, salmon grew more where sculpin were abundant, suggesting that compensatory growth at reduced salmon population density moderated predator-caused mortality. Predator effects on prey energetics can drive variation in survival and growth, with important consequences for population dynamics.

Résumé : Les effets des prédateurs sur les populations de proies sont déterminés par le nombre de proies consommées et les effets sur les traits des proies survivantes. On évalue, néanmoins, rarement les effets des prédateurs sur les traits des proies dans les études sur le terrain. Nous mesurons les effets des prédateurs sur les traits énergétiques (taux de consommation et de croissance) de jeunes saumons atlantiques (*Salmo salar*) dans une étude de terrain à grande échelle. Nous avons libéré des alevins de saumons dans 18 sites qui couvrent une grande étendue d'abondances de prédateurs, des chabots visqueux (*Cottus cognatus*). Nous avons échantillonné les saumons après 21 et 140 jours afin de mesurer la croissance des saumons et d'estimer leur consommation à l'aide d'un modèle de bilan massique d'accumulation de méthylmercure. La densité des saumons a été réduite par un facteur de cinq aux sites où les chabots sont abondants. Durant le début de la saison, les saumons consomment moins là où les chabots sont nombreux, ce qui laisse croire que la recherche réduite de nourriture à cause du risque de prédation contribue à la mortalité due aux prédateurs. En revanche, durant la fin de la saison, les saumons croissent plus lorsque les chabots sont abondants, ce qui indique qu'une croissance compensatoire aux densités réduites de saumons tempère la mortalité due aux prédateurs. Les effets des prédateurs sur l'énergétique des proies peuvent expliquer les variations de la survie et de la croissance, qui ont des conséquences importantes sur la dynamique de la population.

[Traduit par la Rédaction]

Introduction

Heavy predation on small, juvenile size classes directly reduces recruitment of fish cohorts (Hixon and Beets 1993; Walters and Juanes 1993). In addition to direct losses to predators, predation can have a strong effect on average behavioral and physiological traits of prey cohorts. For example, predators can alter the average energetic traits (consumption and growth rates, activity costs) of a cohort through at least three distinct processes (Relyea 2002): first, behavioral responses of prey to predation risk can result in

reduced time spent foraging or elevated energetic costs; second, predator-caused mortality may be biased toward a specific subset of the prey population, such as smaller individuals or more active foragers; third, there may be reduced competition among prey after predators reduce prey population density. These effects of predators on prey traits can have important consequences for population dynamics of prey (Lima 1998; Peckarsky et al. 2008), particularly for species like salmonids (trout and salmon), where survival, fecundity, and the pattern of life history expression are strongly tied to individual consumption and growth rates

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(Metcalf 1998). Yet the strength and mechanisms of predator effects on prey traits are rarely evaluated in field studies of predator effects on prey.

Atlantic salmon (*Salmo salar*) fry are very vulnerable to predators during a critical period early in their first growing season, when they disperse from natal habitat and transition from dependence on yolk reserves to exogenous feeding (Henderson and Letcher 2003; Ward et al. 2008a). Survival during this critical period can largely determine total cohort recruitment for Atlantic salmon (Milner et al. 2003; Nislow et al. 2004) and other stream salmonids (Elliott 1989; Lobón-Cerviá and Rincón 2004). While direct losses to predators can be high, short-term (minutes to hours) behavioral studies show that foraging and activity of juvenile Atlantic salmon are also strongly affected by predation risk (Gotceitas and Godin 1991). Under predation risk, salmon reduce foraging and spend more time hiding in the substrate (Leduc et al. 2004). Yet because of the challenges of estimating longer-term (days to weeks) consumption rates in the field, it is not clear whether the short-term behavioral response to predators is associated with reduced foraging over the critical period. Small-scale studies in field enclosures (Blanchet et al. 2008) and the laboratory (Orpwood et al. 2006; Blanchet et al. 2007) suggest that behavioral compensation may allow salmon to maintain long-term consumption and growth rates despite short-term predator avoidance behavior. Testing the link between predation risk and critical period consumption in the field over larger spatial and temporal scales is crucial because previous work suggests that suppressed consumption over the critical period is a key indicator of sites with poor early survival for Atlantic salmon (Kennedy et al. 2004, 2008).

While the peak vulnerability of newly emerging or newly stocked Atlantic salmon fry to fish predators only lasts a few days (Henderson and Letcher 2003; Ward et al. 2008a), the effects of predators on salmon traits may persist through the growing season (Ward and Hvidsten 2010). High early predation losses could suppress mean growth over the season if early predation mortality is biased towards inherently active foragers. Alternatively, high early predation losses could lead to higher mean growth over the growing season owing to reduced competition at lower salmon population density. Increased mean growth as a response to early predation loss could be a powerful demographic compensation mechanism for Atlantic salmon populations (Vincenzi et al. 2008; Horton et al. 2009) and is consistent with numerous recent observations of density-dependent growth of juvenile Atlantic salmon (Imre et al. 2005; Ward et al. 2009), yet remains untested in the field.

The goal of this study was to evaluate the relationship between predator abundance and survival, growth, and consumption rates of juvenile Atlantic salmon in the field. We were particularly interested in assessing the energetic effects of predators and predation risk over longer time scales than are typically considered in behavioral studies of prey responses to predation risk. This has long been technically challenging for field studies owing to the practical difficulty in measuring time-integrated consumption rates of individual fish over days and weeks. We addressed this challenge by estimating prey consumption using a mass-balance model of methylmercury accumulation, an approach that yields robust, time-integrated individual consumption estimates over peri-

ods of weeks to months (Trudel et al. 2000; Ward et al. 2010a). This approach also allowed us to separate the effects of predators during the early critical period (~20 days after stocking) from long-term or delayed effects over the rest of the growing season (~140 days after stocking) by sampling fish for growth and consumption estimates at these two separate time intervals.

Materials and methods

We conducted the field study at 18 study sites located on six small (<7 m mean summer width) tributary streams of the Connecticut River in Grafton and Sullivan counties in New Hampshire, USA (three sites per stream; general habitat descriptions in Ward et al. 2008b, 2009). All sites on the same tributary were separated by at least 1 km; all tributaries were separated by at least 3 km along the main stem of the Connecticut River or Mascoma River (a larger Connecticut River tributary). The study streams had predominantly forested watersheds and mostly gravel and cobble substrate. Fish communities in the study streams consisted of stocked Atlantic salmon (including an overyearling juvenile cohort from previous years of stocking), brook trout (*Salvelinus fontinalis*), slimy sculpin (*Cottus cognatus*), and minnows (primarily *Rhinichthys atratulus* and *Rhinichthys cataractae*). Our previous work in these streams shows that, of these species, only slimy sculpin are an important determinant of first-summer survival for Atlantic salmon (Ward et al. 2008a, 2008b). Stomach sampling of slimy sculpin revealed that the negative effect of slimy sculpin on Atlantic salmon survival was due at least in part to sculpin predation on salmon fry in the first few days after stocking (Ward et al. 2008a).

On 8–9 May 2007, we released 2000 Atlantic salmon fry at each study site. Fish stocking was conducted as part of an ongoing restoration program for Atlantic salmon in New England (Folt et al. 1998). The salmon were produced at the White River National Fish Hatchery in Bethel, Vermont, and were stocked as unfed fry that had not yet transitioned from yolk resources to independent feeding. We released the fry in 10–15 cm deep water over gravel and small cobble substrate. Fry were released into a stilling well (plastic bucket with the bottom removed) placed over the substrate to protect them from being washed downstream before finding shelter in the substrate. All fry were released at a single location at each study site. We collected a subsample of fry at the time of stocking to measure initial size (0.16 ± 0.03 g; mean \pm SD) and mercury concentration (24 ± 2 ppb dry).

There is no natural Atlantic salmon reproduction in the study streams, as dams on the main stem of the Connecticut River prevent adult return. Further, study sites within a stream were far enough apart that movement of stocked salmon among sites during their first summer was not likely (Ward et al. 2008b). Therefore, we assumed that the young-of-the-year salmon we sampled throughout the summer growing season at each site were from our controlled stocking events.

Fish sampling was conducted in three bouts over the growing season by electrofishing (Smith-Root BP-12 electrofisher at 300–500 V DC) and was conducted under Dartmouth College Animal Care and Use Program protocol 06-02-12. We collected fish from each site for growth and mercury analysis

on two dates, timing sampling to capture conditions just after the critical period (29–30 May 2007, ~20 days after stocking) and at the end of the summer growing season (25–26 September 2007, ~140 days after stocking). These fish were collected in a single electrofishing pass ~20–50 m long at the stocking site. We could not conduct a full population density estimate at all sites during these samples and still complete the time-critical growth and consumption sampling within a short time window, so we conducted a separate sample bout to measure the population density of Atlantic salmon, slimy sculpin, and the rest of the fish community at each site from 3 to 30 August 2007. For population density estimates, we fished three 30 m sample reaches at each study site, with 30 m between reaches (150 m total stream length in the sampled area). Each 30 m reach was isolated with block nets at the upstream and downstream end and fished for two to four passes of removal sampling. All salmon and a subset of all other species were measured to the nearest millimetre (total length). We used a maximum weighted likelihood technique to estimate total abundance of each species in each plot from removal data (Carle and Strub 1978). We separated young-of-the-year salmon from overyearlings based on stream-specific length distributions and estimated density separately for these age classes. Density estimates for slimy sculpin include only individuals >55 mm, based on the minimum-sized sculpin that we have found containing salmon fry in stomach sampling. Atlantic salmon population density in the sample plots is a function of survival of stocked fish and emigration from the study area, but spatially extensive sampling upstream and downstream of sites stocked by the same techniques in previous years showed that population density within 100 m of the stocking site is a reliable index of total first-summer survival of point-stocked Atlantic salmon fry (Ward et al. 2008b).

Mayfly (order Ephemeroptera, family predominantly Baetidae) nymphs were collected for mercury analysis to assess mercury concentrations in salmon prey. Mayflies were by far the dominant prey in diets of Atlantic salmon collected in early-season samples (mean percentage of diet by numbers: $74\% \pm 19\%$ (mean \pm SD)) and remained a substantial component of the diet through the late-season samples ($28\% \pm 22\%$). Further, mayfly mercury concentrations are representative of other abundant aquatic insects at our study sites (D.M. Ward, unpublished data). At each site, we collected three replicate mayfly samples using an electrobugging technique (Taylor et al. 2001). Each sample consisted of three discrete subplots (~1 m \times 0.3 m) treated with a 10 s sweep with the electrofisher anode (300–500 V DC); stunned insects drifted into a 500 μ m mesh Surber net held downstream. This technique yielded sufficient biomass of mayflies (2–17 mg dry mass) for mercury analysis with little detritus. We also used the mean total biomass of mayflies captured via standardized electrobugging as an index of prey biomass available at the study sites.

All biological samples collected for mercury analysis were stored on ice in acid-cleaned vials or sample bags for transportation. We weighed and measured fish and removed their stomach contents before freezing them for storage. Stomach contents were preserved in 70% ethanol and sorted to family level to estimate diet composition. Mayflies were sorted from invertebrate samples within 24 h and frozen for storage. Fro-

zen fish and mayfly samples were freeze-dried, and a 0.1 g homogenized subsample (fish) or the entire sample mass (mayflies) was digested for mercury analysis. Following our established protocols (Chen et al. 2000; Ward et al. 2010b), all samples were digested in ultraclean nitric acid in sealed, acid-cleaned Teflon vessels in a microwave reaction accelerator. Total mercury concentrations in the digested solution were measured by inductively coupled plasma mass spectrometry. Quality control was ensured by analysis of certified reference materials (NIST 2976, mussel tissue; CRC DORM-2, dogfish muscle), duplicate samples, and digestion blanks with every processing batch of 20 samples.

We measured total mercury concentrations in all samples, but methylmercury is the mercury compound that is most prevalent in fish and most prone to bioaccumulation. Variation in the proportion of total mercury that is methylmercury could alter mercury accumulation dynamics and the model parameters required to estimate consumption from the mass-balance model (Lepak et al. 2009). To assess potential variation in methylmercury, we measured a subset of samples for mercury speciation (one fish and one prey sample from each site). Mercury speciation samples were measured by isotope dilution gas chromatography – inductively coupled plasma mass spectrometry (Taylor et al. 2008). In all fish samples, nearly all the mercury was methylmercury ($97\% \pm 2\%$ (mean \pm SD); range 94%–100%), as observed in numerous other studies (Bloom 1992). In prey samples, the mean proportion of mercury as methylmercury was lower, but there was no consistent variation across streams ($86\% \pm 6\%$ (mean \pm SD); range 76%–94%). We assumed that the mean proportions were consistent across all sites, to use literature parameters for methylmercury accumulation in our mercury accumulation model.

Mercury mass-balance model

We used a simple, widely used contaminant accumulation model (Forseth et al. 1992; Rowan and Rasmussen 1996) to estimate consumption rates for young-of-the-year Atlantic salmon. The model, as adapted for stable isotopes and non-reproductive fish, is described in detail elsewhere (Trudel et al. 2000; Kennedy et al. 2004). Briefly, as fish accumulate methylmercury largely from the prey they consume, total prey consumption (C , $\text{g}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$) can be estimated from initial methylmercury body burden (B_i , ng), the final methylmercury body burden (B_{t+d} , where d is the number of days in the interval), the methylmercury concentrations in prey (F , $\text{ng}\cdot\text{g}^{-1}$), and literature estimates for assimilation efficiency (a , proportion) and elimination rate (E , proportion).

For chronically exposed fish, methylmercury elimination rate depends on both temperature and body size as $\ln(E) = 0.066T - 0.2\ln(W) - 5.83$, where T is temperature ($^{\circ}\text{C}$) and W is mass (g) (Trudel and Rasmussen 1997). As temperature and body size varied over time, we iterated the model on a daily time step with mean daily temperature for each site from field data (hourly measurements by temperature loggers anchored to the stream bed; Onset Optic StowAway, Onset Computer Corporation, Pocasset, Mass., USA) and individual daily size estimated by assuming constant instantaneous growth rate between sampling periods. Growth was calculated as $\ln(W_{t+d}/W_t) \cdot d^{-1}$, where W_{t+d} is individual mass at sampling, and W_t is mean mass at stocking (for the early sea-

son) or site-mean mass in the early sample (for the late season). Thus, the daily model for mercury body burden was $B_{t+1} = B_t + aCWF - EB_t$, with B_{t+1} carried over as B_t for the subsequent day. Measured total mercury concentrations were converted to methylmercury as described above. We used an iterative procedure (Hood 2008) to identify the mean daily consumption rate that produced the observed final mercury body burden for each individual after the appropriate number of days (21 days for stocking to early season, 119 days for early season to late season).

For the early-season model and growth calculations, we used the mean size and mercury concentration of fry sampled prior to stocking as initial conditions. All fry originated from the same source with uniform initial mean size and mercury concentration across sites, so this approach does not affect site comparisons. For the late-season model and growth calculations, we used the mean size and mercury concentration of fish at the early sampling date as initial conditions. This approach assumes that the variation in size and mercury concentration across sites is very large compared with the variation among individuals within sites, otherwise site mean values would not be appropriate as initial conditions for individuals in the late-season sample. In our early-season sample, 73% of the variation in size and 95% of the variation in mercury concentration was across sites, suggesting that this was a reasonable approximation.

Data analysis

Our analysis assumes that large differences among sites in survival during the early critical period generate variation in salmon population density that persists through the growing season, as seen for other Atlantic salmon populations (Milner et al. 2003; Nislow et al. 2004) and other stream salmonids (Elliott 1989; Lobón-Cerviá and Rincón 2004). Consistent with this assumption, catch per effort of young-of-the-year salmon during the early-season sample collection was significantly correlated with density from the intensive population samples later in the season, indicating that the density gradient across sites was established early in the season ($r = 0.73$, $n = 18$, $P = 0.0005$). Therefore, we treat the mean population density of the three sample plots fished at each site in August as an index of early survival during the critical period (for survival analyses) as well as a measure of the population density salmon experience between the early- and late-season samples (for density–growth analyses).

Our primary analysis focused on the relationship between predator abundance and mean energetic traits of Atlantic salmon. We first used linear regression to test whether salmon population density was suppressed at high sculpin density. For both the early- and late-season data sets, we used linear regression to determine whether mean salmon prey consumption and growth rates were suppressed at high sculpin density, as predicted for reduced foraging under predation risk or trait-biased predation, or whether consumption and growth were elevated at high sculpin density, as predicted for a compensatory response of salmon to reduced competition. We also used regression to test the direct relationship between salmon population density and late-season growth and consumption. For most regressions, fish population densities were \log_{10} -transformed to equalize variance and linearize re-

lationships ($\log_{10}(x+1)$) for sculpin, which were absent from some sites).

For the primary analysis, our focus was on evaluating specific links between energetic traits and predator abundance, but prey consumption and growth rates can be affected by a suite of factors that affect energetic demand, including temperature, water chemistry, prey availability, and physical habitat. To assess the effects of these factors, we conducted an additional multimodel analysis for early- and late-season consumption and growth rates. For each response, we fit all possible regression models with slimy sculpin population density (\log_{10} -transformed) along with stream gradient (as a percentage, mean of the 30 m sample plots at each site), water temperature (in °C, seasonal mean of hourly measures from in-stream probes installed at each site), depth (in cm, mean of nine transects at each site), mean pH (seasonal mean of biweekly samples), and prey biomass (\log_{10} mean mg dry mass of mayflies in electrobugging samples) as potential predictors. Consumption rate was also included as a predictor for growth rate. We ranked models according to small sample size corrected Akaike information criterion (AIC_c) and report the model-averaged parameter estimates and post hoc probability for each predictor with an AIC_c weight cutoff of 0.95 (Burnham and Anderson 2004).

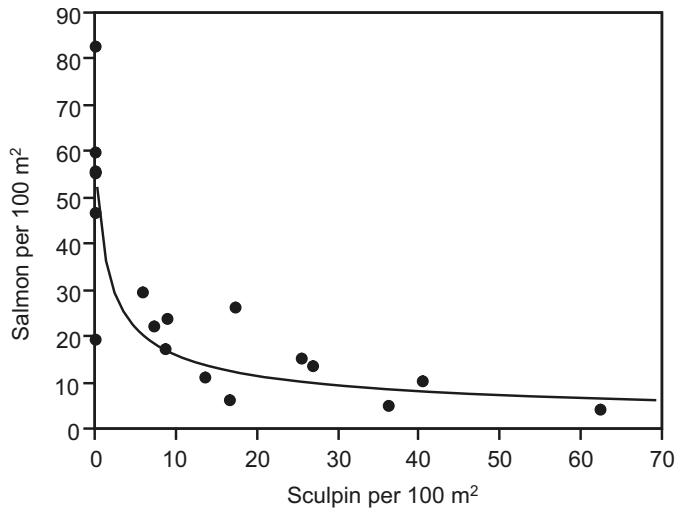
Results

The wide range in sculpin population density (0–60 sculpin per 100 m²) and other conditions across the 18 study locations produced a correspondingly wide range in population density of juvenile Atlantic salmon (range in August: 4–83 salmon per 100 m²). Mean performance as indicated by mass-balance estimated consumption and mean individual growth rates also varied widely across sites. Early-season consumption estimates ranged from 0.10 to 0.37 g·g⁻¹·day⁻¹ and growth from 0.02 to 0.08 g·g⁻¹·day⁻¹, producing mean sizes in May ranging from 0.4 to 1.1 g across sites. Late-season consumption estimates ranged from 0.08 to 0.19 g·g⁻¹·day⁻¹ and growth from 0.01 to 0.02 g·g⁻¹·day⁻¹, producing mean sizes in September ranging from 3.1 to 7.6 g across sites.

Population density of salmon fry was much lower at sites with abundant sculpin (Fig. 1; $\log_{10}(\text{salmon per } 100 \text{ m}^2) = 1.72 - 0.50(\log_{10}(\text{sculpin per } 100 \text{ m}^2 + 1))$, $R^2 = 0.73$, root mean square error (RMSE) = 0.21, $F_{[1,16]} = 43.3$, $P < 0.0001$). Consistent with reduced foraging under sculpin predation risk, salmon early-season prey consumption was also suppressed at sites with abundant sculpin (Fig. 2a; consumption (g·g⁻¹·day⁻¹) = $0.25 - 0.06(\log_{10}(\text{sculpin per } 100 \text{ m}^2 + 1))$, $R^2 = 0.38$, RMSE = 0.06, $F_{[1,16]} = 9.7$, $P = 0.007$). However, mean early-season growth of salmon was not related to sculpin abundance (Fig. 2b; $R^2 = 0.01$, RMSE = 0.02, $F_{[1,16]} = 0.002$, $P = 0.97$).

Consistent with a compensatory response of salmon to reduced competition, late-season mean individual performance was elevated at sites with abundant sculpin and low salmon population density. Mean late-season growth was fastest at sites with low salmon population density (Fig. 3; growth (g·g⁻¹·day⁻¹) = $0.022 - 0.004[\log_{10}(\text{salmon per } 100 \text{ m}^2)]$, $R^2 = 0.43$, RMSE = 0.002, $F_{[1,16]} = 11.9$, $P = 0.003$), resulting in a positive relationship between late-season salmon growth and sculpin density (Fig. 2d; growth (g·g⁻¹·day⁻¹) = $0.016 +$

Fig. 1. Atlantic salmon summer population density from standardized stocking related to slimy sculpin population density. Each point is the mean population density from three 30 m sample reaches at each study site. The line is the regression fit to \log_{10} -transformed data.



0.00008(sculpin per 100 m²), $R^2 = 0.36$, RMSE = 0.002, $F_{[1,16]} = 8.9$, $P = 0.009$). However, mean late-season prey consumption was not significantly elevated at sites with abundant sculpin (Fig. 2c; $R^2 = 0.09$, RMSE = 0.027, $F_{[1,16]} = 1.6$, $P = 0.23$). Thus, salmon experiencing low population density grew faster than salmon at high population density without consuming more prey, suggesting that energetic costs were reduced at low population density. This pattern in late-season growth drove variation in final size of salmon across sites, such that salmon were larger at the end of summer at sites with abundant sculpin (\log_{10} mean mass (g) = $0.67 + 0.004(\text{sculpin per } 100 \text{ m}^2)$, $R^2 = 0.42$, RMSE = 0.08, $F_{[1,16]} = 11.5$, $P = 0.003$) and low salmon population density (\log_{10} mean mass (g) = $0.89 - 0.17[\log_{10}(\text{salmon per } 100 \text{ m}^2)]$, $R^2 = 0.44$, RMSE = 0.08, $F_{[1,16]} = 12.6$, $P = 0.003$).

Beyond the effects of predators and population density, salmon consumption rates were most strongly correlated with mean prey biomass, with higher consumption rates at sites with higher prey biomass in both the early and late season (Table 1). Stream depth and gradient may also explain some variation in early-season consumption, with consumption greatest at deeper and lower-gradient sites, potentially reflecting drivers of profitable foraging habitat. Increased prey consumption was associated with faster growth in the early season, but not in the late season, suggesting that variation in late-season growth was associated with energetic expenditures, not intake (Table 1). Other factors that explained variation in growth rate include pH, with suppressed growth at acidic sites in early season and the reverse in the late season, suggesting a potential compensatory effect. The effect of sculpin population density on late-season growth reflects the closely correlated effect of salmon population density discussed above.

Discussion

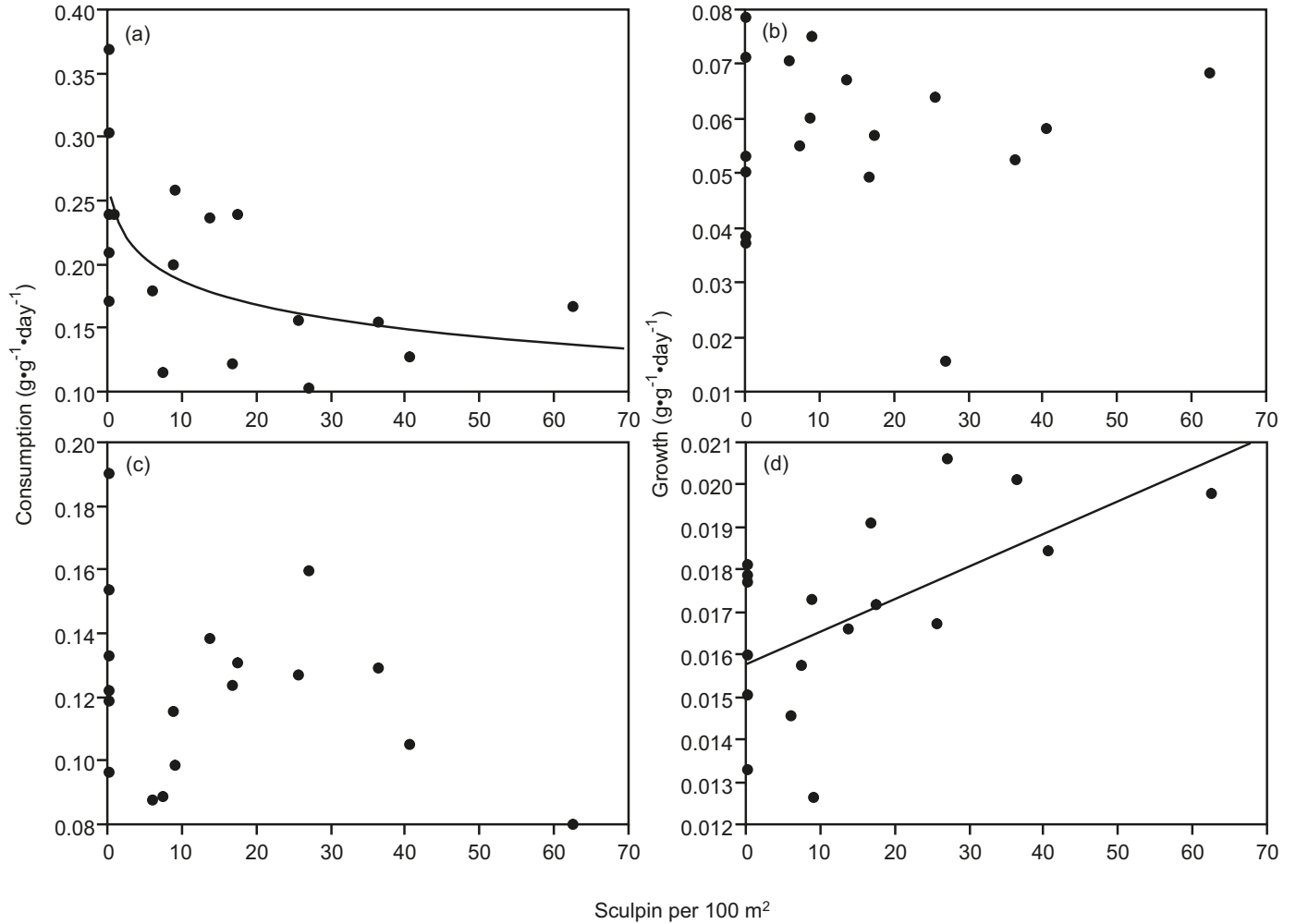
Using robust, trace-element derived consumption rates of

juvenile Atlantic salmon in the field, combined with controlled stocking across spatial and temporal variation in the biotic and abiotic environment, we were able to elucidate some of the basic mechanisms underlying variation in growth and survival of juvenile stream salmonids. In combination with our earlier work documenting sculpin predation on salmon fry (Ward et al. 2008a, 2008b), these results suggest that slimy sculpin predation strongly increased salmon mortality, likely compounded by a short-term effect on salmon traits (early-season consumption) but moderated by a delayed compensatory effect on salmon traits (late-season growth). These results are consistent with the idea that predator effects on prey traits are ubiquitous (Lima 1998) and that these effects are important for determining the effects of predators on populations (Werner and Peacor 2003; Peckarsky et al. 2008). Further, our seasonal sampling provides a compelling example of a temporal reversal of such effects.

Use of contaminant accumulation models to estimate consumption rates of free-living fish in the field is becoming increasingly common (Trudel et al. 2001; Rennie et al. 2008). These models have been shown to yield consumption estimates similar to those obtained with techniques that rely on direct measurement of stomach contents (Trudel et al. 2000) and capture ecologically meaningful differences across locations (Kennedy et al. 2004, 2008). A primary advantage of the contaminant mass-balance approach over standard bioenergetics models is the estimation of integrated consumption rates that are not confounded by problematic assumptions about the proportion of total energy consumed that is allocated to growth versus activity (Chippis and Wahl 2008) and so allow for assessment of the relative importance of energy intake and energy expenditure in driving patterns of growth (Rennie et al. 2005). For example, the factors that we identified in the multimodel analysis as important drivers of growth variation after accounting for variation in consumption may act by mediating energetic costs of maintaining osmotic balance (e.g., effect of pH in the early season) or activity costs associated with behavior or habitat use (e.g., effect of sculpin population density in the late season, reflecting density-dependent growth).

The utility of the contaminant mass-balance model approach for answering ecological questions about energy acquisition and use is not without limits. Accurate estimates of consumption require reliable estimates of model parameters. Of particular importance is adequate representation of contaminant concentration in the diet (Kennedy et al. 2004). Site-level bias in the estimate of contaminant concentrations in prey will confound site-level estimates of mean consumption rate of fish. Here, we used mercury in mayflies as a surrogate for the salmon diet, as they were a dominant prey item, they reflect mercury concentrations in other aquatic insect prey for juvenile salmon (Ward et al. 2010a), and contaminant accumulation in salmon generally tracks that in mayflies across sites (Ward et al. 2010b, 2010c). This approach is only valid as long as salmon did not disproportionately consume prey with very distinct mercury concentrations from mayflies at some sites. However, we found no evidence of a shift in the use of mayflies along the sculpin population gradient that could explain the pattern of reduced consumption under predation risk that we observed (correlation of proportion of mayflies in the diet with sculpin population

Fig. 2. Early-season (*a, b*) and late-season (*c, d*) consumption (*a, c*) and growth rates (*b, d*) of juvenile Atlantic salmon related to slimy sculpin population density. Each consumption or growth estimate is the mean of four or five salmon sampled at each study site; sculpin population density is the mean from three 30 m sample reaches at each study site. Regression lines are shown for significant fits to log₁₀-transformed (*a*) or untransformed (*d*) data.



density; early season: $r = 0.25$, $P = 0.31$; late season: $r = 0.05$, $P = 0.84$).

Early season

Our results are particularly relevant to understanding the functional role of predators during early life history of stream-dwelling salmonids. This role has been difficult to elucidate. On one hand, small postemergent fry appear to be highly vulnerable to predatory fish (Ward et al. 2008a, 2008b), which are the likely major predators of juveniles before they become large enough to be preyed on by birds or mammals (Ward and Hvidsten 2010). At the same time, peak vulnerability may only extend for a brief period after emergence (Brännäs 1995; Henderson and Letcher 2003), potentially limiting the total predation rate. We have observed in this and previous studies that locations containing predatory sculpins have lower salmon first-summer recruitment rates than low-sculpin or sculpin-free sites (Ward et al. 2008a, 2008b). Yet when initial densities of salmon fry are very high, observed sculpin predation rates do not seem able to explain the magnitude of this decrease in survival (Ward et al. 2008b). This potential mismatch could be explained if

Fig. 3. Late-season growth rates of juvenile Atlantic salmon related to salmon population density. Each growth estimate is the mean of five salmon sampled at each study site, salmon population density is the mean from three 30 m sample reaches at each study site. The line is the regression fit to log₁₀-transformed data.

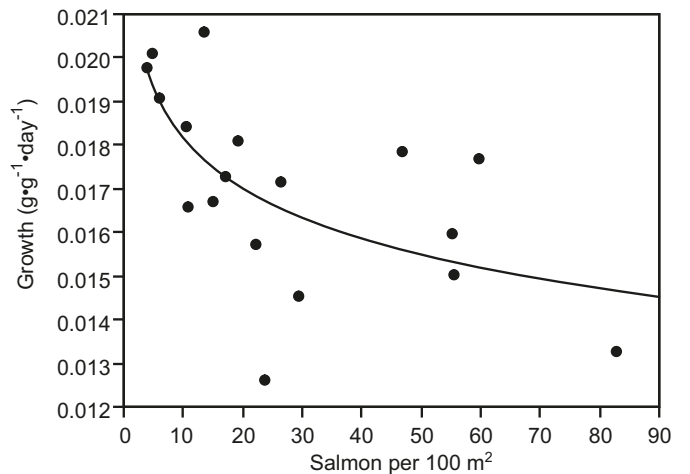


Table 1. Model-averaged regression coefficients, standard errors (SE), and the post hoc probability that the coefficient does not equal zero for predictors of seasonal growth and consumption by Atlantic salmon.

| | Early consumption | | Late consumption | | Early growth | | Late growth | |
|-------------------|----------------------|-------|---------------------|-------|---------------------|-------|-----------------------|-------|
| | Coefficient (SE) | P ≠ 0 | Coefficient (SE) | P ≠ 0 | Coefficient (SE) | P ≠ 0 | Coefficient (SE) | P ≠ 0 |
| Prey biomass | 0.2 (0.06) | 1 | 0.07 (0.03) | 1 | 0.006 (0.006) | 0.6 | -0.002 (0.002) | 0.6 |
| Stream gradient | -0.008 (0.007) | 0.7 | 0.0004 (0.003) | 0.1 | -0.0004 (0.0009) | 0.3 | 0.00002 (0.0002) | 0.1 |
| Mean depth | 0.009 (0.003) | 1 | -0.00003 (0.0005) | 0 | 0.00008 (0.0002) | 0.3 | 0.000003 (0.00004) | 0.1 |
| Mean temperature | -0.00005 (0.0006) | 0 | -0.004 (0.005) | 0.5 | 0.0005 (0.001) | 0.3 | 0.00004 (0.0003) | 0.1 |
| Sculpin density | -0.05 (0.02) | 1 | -0.0004 (0.003) | 0.1 | 0.001 (0.002) | 0.5 | 0.001 (0.0006) | 0.9 |
| pH | 0.005 (0.01) | 0.2 | -0.02 (0.02) | 0.8 | 0.05 (0.008) | 1 | -0.002 (0.001) | 0.9 |
| Early consumption | — | — | — | — | 0.04 (0.02) | 0.9 | — | — |
| Late consumption | — | — | — | — | — | — | 0.009 (0.01) | 0.6 |

Note: Missing coefficients indicate that the predictor was not included in the model. Coefficients in bold are for predictors included in the best model for each response (lowest corrected Akaike information criterion (AIC_c) values: -52.8 for early consumption, -79.1 for late consumption, -115.1 for early growth, -168.2 for late growth); coefficients in italics are for predictors included in additional models within 2 AIC_c units of the best model (ΔAIC_c values: 1.3 for early consumption, 1.5 for late consumption, 1.0 for early growth, 2.1 for late growth).

predators had other negative effects in addition to direct predation, such as the reduced consumption rates that we observed.

Effects of predators on consumption rate during the critical period are likely to be particularly important for young-of-the-year Atlantic salmon. Previous research on Atlantic salmon survival through the critical period indicates that increased foraging opportunity (Nislow et al. 1998, 1999) or consumption rate (Kennedy et al. 2004, 2008) is associated with increased survival. Somewhat surprisingly, despite suppressed consumption at high predator density, we did not observe direct effects of predators on growth of juvenile salmon in the early season. However, increased early-season consumption was associated with rapid growth after accounting for variation in abiotic factors, particularly pH. Further, the absence of a simple negative relationship between predation risk and growth is consistent with the observation in previous studies that critical-period stressors are manifest by effects on survival and not individual growth (Einum et al. 2006; Kennedy et al. 2008). Reduced activity costs for fish that seek shelter to avoid predators might to some extent offset effects of reduced consumption on growth (Orpwood et al. 2006; Blanchet et al. 2008). Finally, while we cannot determine whether the effects of sculpin on mean consumption rates that we observed are the result of reductions in foraging rate or selective predation on individuals with higher foraging rates, the net result is the same — reductions in overall survival during an early critical period.

Late season

Low salmon population density in streams with abundant sculpin was associated with high growth rates during the late season, yielding mean salmon mass up to 50% larger at the end of summer in streams with abundant sculpin than in those without sculpin. This finding is concordant with a large body of work demonstrating strong density dependence of stream salmonid growth rates (Grant and Imre 2005; Ward et al. 2009). However, this is the first study to explicitly link predator-associated early mortality of salmon to increased later growth of survivors. This late-season, density-dependent growth has potentially important implications for the effects of predators on salmon populations. Fast-growing salmon migrate to sea sooner, and males mature earlier than slow growers (Letcher and Terrick 1998; Horton et al. 2009), suggesting the potential for strong compensation for early predator losses via increased individual growth (Ward and Hvidsten 2010).

While density-dependent growth of stream-dwelling salmonids clearly occurs, the precise mechanisms remain controversial (Ward et al. 2007). Our measured consumption rates indicate that energetic costs play an important role in determining the effect of changes in population density on growth. Consumption rates were not elevated at low-density, high-growth sites, suggesting that reduced energetic costs were the likely mechanism underlying increased individual growth at low density. While we cannot eliminate the possibility that shifts in diet composition or other factors drive the growth effect, reduced energetic costs are consistent with recent laboratory studies showing that juvenile salmonids respond to increases in resources or reduction in population density by reducing energetic expenditures rather than increasing their

prey intake rates (Orpwood et al. 2006; Kaspersson et al. 2010). Interestingly, our field studies (Ward et al. 2009; current study) suggest that, in contrast to reduced competitor density, increased prey availability is associated with increased growth and prey consumption. This suggests that fundamentally different mechanisms underlie growth responses to increased resource availability versus increased competition for a given level of resources: the relative scope for compensatory growth is set by reduced energetic costs at low population density, but the absolute scope is set by resource availability and consumption rates. Clearly, further work is necessary to evaluate these hypotheses in the field.

Taken together, our results support an emerging “general model” of biotic factors that affect recruitment through the first summer for Atlantic salmon and similar stream salmonids. Building on earlier work on recruitment of stream salmonids (Le Cren 1973; Elliott 1989), this model predicts that total cohort strength is largely determined during the early critical period by predation (Ward et al. 2008a, 2008b), limited suitable habitat (Lobón-Cerviá and Rincón 2004; Nislow et al. 2004), and other factors that reduce foraging success (Kennedy et al. 2008). Thereafter, compensatory responses, constrained by habitat and prey availability (Ward et al. 2009), primarily affect mean individual traits (growth, condition) rather than abundance (Einum et al. 2006; Nislow et al. 2011). By using a tracer approach to estimate time-integrated consumption, we were able to evaluate for the first time the energetic mechanisms underlying this transition from the critical period to subsequent compensatory performance for free-living fish.

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References

- Blanchet, S., Bernatchez, L., and Dodson, J.J. 2007. Behavioural and growth responses of a territorial fish (Atlantic salmon, *Salmo salar*, L.) to multiple predatory cues. *Ethology*, **113**(11): 1061–1072. doi:10.1111/j.1439-0310.2007.01410.x.
- Blanchet, S., Loot, G., and Dodson, J.J. 2008. Competition, predation and flow rate as mediators of direct and indirect effects in a stream food chain. *Oecologia* (Berl.), **157**(1): 93–104. doi:10.1007/s00442-008-1044-8. PMID:18465148.
- Bloom, N.S. 1992. On the chemical form of mercury in edible fish and marine invertebrate tissue. *Can. J. Fish. Aquat. Sci.* **49**(5): 1010–1017. doi:10.1139/f92-113.
- Brännäs, E. 1995. First access to territorial space and exposure to strong predation pressure: a conflict in early emerging Atlantic salmon (*Salmo salar* L.) fry. *Evol. Ecol.* **9**: 411–420. doi:10.1007/BF01237763.
- Burnham, K.P., and Anderson, D.R. 2004. Multimodel inference: understanding AIC and BIC in model selection. *Sociol. Methods Res.* **33**(2): 261–304. doi:10.1177/0049124104268644.
- Carle, F.L., and Strub, M.R. 1978. A new method for estimating population size from removal data. *Biometrics*, **34**(4): 621–630. doi:10.2307/2530381.
- Chen, C.Y., Stemberger, R.S., Klaue, B., Blum, J.D., Pickhardt, P.C., and Folt, C.L. 2000. Accumulation of heavy metals in food web components across a gradient of lakes. *Limnol. Oceanogr.* **45**(7): 1525–1536. doi:10.4319/lo.2000.45.7.1525.
- Chipps, S.R., and Wahl, D.H. 2008. Fish bioenergetics modeling in the 21st century: reviewing new insights and revisiting old constraints. *Trans. Am. Fish. Soc.* **137**(1): 298–313. doi:10.1577/T05-236.1.
- Einum, S., Sundt-Hansen, L., and Nislow, K.H. 2006. The partitioning of density-dependent dispersal, growth and survival throughout ontogeny in a highly fecund organism. *Oikos*, **113**(3): 489–496. doi:10.1111/j.2006.0030-1299.14806.x.
- Elliott, J.M. 1989. The critical period concept for juvenile survival and its relevance for population regulation in young sea trout, *Salmo trutta*. *J. Fish Biol.* **35**: 91–98. doi:10.1111/j.1095-8649.1989.tb03049.x.
- Folt, C.L., Nislow, K.H., and Power, M.E. 1998. Implications of temporal and spatial scale for Atlantic salmon (*Salmo salar*) research. *Can. J. Fish. Aquat. Sci.* **55**(S1): 9–21. doi:10.1139/d98-017.
- Forseth, T., Jonsson, B., Næumann, R., and Ugedal, O. 1992. Radioisotope method for estimating food consumption by brown trout (*Salmo trutta*). *Can. J. Fish. Aquat. Sci.* **49**(7): 1328–1335. doi:10.1139/f92-148.
- Gotceitas, V., and Godin, J.G.J. 1991. Foraging under the risk of predation in juvenile Atlantic salmon (*Salmo salar* L.): effects of social status and hunger. *Behav. Ecol. Sociobiol.* **29**(4): 255–261. doi:10.1007/BF00163982.
- Grant, J.W.A., and Imre, I. 2005. Patterns of density-dependent growth in juvenile stream-dwelling salmonids. *J. Fish Biol.* **67**(Suppl. B): 100–110. doi:10.1111/j.0022-1112.2005.00916.x.
- Henderson, J.N., and Letcher, B.H. 2003. Predation on stocked Atlantic salmon (*Salmo salar*) fry. *Can. J. Fish. Aquat. Sci.* **60**(1): 32–42. doi:10.1139/f03-001.
- Hixon, M.A., and Beets, J.P. 1993. Predation, prey refuges, and the structure of coral reef fish assemblages. *Ecol. Monogr.* **63**(1): 77–101. doi:10.2307/2937124.
- Hood, G.M. 2008. PopTools version 3.0.6 [computer program]. Available from <http://www.cse.csiro.au/poptools> [accessed 11 October 2008].
- Horton, G.E., Letcher, B.H., Bailey, M.M., and Kinnison, M.T. 2009. Atlantic salmon (*Salmo salar*) smolt production: the relative importance of survival and body growth. *Can. J. Fish. Aquat. Sci.* **66**(3): 471–483. doi:10.1139/F09-005.
- Imre, I., Grant, J.W.A., and Cunjak, R.A. 2005. Density-dependent growth of young-of-the-year Atlantic salmon *Salmo salar* in Catamaran Brook, New Brunswick. *J. Anim. Ecol.* **74**(3): 508–516. doi:10.1111/j.1365-2656.2005.00949.x.
- Kaspersson, R., Hojesjo, J., and Pedersen, S. 2010. Effects of density on foraging success and aggression in age-structured groups of brown trout. *Anim. Behav.* **79**(3): 709–715. doi:10.1016/j.anbehav.2009.12.025.
- Kennedy, B.P., Klaue, B., Blum, J.D., and Folt, C. 2004. Integrative measures of consumption rates in salmon: expansion and application of a trace element approach. *J. Appl. Ecol.* **41**(5): 1009–1020. doi:10.1111/j.0021-8901.2004.00956.x.
- Kennedy, B.P., Nislow, K.H., and Folt, C.L. 2008. Habitat-mediated foraging limitations drive survival bottlenecks for juvenile salmon. *Ecology*, **89**(9): 2529–2541. doi:10.1890/06-1353.1. PMID:18831174.
- Le Cren, E.D. 1973. The population dynamics of young trout (*Salmo*

- trutta*) in relation to density and territorial behavior. Rapp. P.-V. Reun.- Cons. Int. Explor. Mer, **164**: 241–246.
- Leduc, A.O.H.C., Kelly, J.M., and Brown, G.E. 2004. Detection of conspecific alarm cues by juvenile salmonids under neutral and weakly acidic conditions: laboratory and field tests. *Oecologia (Berl.)*, **139**(2): 318–324. doi:10.1007/s00442-004-1492-8. PMID: 14758533.
- Lepak, J.M., Robinson, J.M., Kraft, C.E., and Josephson, D.C. 2009. Changes in mercury bioaccumulation in an apex predator in response to removal of an introduced competitor. *Ecotoxicology*, **18**(5): 488–498. doi:10.1007/s10646-009-0306-5. PMID:19277860.
- Letcher, B.H., and Terrick, T.D. 1998. Maturation of male age-0 Atlantic salmon following a massive, localized flood. *J. Fish Biol.* **53**(6): 1243–1252. doi:10.1111/j.1095-8649.1998.tb00245.x.
- Lima, S.L. 1998. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. *Adv. Stud. Behav.* **27**: 215–290. doi:10.1016/S0065-3454(08)60366-6.
- Lobón-Cerviá, J., and Rincón, P.A. 2004. Environmental determinants of recruitment and their influence on the population dynamics of stream-living brown trout *Salmo trutta*. *Oikos*, **105**(3): 641–646. doi:10.1111/j.0030-1299.2004.12989.x.
- Metcalf, N.B. 1998. The interaction between behavior and physiology in determining life history patterns in Atlantic salmon (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* **55**(S1): 93–103. doi:10.1139/d98-005.
- Milner, N.J., Elliott, J.M., Armstrong, J.D., Gardiner, R., Welton, J.S., and Ladle, M. 2003. The natural control of salmon and trout populations in streams. *Fish. Res.* **62**(2): 111–125. doi:10.1016/S0165-7836(02)00157-1.
- Nislow, K.H., Folt, C., and Seandel, M. 1998. Food and foraging behavior in relation to microhabitat use and survival of age-0 Atlantic salmon. *Can. J. Fish. Aquat. Sci.* **55**(1): 116–127. doi:10.1139/f97-222.
- Nislow, K.H., Folt, C.L., and Parrish, D.L. 1999. Favorable foraging locations for young Atlantic salmon: application to habitat and population restoration. *Ecol. Appl.* **9**(3): 1085–1099. doi:10.1890/1051-0761(1999)009[1085:FFLFYA]2.0.CO;2.
- Nislow, K.H., Einum, S., and Folt, C. 2004. Testing predictions of the critical period for survival concept using experiments with stocked Atlantic salmon. *J. Fish Biol.* **65**(Suppl. s1): 188–200. doi:10.1111/j.0022-1112.2004.00561.x.
- Nislow, K.H., Armstrong, J.D., and Grant, J.W.A. 2011. The role of competition in the ecology of juvenile Atlantic salmon. *In Atlantic salmon Ecology. Edited by Ø. Aas, S. Einum, A. Klemetsen, and J. Skurdal.* Wiley-Blackwell, Oxford, UK. pp. 171–190.
- Orpwood, J.E., Griffiths, S.W., and Armstrong, J.D. 2006. Effects of food availability on temporal activity patterns and growth of Atlantic salmon. *J. Anim. Ecol.* **75**(3): 677–685. doi:10.1111/j.1365-2656.2006.01088.x. PMID:16689950.
- Peckarsky, B.L., Abrams, P.A., Bolnick, D.I., Dill, L.M., Grabowski, J.H., Luttbeg, B., Orrock, J.L., Peacor, S.D., Preisser, E.L., Schmitz, O.J., and Trussell, G.C. 2008. Revisiting the classics: considering nonconsumptive effects in textbook examples of predator-prey interactions. *Ecology*, **89**(9): 2416–2425. doi:10.1890/07-1131.1. PMID:18831163.
- Relyea, R.A. 2002. The many faces of predation: how induction, selection, and thinning combine to alter prey phenotypes. *Ecology*, **83**(7): 1953–1964. doi:10.1890/0012-9658(2002)083[1953:TMFOPH]2.0.CO;2.
- Rennie, M.D., Collins, N.C., Shuter, B.J., Rajotte, J.W., and Couture, P. 2005. A comparison of methods for estimating activity costs of wild fish populations: more active fish observed to grow slower. *Can. J. Fish. Aquat. Sci.* **62**(4): 767–780. doi:10.1139/f05-052.
- Rennie, M.D., Purchase, C.F., Lester, N., Collins, N.C., Shuter, B.J., and Abrams, P.A. 2008. Lazy males? Bioenergetic differences in energy acquisition and metabolism help to explain sexual size dimorphism in percids. *J. Anim. Ecol.* **77**(5): 916–926. doi:10.1111/j.1365-2656.2008.01412.x. PMID:18557958.
- Rowan, D.J., and Rasmussen, J.B. 1996. Measuring the bioenergetic cost of fish activity in situ using a globally dispersed radiotracer (Cs-137). *Can. J. Fish. Aquat. Sci.* **53**(4): 734–745. doi:10.1139/f95-046.
- Taylor, B.W., McIntosh, A.R., and Peckarsky, B.L. 2001. Sampling stream invertebrates using electroshocking techniques: implications for basic and applied research. *Can. J. Fish. Aquat. Sci.* **58**(3): 437–445. doi:10.1139/f00-255.
- Taylor, V.F., Jackson, B.P., and Chen, C.Y. 2008. Mercury speciation and total trace element determination of low-biomass biological samples. *Anal. Bioanal. Chem.* **392**(7–8): 1283–1290. doi:10.1007/s00216-008-2403-3. PMID:18828006.
- Trudel, M., and Rasmussen, J.B. 1997. Modeling the elimination of mercury by fish. *Environ. Sci. Technol.* **31**(6): 1716–1722. doi:10.1021/es960609t.
- Trudel, M., Tremblay, A., Schetagne, R., and Rasmussen, J.B. 2000. Estimating food consumption rates of fish using a mercury mass balance model. *Can. J. Fish. Aquat. Sci.* **57**(2): 414–428. doi:10.1139/f99-262.
- Trudel, M., Tremblay, A., Schetagne, R., and Rasmussen, J.B. 2001. Why are dwarf fish so small? An energetic analysis of polymorphism in lake whitefish (*Coregonus clupeaformis*). *Can. J. Fish. Aquat. Sci.* **58**(2): 394–405. doi:10.1139/f00-252.
- Vincenzi, S., Crivelli, A.J., Jesensek, D., and De Leo, G.A. 2008. The role of density-dependent individual growth in the persistence of freshwater salmonid populations. *Oecologia (Berl.)*, **156**(3): 523–534. doi:10.1007/s00442-008-1012-3. PMID:18386068.
- Walters, C.J., and Juanes, F. 1993. Recruitment limitation as a consequence of natural selection for use of restricted feeding habitats and predation risk taking by juvenile fishes. *Can. J. Fish. Aquat. Sci.* **50**(10): 2058–2070. doi:10.1139/f93-229.
- Ward, D.M., and Hvidsten, N.A. 2010. Predation: compensation and context dependence. *In Atlantic salmon ecology. Edited by Ø. Aas, A. Klemetsen, S. Einum, and J. Skurdal.* Wiley-Blackwell, Oxford, UK. pp. 199–220.
- Ward, D.M., Nislow, K.H., Armstrong, J.D., Einum, S., and Folt, C. L. 2007. Is the shape of the density–growth relationship for stream salmonids evidence for exploitative rather than interference competition? *J. Anim. Ecol.* **76**(1): 135–138. doi:10.1111/j.1365-2656.2006.01169.x. PMID:17184361.
- Ward, D.M., Nislow, K.H., and Folt, C. 2008a. Do native species limit survival of reintroduced Atlantic salmon in historic rearing streams? *Biol. Conserv.* **141**(1): 146–152. doi:10.1016/j.biocon.2007.09.006.
- Ward, D.M., Nislow, K.H., and Folt, C.L. 2008b. Predators reverse the direction of density dependence for juvenile salmon mortality. *Oecologia (Berl.)*, **156**(3): 515–522. doi:10.1007/s00442-008-1011-4. PMID:18317816.
- Ward, D.M., Nislow, K.H., and Folt, C.L. 2009. Increased population density and suppressed prey biomass: relative impacts on juvenile Atlantic salmon growth. *Trans. Am. Fish. Soc.* **138**(1): 135–143. doi:10.1577/T08-128.1.
- Ward, D.M., Nislow, K.H., Chen, C.Y., and Folt, C.L. 2010a. Rapid, efficient growth reduces mercury concentrations in stream-dwelling Atlantic salmon. *Trans. Am. Fish. Soc.* **139**(1): 1–10. doi:10.1577/T09-032.1. PMID:20436784.
- Ward, D.M., Nislow, K.H., Chen, C.Y., and Folt, C.L. 2010b.

- Reduced trace element concentrations in fast-growing juvenile Atlantic salmon in natural streams. *Environ. Sci. Technol.* **44**(9): 3245–3251. doi:10.1021/es902639a. PMID:20356034.
- Ward, D.M., Nislow, K.H., and Folt, C.L. 2010c. Bioaccumulation syndrome: identifying factors that make some stream food webs prone to elevated mercury bioaccumulation. *Ann. N. Y. Acad. Sci.* **1195**(1): 62–83. doi:10.1111/j.1749-6632.2010.05456.x. PMID:20536817.
- Werner, E.E., and Peacor, S.D. 2003. A review of trait-mediated indirect interactions in ecological communities. *Ecology*, **84**(5): 1083–1100. doi:10.1890/0012-9658(2003)084[1083:AROTII]2.0.CO;2.