Failure of physiological metrics to predict dominance in juvenile Pacific salmon (Oncorhynchus spp.): habitat effects on the allometry of growth in dominance hierarchies

Travis E. Van Leeuwen, Jordan S. Rosenfeld, and Jeffrey G. Richards

Abstract: Territoriality is one of the best examples of interference competition and generally results in larger, dominant individuals gaining preferential access to food. However, the expectation of higher growth of dominant individuals among juvenile salmonids has received only mixed support. We used outdoor semi-natural stream channels stocked with varying sizes of young of the year juvenile salmonids under high and low food rations (i) to examine the mechanisms underlying variation in the benefits of dominance and (ii) to demonstrate that inconsistencies in the apparent benefits of dominance are a logical outcome of the allometry of growth and differential energy intake among fish of different size in a dominance hierarchy. Growth of dominants exceeded that of subordinates when food was abundant, but subordinates grew faster than dominants in low food treatments and when dominant fish increased in size and approached the capacity of their habitat. In general, size disparity within a dominance hierarchy may promote higher growth of subordinates because of the lower energetic requirements of smaller individuals, and the allometry of fish growth, relative to habitat capacity, can reverse the expected growth and condition of dominant and subordinate fish.

Introduction

Territoriality is one of the best examples of interference competition and generally results in larger dominant individuals gaining preferential access to food, shelter, or mates. Territoriality occurs across a broad range of taxa (e.g., Huntington and Turner 1987; Harwood et al. 2003) and is especially common among juvenile drift-feeding salmon, which rapidly establish size-based dominance hierarchies both in laboratory settings (Reinhardt 1999; Sloman et al. 2000, 2001) and in the wild (Nakano 1995). Dominance hierarchies form soon after emergence as juveniles engage in intra- and inter-specific competition for preferred feeding territories (Hartman 1965; Chapman 1966; Cutts et al. 1999). It is generally accepted that dominance is advantageous as preferential access to food (Cutts et al. 1999) facilitates increased growth (Metcalfe et al. 1995), as well as survival (Huntingford and Turner 1987), as mortality rate tends to decline with fish size (Post and Evans 1989; Shut her and Post 1990; Post and Parkinson 2001).
The ability to obtain preferential access to food in dominance hierarchies that are temporally stable (Bachman 1984; Abbott et al. 1985; Nakano 1995) generates an expectation that dominant fish should experience high growth. Laboratory experiments have generally found positive correlations between dominance and growth (e.g., Thorpe et al. 1992; Metcalfe et al. 1995; Sloman et al. 2001), with some notable exceptions (e.g., experiments by Huntingford and Garcia de Leániz 1997 carried out in semi-natural stream channels). However, despite the expectation of higher growth of dominant fish from laboratory studies, relationships between dominance, growth, and physiological diagnostics in wild salmonids have been mixed. Although several studies have shown positive correlations between dominance and physiological metrics of performance such as growth hormone (GH) levels (Johnsson and Bjornsson 1994) or standard metabolic rate (SMR) (Metcalfe et al. 1995), other studies have found no relationship between dominance and physiological condition in wild populations or negative relationships (e.g., Martin-Smith and Armstrong 2002; Sloman et al. 2008).

Contrary to expectation, dominant or larger wild fish may exhibit lower growth rates (Harvey et al. 2005, Hansen and Closs 2009) and higher cortisol (stress) levels than smaller subordinates (Sloman et al. 2008). This has caused puzzlement, as dominant or larger wild fish are typically expected to have higher SMR (prior to agonistic encounters) and growth rates (Cutts et al. 1999; Álvarez and Nicieza 2005) and lower cortisol levels, which are usually found in high concentrations in subordinates (Eijke and Schreck 1980). These conflicting results between correlates of dominance in the lab and field are attributed to the general complexity and unpredictability of natural habitats (Martin-Smith and Armstrong 2002; Álvarez and Nicieza 2005; Sloman et al. 2008), although the specific mechanism(s) underlying variation in the benefits of dominance remain unclear.

Various studies have suggested that greater time spent foraging and risk-taking, and the subsequent exposure to predation, by dominant or faster-growing fish may result in higher mortality rates for dominants (Nakano 1995; Finstad et al. 2007; Biro and Post 2008), but this should not cause lower growth or elevated stress. Vøllestad and Quinn (2003) demonstrated that being dominant may only be advantageous when food availability is limiting or predictable, allowing monopolization of the food supply. When dominants were unable to monopolize resources, Vøllestad and Quinn (2003) found a negative relationship between growth and dominance in juvenile coho salmon (Oncorhynchus kisutch), presumably because of greater energetic costs and stress of territorial defense.

Here we build on the observations of earlier researchers (e.g., Grand and Grant 1994; Vøllestad and Quinn 2003) to demonstrate that inconsistencies in the apparent benefits of dominance are not unexpected but are a logical outcome of the allometry of growth and differential energy intake among fish in a dominance hierarchy (where allometry refers to non-linear changes in the relationship between maximum food ration and growth with increasing body size). Hierarchies are not all of equal benefit to dominant and subordinate fish, and net energy intake in a hierarchy will depend on body size and energetic demands of a fish relative to the food supply, which will vary with habitat type and configuration (e.g., pool size and shape, drift concentration, and discharge from the upstream riffle; Harvey et al. 2005; Hansen and Closs 2009). A large fish in a habitat with abundant food that it can monopolize may experience higher growth than a subordinate, particularly if they are of similar size; however, a large dominant fish in an unproductive habitat may conceivably experience lower growth than a smaller subordinate that has a smaller absolute energy requirement for growth (Hansen and Closs 2009).

As part of a larger study to assess metabolic differences in juvenile steelhead trout (Oncorhynchus mykiss) and coho salmon (Van Leeuwen et al. 2011), we reared fish at different food rations in a set of outdoor artificial stream channels. Because fish increased in size throughout the experiment, it provided an opportunity to analyze size-based patterns of growth to understand (i) the allometric effects of body size on relative growth of fish in dominance hierarchies and (ii) the effects of increasing food ration on the relative growth rates of dominants and subordinates. Based on the allometry of juvenile salmonid growth (e.g., Rosenfeld and Taylor 2009), we expect that (i) relative growth rates of dominants will decrease as fish increase in size and approach the capacity of their habitat, (ii) enhanced ability of the dominant to monopolize resources will increase the disparity in growth between the dominant and subordinates, and (iii) size disparity within a dominance hierarchy will promote higher growth of subordinates because of the lower energetic requirements of smaller individuals.

Materials and methods

Experimental fish

Twenty-four young of the year (YOY) wild steelhead trout and 24 YOY coho salmon were captured from McNab Creek, Port Mellon, British Columbia, Canada (Universal Transverse Mercator (UTM) 471738E 5490574N), on 27 August 2009 using a combination of dip netting, minnow trapping, and seining. The fish collected from McNab Creek are presumed to be of wild origin because there is no history of hatchery releases into the creek. Wild steelhead and coho salmon averaged 0.53 ± 0.19 g (± standard deviation (SD)) and 1.99 ± 0.64 g in mass and 3.93 ± 0.40 cm and 5.72 ± 0.58 cm in fork length (FL), respectively, at time of collection. Fish were transported to Chapman Creek (where the experimental channels were located) and individually marked with visible implant elastomers (Northwest Marine Technology, Inc., Shaw Island, Washington) so that growth of individuals could be monitored. Average water temperature was 14.0 ± 1.4 °C for the first growth interval (interval 1; 29 August 2009 – 24 September 2009) of the experiment and 9.7 ± 1.8 °C for the second growth interval (interval 2; 24 September 2009 – 7 October 2009).

Experimental setup

This experiment was set up as part of a broader study to assess differences in growth and metabolism between juvenile steelhead trout and coho salmon (Van Leeuwen et al. 2011); however, it became apparent that allometric patterns in growth over time, as described below, could provide unique insight into the costs and benefits of dominance within hierarchies. In addition, differences in initial body size between species (steelhead are much smaller than coho...
Table 1. Average mass and food rations (estimated percentage of satiation diet) of juvenile steelhead (Oncorhynchus mykiss) and coho salmon (Oncorhynchus kisutch) in the high and low food treatments during intervals 1 and 2 of the growth experiment.

<table>
<thead>
<tr>
<th>Food ration</th>
<th>Average mass (g; ±SD)</th>
<th>Satiation diet (%; ±SD)</th>
<th>Blood worms added (% body mass·day⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Steelhead</td>
<td>Coho</td>
<td>Steelhead</td>
</tr>
<tr>
<td>Interval 1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>High</td>
<td>0.55±0.01</td>
<td>2.09±0.04</td>
<td>100±0</td>
</tr>
<tr>
<td>Low</td>
<td>0.52±0.07</td>
<td>1.90±0.01</td>
<td>100±0</td>
</tr>
<tr>
<td>Interval 2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>High</td>
<td>1.35±0.17</td>
<td>2.82±0.15</td>
<td>100±0</td>
</tr>
<tr>
<td>Low</td>
<td>1.35±0.13</td>
<td>2.26±0.08</td>
<td>22±6</td>
</tr>
</tbody>
</table>

Note: SD (standard deviation) equal to zero indicates that modeled satiation in all replicate channels equaled or exceeded 100%. Suppl.+, supplemented with natural invertebrate drift collected from drift nets; 1/2 Ambient, half of the inflow water volume entering the channels was filtered through a 250 µm mesh net to reduce invertebrate drift. N/A, frozen blood worms were not supplemented during interval 1.

because of their later fry emergence date) allowed us to consider how size of fish relative to the capacity of their habitat affects growth trajectories in dominance hierarchies.

The experiment was conducted in 12 outdoor artificial stream channels installed in a side channel of Chapman Creek, Sechelt, British Columbia, Canada (UTM 448100E 5478100N). Channels were constructed and designed in a similar fashion to those described in Rosenfeld et al. (2005), although at a larger scale. Channels were 2.5 m long, 1 m wide, and 60 cm deep and constructed out of 6.4 mm plywood coated with epoxy resin and lined with plastic sheeting to prevent leakage. Channel boxes were supported above the stream on wooden frames arranged in three rows of four channels in a staircase design (for schematic, see Rosenfeld et al. 2005). Water from each channel spilled into a smaller box that was 60 cm long, 1 m wide, and 60 cm deep to dispel turbulence before water entered the next experimental channel downstream. A 6 mm mesh screen at both ends of each channel prevented fish escape. Water was gravity fed into the channels through an intake pipe from Chapman Creek and a header box upstream of the channels. Flow through each of the 12 channels was held constant throughout the experiment at approximately 7.5 L·s⁻¹. Stream channels were filled with equal amounts of 2 to 4 cm diameter river-washed gravel arranged so that each channel had an upstream riffle (average water depth ± SD, 6 ± 2 cm; average velocity, 16 ± 6 cm·s⁻¹) and a downstream pool (maximum depth, 26 cm; average water depth, 20 ± 5 cm; velocity, 3 ± 2 cm·s⁻¹) of approximately equal lengths. Habitat in each channel was characterized by measuring velocity and depth with a Marsh–McBirney model 2000 flowmeter at four points along 10 transects spaced 20 cm apart in each channel. Channels were flowing for approximately two weeks prior to stocking fish to allow colonization of aquatic invertebrates and were covered with a coarse plastic net to protect against avian predators.

Two 45 cm × 30 cm Plexiglas panels coated with reflective film were installed above each channel to allow observations of fish from a concealed location. Covered canopies of dark plastic sheeting were constructed between the channels to maximize the reflective properties of the film and allow better viewing of fish in the stream channels.

Experimental design
Experimental treatments included two levels of food rations (high and low) for each of two salmonid species (juvenile coho and steelhead) applied over two sequential time intervals (26- and 14-day durations, respectively) from 29 August 2009 – 7 October 2009. This allowed us to assess the allometry of growth within dominance hierarchies under contrasting degrees of food limitation (habitat capacity) determined by food abundance. Experimental treatments varied in length due to time constraints and concern that the onset of cooler water temperatures during interval 2 might confound growth relationships because steelhead are somewhat more cold-adapted than coho. Fish were weighed at the end of each time interval to track the allometry of growth as fish increased in size and became increasingly limited by the capacity of the channel habitat. Food levels in interval 2 were increased in the high food treatment to assess how the benefits of dominance responded to increased food ration. Because coho hatch approximately 4–6 weeks earlier than steelhead, coho juveniles are larger at any given time so that the primary contrast of interest between species in this experiment involved initial body size, rather than intrinsic differences in growth between species.

Four juvenile steelhead or coho were systematically assigned to each of the 12 channels for a density of 1.6 fish·m⁻². In interval 1, the high food treatment involved supplementing the first and fourth rows of channels (n = 6) with natural invertebrate drift collected from drift nets set overnight in Chapman Creek. To increase contrast in food availability, invertebrate drift in the low food treatment (second and third rows of channels, n = 6) was reduced by filtering half of the inflow water volume entering the channels through a 250 µm mesh net. To determine food ration as a percentage of satiation in the two treatments, we used a bioenergetic model for juvenile steelhead and coho salmon (Sullivan et al. 2001) to back-calculate estimated consumption based on observed growth at the end of each time interval (Table 1).

Because of their small initial size, steelhead at high and low food rations were growing at a rate consistent with satiation (i.e., experiencing maximum growth rates) in interval 1, whereas coho at high and low food rations were growing at an estimated 84% and 57% of satiation, respectively (Table 1). During interval 2, the high food treatment was increased further by supplementing drift with blood worms (frozen chironomids) to meet the increasing demand of growing fish and ensure that the high food treatment would be at satiation. During interval 2, steelhead and coho at high food ration...
were estimated to be growing at a rate consistent with satiation, whereas coho and steelhead on low food ration were growing at 63% and 22% of satiation, respectively (Table 1).

Invertebrates for supplementing prey abundance in the high food treatments were collected three times daily by lifting 12 drift nets placed in the side channel of Chapman Creek; this level of addition was observed to increase invertebrate drift approximately three to four times above ambient in an earlier study (Rosenfeld et al. 2005). Invertebrates and blood worms were then incrementally added in equal amounts to the head of each of the high food ration channels (n = 6) by overflow from inclined buckets receiving water from a 12V bilge pump. Blood worms were boiled for 10–20 min and refrozen prior to use to prevent unintentional introduction of exotic pathogens into receiving waters. All but two steelhead trout were recovered at the end of the experiment.

Dominance rank of fish in the stream channels were assigned based on final size of fish. Juvenile salmonids are known to be extremely aggressive and quickly establish dominance hierarchies (Reinhardt 1999; Sloman et al. 2000, 2001) that are almost exclusively size-based (Chapman 1966; Nakano 1995; Young 2003). Size only becomes a poor predictor of dominance when fish are nearly size-matched, and then factors such as prior residence or outcome of aggressive encounters become important (Sloman and Armstrong 2002). Each channel was deliberately stocked with a similarly wide range of fish sizes (average mass and fork length of steelhead and coho were 0.53 ± 0.19 g and 1.99 ± 0.64 g and 3.93 ± 0.40 cm and 5.72 ± 0.58 cm, respectively). The average difference between the smallest and largest fish in each channel for steelhead and coho was 0.47 ± 0.12 g and 1.61 ± 0.22 g, making it reasonable to infer that dominance was well correlated with body size. Casual observations during the experiment confirmed strong dominance hierarchies within the stream channels, with the largest fish typically defending the most upstream position, as noted during more systematic behavioural observations in earlier experiments in a similar study system (Rosenfeld et al. 2005).

Modeling effects of prey abundance and size disparity on growth in a dominance hierarchy

We used the bioenergetic model of Sullivan et al. (2001; set at 15 °C) to assess the effects of size disparity and food abundance on relative growth rates of juvenile coho in a simplified dominance hierarchy of three individuals occupying a hypothetical stream pool. The purpose of this modeling was not to precisely mimic conditions in the experimental channels, but rather to demonstrate the interactive effects of size disparity and food availability on relative growth in a dominance hierarchy and to test whether varying both food abundance and size disparity can generate similar trends to those observed in the channel experiments. For simplicity of modeling, a hierarchy with only three fish was used. Size disparity had three levels: low (range of fish mass 3.6–4.0 g), intermediate (2.5–4.0 g), and high (0.7–4.0 g). Food was assumed to enter the pool from an upstream riffle at a delivery rate of either 0.10 (high food ration) or 0.03 (low food ration) g dry mass per day. This would simulate, for example, differences in prey abundance among physically identical pools that differed only in rate of invertebrate drift (e.g., Hansen and Closs 2009). The high food level represents a relatively high capacity habitat, with sufficient energy to generate moderate growth for a 4.0 g coho, whereas the low food ration scenario is below maintenance for a 4.0 g fish. Modeled energy intake, fish size, and growth were within the range observed in the stream channel experiments. Experimental studies have shown that capture success of dominants over subdominants ranges around 60%–75% for drifting prey (e.g., Rincon and Grossman 2001; Hazelton and Grossman 2009); we therefore assumed that each fish in the dominance hierarchy consumed 60% of upstream prey at a 90% capture efficiency (Hill and Grossman 1993), with the remaining prey available to the next fish downstream.

This basic modeling incorporates only the effects of dominants on resource monopolization and the allometric effects of body size on energy demand and growth and ignores the effects of differential activity costs, stress, or aggressive interactions in dominance hierarchies. However, the purpose of this exercise was to test whether the allometry of energy supply and growth within hierarchies was sufficient to account for variation in the benefits of dominants, rather than to precisely reproduce observed growth rates.

Data analysis

Daily instantaneous growth rates of fish (%·day−1) were calculated as \[ \left[ \log_{10}(\text{final mass}) - \log_{10}(\text{initial mass}) \right] / \text{duration} \times 100 \] (Ricker 1975). Absolute growth rate was calculated as (final mass – initial mass)/duration.

The slope of the absolute growth (g·day−1) vs. individual mass (average mass over the growth interval) relationships was used as a conservative index of the benefits of dominance in each treatment. A growth–body mass relationship with a positive slope indicates that growth of dominants exceeds that of subordinate fish, whereas a negative slope would indicate lower absolute growth of dominant fish despite their competitive advantage. We used absolute rather than relative growth (% body mass·day−1; Fig. 1) because relative growth systematically declines with fish size even at maximum growth rates.

**Fig. 1.** Instantaneous growth rate vs. average mass (interval 1) for juvenile steelhead (*Oncorhynchus mykiss*) (squares) and coho (*Oncorhynchus kisutch*) (circles) salmon in supplemented – high food ration (solid symbols) and nonsupplemented – low food ration (open symbols) stream channels.
We tested for the effects of food, species, channel identity, and individual fish mass (average mass over the growth interval) on absolute growth using analysis of covariance (ANCOVA), including mass × food and species × food interaction terms. Intrinsic species effects should be manifest as differences in average growth between species (i.e., intercepts or elevations of lines in Figs. 1 and 2); any species effect related to differences in initial body size should be represented by the mass covariate. If a significant interaction was found, coho and steelhead data were separated and analyzed independently. Interaction terms and independent variables that were not significant at $p < 0.05$ were removed from the model. All data passed assumptions of normality and homogeneity of variance. Analysis was conducted using R version 2.8.1 statistical software (www.r-project.org/).

To assess the effects of food ration and size disparity on growth in our modeling scenarios, we also used the slope of the relationship between absolute growth and mass as a metric of the benefits of dominance. We modeled the relationship between absolute growth and mass as a function of food level (high or low) and size disparity within each three-fish hierarchy (three levels) using ANOVA. We included food × mass and size disparity × mass interaction terms to evaluate whether the slope of the relationship between growth and mass (i.e., the benefits of dominance) was sensitive to food level or differences in size among fish in a hierarchy.

**Results**

**Instantaneous growth rate (interval 1)**

We found that smaller fish had a higher instantaneous growth rate ($F_{[4,41]} = 8.21$, $p = 0.007$; Fig. 1), as expected based on the allometry of growth (i.e., maximum growth declines allometrically with body size). Steelhead had a higher growth rate than coho ($F_{[4,41]} = 34.9$, $p < 0.001$; Fig. 1). There was also a significant mass × food interaction ($F_{[4,41]} = 4.11$, $p = 0.049$; Fig. 1), with smaller fish (steelhead) showing no difference in instantaneous growth rate at high and low food rations ($F_{[3,18]} = 0.66$, $p = 0.43$), whereas larger fish (coho) growth was significantly reduced on the low food ration.

**Absolute growth rate (interval 1)**

There was no significant effect of channel identity on absolute growth rate ($F_{[5,40]} = 0.68$, $p = 0.41$), and therefore it was dropped from the analysis. There was a significant interaction between body mass and food with species combined ($F_{[5,40]} = 6.20$, $p = 0.02$; Fig. 2a), indicating that the effect of body mass on growth varied with food ration. For steelhead (smaller on average than coho), there was no difference in growth at high and low food levels ($F_{[3,18]} = 0.17$, $p = 0.68$), and a positive slope indicated that dominants grew faster at both food rations. However, analysis of the coho data separately revealed an interaction between body mass and food ($F_{[3,20]} = 5.00$, $p = 0.04$), indicating that dominant (larger) coho at high food ration experienced higher absolute growth than subordinates (positive slope), whereas dominant coho had lower absolute growth at low food ration (negative slope; Fig. 2a).

**Interval 2**

As with interval 1, there was no significant effect of channel identity on absolute growth rate ($F_{[6,37]} = 0.19$, $p = 0.66$), and therefore it was again dropped from the analysis. There was a significant interaction between mass and food level ($F_{[4,37]} = 39.96$, $p < 0.001$; Fig. 2b) across the entire data set. Although steelhead grew faster on the high food ration (Fig. 2b), slopes were similarly positive at both high and low food rations ($F_{[3,17]} = 0.12$, $p = 0.73$), but this was not the case for coho. Analysis of the coho data separately revealed a significant interaction between food and mass ($F_{[3,18]} = 24.58$, $p < 0.001$); the positive slope at the enhanced high food level indicated that larger (dominant) coho did better than subordinates when food was abundant, but the relationship was again negative at low food ration, with the largest dominant fish exhibiting the lowest absolute growth (Fig. 2b).
largest fish lost mass). In contrast, the increase in food ration in the high food treatment (relative to interval 1) increased the slope of the coho growth line at high food ration (Fig. 2b), despite the increase in average fish size.

**Modelling effects of prey abundance and size disparity on growth in a dominance hierarchy**

There was a significant effect of size disparity on modeled growth ($F_{[2,10]} = 17.8, p = 0.001$), and a significant size disparity by mass interaction ($F_{[2,10]} = 13.9, p = 0.001$), indicating that the slope of the relationship between growth and body mass varied with size disparity in the dominance hierarchy (Fig. 3). Similar to the channel growth experiments, there was also a significant interaction between body mass and food ($F_{[1,10]} = 16.3, p = 0.002$), indicating that the effect of dominance on growth varied with food ration. As predicted, the benefits of dominance (a steeply positive growth—mass relationship) were most pronounced at high food ration and when fish in the dominance hierarchy were similar in size. The relative benefits of dominance were reversed in the low food ration scenario with the greatest size disparity (Fig. 3c), where the smallest fish in the hierarchy was able to achieve positive growth, but not the dominant.

**Discussion**

By controlling channel structure and fish density in outdoor artificial stream channels, we were able to examine how fish size and the allometry of growth affect the benefits of dominance in competitive hierarchies. We show that conflicting results among correlates of dominance in the literature are not unexpected but are the outcome of allometric effects of body size on energy requirement and absolute growth of fish in a dominance hierarchy, which depend on habitat capacity and the ability of dominant fish to defend preferred feeding territories.

Consistent with expectation, we found that dominant fish experienced higher growth rates than subordinates when food was abundant. However, at low food ration (low habitat capacity), large juveniles (i.e., coho) clearly demonstrated a negative relationship between absolute growth rate and dominance, whereas subordinates achieved higher absolute growth rates. This result can be attributed to the higher net energetic requirement of larger dominant fish compared with smaller subordinates, which have a lower absolute energy requirement and per-capita food consumption allowing them to achieve greater growth on a smaller food ration. This interpretation is supported by our simple modeling scenarios, which demonstrate that the benefits of dominance (i.e., higher growth) can be reversed if the dominant is large relative to the capacity of the habitat and size disparity in the dominance hierarchy is substantial.

The ability of smaller fish to grow at a lower absolute food ration was validated by near-maximal growth of smaller fish (i.e., steelhead) at food rations that were inadequate to satiate larger coho. Steelhead trout were very small relative to channel size during interval 1, similar to recently emerged salmonids. Steelhead were able to achieve equal and near-maximal growth at both low and high food rations in interval 1 due to their small size and low net energetic requirement relative to channel habitat capacity. Presumably, had steelhead been allowed to grow large enough to approach the capacity of the stream channels, growth of dominant steelhead would also have declined below that of subdominants, as with coho.

An earlier study (Rosenfeld et al. 2005) investigating the effects of fish density and food availability on growth of juvenile coho salmon found patterns of growth at high and low food levels similar to those reported here, but with key differences. In particular, the smallest fish in a hierarchy experienced near-zero growth despite their lower energy requirements. This was likely due to narrower channels in the 2005 study that allowed dominants to intercept a higher proportion of available prey (e.g., Piccolo et al. 2007), and much higher densities of fish (up to 10 fish·m⁻²). Increased density of fish should decrease growth rates of subordinates as upstream predation will act as a filter to reduce delivery of drift to downstream fish (Elliott 2002), and variation in den-
sity between habitats and streams should also contribute to variation in relative growth within hierarchies.

Both fish density and size disparity will also affect the intensity of behavioural interactions and, therefore, associated costs and benefits of rank in a dominance hierarchy (Metcalfe 1986). For instance, the ability of dominants to monopolize resources may decline with density despite increased aggression, and a greater size disparity could facilitate greater behavioural suppression of subdominant growth. However, the allometry of growth alone appears sufficient to account for the broad patterns of size-based growth in dominance hierarchies observed in this study, despite the potential for the intensity of behaviour to modify the costs and benefits of dominance.

Our data also suggest that a larger size disparity within a dominance hierarchy will promote higher growth of subdominants because of the lower energetic requirement of smaller individuals. This suggests that an extended hatch time of juvenile salmonids (resulting in differential fish size) could reduce intraspecific competition and increase cohort production, provided that growing fish can serially recruit to new habitats that deliver more energy as they grow (Armstrong 1997), thereby releasing subdominants from competition. When opportunities for recruitment to new habitat are limited (i.e., in small streams where deeper habitat for larger fish is scarce), dominant fish will continue to suppress the growth of subordinates, even as their own growth declines as they approach the limits of their habitat (Rincon and Lobón-Cerviá 2002; Armstrong and Nislow 2006).

A number of studies have failed to find consistent positive correlations between dominance and growth or other physiological diagnostics of condition in wild fish. Dominants or larger individuals are expected to have higher SMR (prior to agonistic encounters), growth (Cutts et al. 1999; Alvarez and Nicieza 2005), and lower cortisol levels, but studies have shown that dominant or larger fish in the wild may exhibit lower growth (Harvey et al. 2005; Hansen and Closs 2009) and higher cortisol levels (Sloman et al. 2008) than subordinates. This study clearly shows that the relative benefits of dominance depend on the size of the dominant relative to the capacity of the habitat, which will depend on prey abundance and the configuration of the habitat (e.g., pool width or depth, length of the upstream riffle; Hansen and Closs 2009). Similarly, relative growth rates of subordinates (and therefore their SMR and stress levels) will depend on their size relative to prey availability, as well as the density of upstream conspecifics and the ability of the dominant to monopolize resources. Realized energy intake and growth of subordinates will also influence decisions to remain in a hierarchy or move in search of more profitable microhabitats. The greater tendency of larger subordinates to move (Kahler et al. 2001; Hansen and Closs 2009) suggests a response to rapidly declining growth as larger fish approach the capacity of their habitat, as we observed in our coho low food treatments.

Unlike most laboratory environments, natural stream channels encompass a variety of habitats that differ in their ability to support fish production. Even among a single habitat class such as pools, individual habitat units differ greatly in the energy available to drift-feeding fish and the number and size of fish that can be supported (e.g., Hansen and Closs 2009). Given these natural sources of variation in the expected benefits of dominance, random sampling of fish from different habitats in a stream would not necessarily generate clear relationships between dominance and growth or other physiological indices of performance. Although a number of studies have explored the costs and benefits of dominance, they have not explicitly considered how the allometry of fish growth relative to habitat capacity can reverse the expected growth and condition of dominant and subordinate fish. Here we show that allometric effects of body size on relative growth rate in dominance hierarchies can account for much of the discrepancy among fitness-related correlates of dominance between fish in the wild and in the laboratory and demonstrates the importance of considering ecological processes within the context of a natural habitat template.

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