How fish cope in a world of feast and famine: behavioral and physiological adaptations to ecological heterogeneity

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Abstract

How fish cope in a world of feast and famine: behavioral and physiological adaptations to ecological heterogeneity

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Predator-prey interactions are patchy in space and time due to a variety of interactions between predator behavior, prey behavior, and landscape heterogeneity. To survive in a patchy world, predators must capitalize on high quality foraging opportunities and store energy to survive periods of resource scarcity. In this dissertation, I explore the behavioral and physiological adaptations that enable predators to survive and thrive in a world of feast and famine. I begin with a broad analysis that asks: just how patchy are the foraging opportunities of predatory fishes? Since variation in foraging opportunities is extremely difficult to measure in the wild, I instead look to the digestive systems of fish, and explore what levels of variation would have led natural selection to favor the observed levels of excess digestive capacity seen across ~40 species of fish. I discovered high levels of excess digestive capacity that suggest variation in foraging opportunities may be 10-times higher than ecologists typically assume. This indicates that the ability of predators to exploit pulses of food is likely critical to the survival of individuals and the productivity of populations. In the subsequent chapters, I conduct

case studies in the Bristol Bay region of Alaska to explore how animal behavior and physiology interact with landscape heterogeneity to influence the ability of predators to exploit an annual resource pulse.

My field research explores the foraging ecology of juvenile coho salmon as they exploit pulsed sockeye salmon subsidies in thermally heterogeneous riverscapes. In Chapter 2, I explore how differences in water temperature among streams influence the potential for age-zero coho salmon to grow large enough to consume sockeye salmon eggs. The research in Chapter 3 occurs at the scale of a single stream, Bear Creek, and explores how coho salmon foraging behavior copes with trade-offs in the spatial distribution of thermal and trophic resources. I find that individuals actively exploit habitat heterogeneity to increase their digestive capacity, exhibiting feeding forays into cold habitats where sockeye salmon spawn, but spending the majority of their time residing in warmer habitats that provide higher digestive capacity. In Chapter 4, I explore how spatial patterns of water temperature vary at inter-annual timescales due to the episodic nature of summer precipitation events, and how the foraging behavior of juvenile coho salmon responds to a shifting mosaic of water temperature in Bear Creek. I find that precipitation events during wet summers trigger high flows that eliminate warm water habitat in the upstream thalweg of Bear Creek, but generate new warm water habitat in off-channel areas downstream. The spatial distribution of juvenile coho salmon tracked warm water habitat as it shifted across space, suggesting that their behavioral thermoregulatory behavior persists across highly variable flow conditions by exploiting the portfolio of habitat options provided by an intact floodplain.

In summary, this dissertation seeks to understand how juvenile coho salmon (in particular) and aquatic predators (in general) capitalize on prey resources that are distributed heterogeneously in space and time. My research explores the interplay between intrinsic factors of behavior and physiology, and extrinsic factors of habitat conditions and their patterning across space and time.

Chapter 1: Excess digestive capacity in predators reflects a life of feast and famine

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Summary

A central challenge for predators is achieving positive energy balance when prey are spatially and temporally heterogeneous. Ecological heterogeneity produces evolutionary trade-offs in the physiological design of predators because the ability to capitalize on pulses of food abundance requires high capacity for food-processing yet maintaining such capacity imposes energetic costs that are taxing during periods of food scarcity[1,2]. Recent advances in physiology show that when variation in foraging opportunities is predictable, animals may adjust energetic trade-offs by rapidly modulating their digestive system to track variation in foraging opportunities[1]. However, it is increasingly recognized that foraging opportunities for animals are unpredictable[3], which should favor animals that maintain a capacity for food-processing that exceeds average levels of consumption (loads)[2,4]. Despite this basic principle of quantitative evolutionary design, estimates of digestive load: capacity ratios in wild animals are virtually non-existent[1]. Here we provide the first extensive assessment of load: capacity ratios for the digestive systems of predators in the wild, compiling 639 estimates across 38 species of fish. We found that piscine predators typically maintain the physiological capacity to feed at daily rates 2-3-times higher than what they experience on average. A numerical simulation of the trade-off between food-processing capacity and metabolic cost suggests the observed level of physiological opportunism is profitable only if predator-prey encounters, and thus predator energy budgets, are far more variable in nature than currently assumed.

Main Text

Predation opportunities for animals in the wild are distributed heterogeneously in space and time due to a variety of interactions between predator behaviour[5] (e.g., how they allocate time to foraging, avoiding predators, and finding mates), prey behaviour[6], and heterogeneity in the physical attributes of habitats where predator-prey interactions occur[7,8]. As a result, encounter rates between predators and prey in their natural habitats are exceedingly difficult to estimate[6] and may be far more heterogeneous than assumed. To cope with such ecological heterogeneity, predators employ behavioural and physiological tactics that allow them to store energy when food is plentiful, and utilize such reserves when food is scarce. For predators that store energy internally (e.g., as fat reserves or somatic growth), physiological constraints on food-processing may limit rates of energy storage[9] and compensatory growth[10] and thus the potential to capitalize on pulses of food. To thrive in an environment where foraging opportunities vary widely but unpredictably, predators should maintain physiological opportunism and exhibit maximum capacities for food-processing that considerably exceed the average capacity required.

Acquiring energy from prey is a serial process that spans from foraging (attacking, handling, and ingesting prey) to assimilation (digesting food and absorbing nutrients) [11]. In a homogeneous world the most economic pathway would exhibit symmorphosis where the maximal processing rate at each stage is equal to the average input rate (load) from the prior stage[12]. However, if the load at any stage varies in time, performance at that stage should exhibit excess capacity, such that the maximal rate exceeds the mean and the system can accommodate spikes in load[4]. Surprisingly, the role of excess capacity along the food-to-fuel pathway is poorly understood. It is known that parts of the foregut (e.g., the oesophagus, stomach, or other comparable structures) can act as food storage reservoirs, enabling predators to ingest prey faster than they can process it[13,14]. This excess capacity for feeding accommodates short-term variation in prey encounters[14] but it does not facilitate sustained increases in energy gain, which predators would require in order to build energy reserves or achieve compensatory growth. To sustain increased consumption rates predators require excess capacity for assimilation (i.e., digestion and absorption). Current knowledge of excess capacity in the digestive system is primarily limited to measurements at the cellular level[2], and estimates of load:capacity ratios for integrated rates of assimilation are virtually non-existent in wild animals. Measurements of excess assimilation capacity are important for both physiologists, who seek to evaluate symmorphosis (or lack thereof) across the energy intake chain, and ecologists, who lack reliable data to characterize the variation in foraging opportunities experienced by predators in the wild. Here we quantitatively assess how daily variation in foraging opportunity should affect the profitability of excess assimilative capacity, and use our results to interpret observed load:capacity ratios from animals in the wild.

Predators require excess assimilative capacity to capitalize on large pulses of prey abundance as reflected in the right tail of the distribution of predator foraging opportunities[8,14]. However, increasing assimilative capacity also increases the energetic costs of physiological maintenance and locomotion[1]. We developed a simple numerical simulation to characterize this trade-off and explore its response to the underlying distribution describing daily variation in foraging opportunity. We simulated variation in daily foraging opportunities using a gamma distribution with a fixed arbitrary value for the mean, but different coefficients of variation [CV: (standard deviation/mean)·100] (see supplementary material) to simulate different levels of variability in the environment. A type I functional response[15] modeled how assimilative capacity

(*Cmax* : the maximum amount of food that can be consumed in one day) determines the daily food consumption, *C*, that a predator derives from a daily foraging opportunity, *x*:

$$(1) \qquad C(x) = \begin{cases} x \; if \; x < C\max \\ C\max \, if \; x \geq C\max \end{cases}$$

The expected consumption rate (energy·day^{-1}) for an individual with a specified *Cmax* and gamma-distributed variation in daily foraging opportunity is:

$$(2) \qquad E(C\max) = \int_0^\infty C(x)g(x|k,\theta)dx$$

where *C(x)* is the type I functional response of equation (1), and *g(x)* is the gamma distribution with shape and scale parameters (*k* and *θ*) varied to produce specified levels of mean and CV. The load: capacity ratio for assimilation is equal to the expected consumption rate divided by *Cmax* and its inverse is synonymous with excess capacity.

$$(3) \qquad Load\text{: } Capacity\ ratio = E(C\max)/\ C\max = 1/excess\ capacity$$

The net energetic profit (*N*) is the energy remaining after gains from consumption are paid to maintenance and activity costs, *M*.

$$(4) \qquad N = E(C\max) - M$$

The energetic costs associated with increased assimilative capacity are poorly described and likely vary among taxa. We model *M* as a constant fraction, *r*, of *Cmax* (see supplementary material):

$$(5) \qquad M = r \cdot C\max \ldots 0 < r < 1,$$

thus

$$(6) \qquad N = E(C\max) - r \cdot C\max$$

In our analysis, we used numerical simulation to calculate the load:capacity ratio that maximized the net profit function (eq. 6), given the CV in daily foraging opportunity and the cost of the gut.

The optimal load:capacity ratio for assimilation decreased with increasing variation in foraging opportunity, but did not exhibit substantial levels of excess capacity until the CV was very high, indicating strong right-skew in the distribution of foraging opportunities (Fig.1, Fig. S1). For example, the optimal load: capacity ratio reached ~0.4 when the CV in foraging opportunity ranged from 70-150%, depending on the costs of maintaining excess capacity (Fig. 1e). This suggests that, in order for integrated rates of assimilation to exhibit levels of excess capacity seen in many other biological structures[2] (*e.g.,* load:capacity ratios <0.5), predator-prey encounters would need to be extremely heterogeneous in time.

To assess the variation in foraging opportunities that predators experience in nature, we compared our model scenarios to assimilative load:capacity ratios estimated for piscine predators in the wild. We compiled 639 estimates of mean daily consumption rate in fishes. The estimates were calculated from bioenergetics models that integrate across field measurements of growth and express consumption relative to maximum physiological rates. This bioenergetics framework[16,17] (described in supplementary material) has been parameterized for different species through laboratory studies that measure the effects of water temperature and body mass on both metabolism and *Cmax,* the daily consumption rate observed under *ad libitum* feeding. *Cmax* is determined by assimilative capacity[18] and corresponds well to the consumption rates of wild fish in conditions where food is unlimited[19]. The model uses field data on predator growth achieved over a defined time period, diet composition and quality, and water temperature to estimate the proportion of *Cmax* (p) that balances an energy budget where growth is surplus energy after energetic gains from consumption are paid to metabolism, excretion, and specific dynamic action. Thus, p represents the load: capacity ratio for assimilation. We searched research databases for all papers citing this bioenergetics model and compiled all estimates of p

recorded in the wild (Table S1). We grouped p estimates by population (unique combinations of species and publication, n=66). The mean length of time over which p was estimated was 208 days ($s.d.$= 143 days).

Across 66 populations from 38 species, the median p was 43% ($s.d.$= 16%), indicating a load:capacity ratio for assimilation of 0.43. The distribution of p was right-skewed and similar in shape whether grouped by population or not (Fig. 2). Populations from marine (n=11), lake (n=49), and stream (n=6) environments did not exhibit significantly different load:capacity ratios (Kruskal-Wallis test: P=0.10, DF=2) and less than 5% of populations exhibited load:capacity ratios greater than 0.8. Among the >60% of populations that exhibited load: capacity ratios less than 0.5, all functional guilds of predators were represented, including planktivores, benthivores, and piscivores.

Digestive machinery is expensive[1,20], so why do piscine predators maintain the physiological capacity to feed at daily rates that are 2-3-times higher than what they achieve on average? Our numerical simulation demonstrates that such low ratios of assimilative load: capacity become energetically profitable when the distribution of daily foraging opportunities is highly heterogeneous (i.e., right-skewed; Fig. 1, Fig. S1). This suggests that episodes of gorging and fasting are common in fishes, and occur not only in ambush predators that pursue large prey[21], but also in predators that feed on insects and zooplankton. These results question common assumptions regarding the variance in foraging opportunities experienced by predators in the wild.

Foraging models frequently simulate variation in a predator's feeding opportunities by drawing prey encounters from the Poisson distribution[21,22], which exhibits equal mean and variance (λ). Under most configurations of the Poisson (e.g., if λ >~3), values greater than twice the mean have extremely low probabilities (0-2% of occurrences). Thus, foraging models frequently simulate a world in which predators would almost never take advantage of the excess assimilative capacity that we have shown in fishes (i.e., median capacity=2.3X expected load). This suggests that the feeding opportunities of piscine predators, and perhaps many others, are more heterogeneous than has been appreciated in ecology.

In the last decade, three meta-analyses have concluded that lizards[23], fish[24], birds, and mammals [25] rarely exhibit negative energy budgets at daily timescales, based on observations that predators rarely have completely empty stomachs[23,24], or that their integrated rates of energy gain exceed losses at seasonal to annual timescales[25]. In our analysis, we found that piscine predators likely experience foraging opportunities that are distributed extremely patchily in time, such that the median population would actually spend 18-53% of days feeding at levels that are lower than a typical maintenance ration (~20% of Cmax[17]). This suggests that fishes routinely run negative energy budgets and cautions that prior syntheses of empirical data may have underestimated variability in the daily energy balance of not only fishes, but other taxa as well. Future work should consider how patterns of capacity through the food-fuel-pathway are associated with different strategies of energy regulation. For example, many small birds and mammals hoard food during resource pulses or employ torpor to avoid energy deficits[26]. These mechanisms may stabilize consumption rates and energy budgets enough to make maintaining excess capacity for assimilating food unnecessary, but would likely require increased capacity for handling food.

We have assumed that the assimilative capacity observed in fishes has evolved to optimize energy budgets under trade-offs between the capacity and metabolic cost of the gut. There is widespread evidence that the energetic profitability of the gut has strong fitness consequences[1,20] and that its morphology and function evolve in response to energetic demands[27]. Further, the fishes in our analyses exhibit indeterminate somatic growth that is indeed limited by energy aquisition[28]. Therefore it is reasonable to use an energy maximization model to interpret the function of physiological capacity. The temporal pattern of foraging opportunities may vary among generations such that the optimal level of digestive capacity is not static in time. Our general conclusions are robust to such evolutionary disequilibrium because we found high levels of excess digestive capacity across numerous taxa inhabiting diverse environments. The most parsimonious explanation of these findings is that piscine predators have evolved excess assimilative capacity to profit in a world where binging and fasting are regular occurrences.

Phenotypic flexibility can improve performance if energy budgets vary predictably[1]. For example, female mammals increase digestive capacity during pregnancy, and birds adjust digestive capacity during migration as they alternate between fueling and flight[1]. Although seasonal changes in food abundance may be predictable, pulses of food are frequently both unpredictable and ephemeral[29] causing the performance of consumers to be measured by the guts they possess in the moment and not the ones they can construct days or weeks later (except certain sit-and-wait predators that are capable of rapid intestinal regulation[20]). Similar to the fishes in our analysis, birds may maintain excess capacity for consumption despite their ability to modify gut size over relatively short time-scales[30]. McWilliams and Karasov[30] suggest flexibility in gut size facilitates adaptive responses to long- but not short-term variation in resource abundance. Our meta-analysis and model strongly suggest that predator-prey encounters are patchier than most ecologists assume, that fish run negative energy budgets more frequently than assumed, and that eco-physiology should consider the combined roles of excess capacity and phenotypic flexibility when considering how organisms cope with a world far more heterogeneous than the laboratory or treadmill. The insights derived from our analysis have important implications for models of predator-prey dynamics, community structure, and the stability of food webs, which can be sensitive to heterogeneity in predator-prey interactions[6].

References

1 Piersma, T., and van Gils J.A. *The Flexible Phenotype*. (Oxford University Press, 2011).

2 Diamond, J. Quantitative evolutionary design. *Journal of Physiology-London* **542**, 337-345, doi:10.1113/physiol.2002.018366 (2002).

3 Humphries, N. E. *et al.* Environmental context explains Levy and Brownian movement patterns of marine predators. *Nature* **465**, 1066-1069, doi:10.1038/nature09116 (2010).

4 Gans, C. Momentarily excessive construction as the basis for protoadaptation. *Evolution* **33**, 227-233 (1979).

5 Ritchie, E. G. & Johnson, C. N. Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters* **12**, 982-998, doi:10.1111/j.1461-0248.2009.01347.x (2009).

6 Walters, C. J. a. M., S.J.D. *Fisheries Ecology and Management*. (Princeton University Press, 2004).

7 Kauffman, M. J. *et al.* Landscape heterogeneity shapes predation in a newly restored predator-prey system. *Ecology Letters* **10**, 690-700, doi:10.1111/j.1461-0248.2007.01059.x (2007).

8 Armstrong, J.B, *et al.* Thermal heterogeneity mediates the effects of pulsed subsidies across a landscape. *Ecology* **91**, 1445-1454, doi: 10.1890/09-0790.1 (2010)

9 Klaassen, M., Lindstrom, A. & Zijlstra, R. Composition of fuel stores and digestive limitations to fuel deposition rate in the long-distance migratory thrush nightingale, Luscinia luscinia. *Physiol. Zool.* **70**, 125-133 (1997).

10 Dupont-Prinet, A. *et al.* Physiological mechanisms underlying a trade-off between growth rate and tolerance of feed deprivation in the European sea bass (*Dicentrarchus labrax*). *J. Exp. Biol.* **213**, 1143-1152, doi:10.1242/jeb.037812 (2010).

11 Weiner, J. Physiological limits to sustainable energy budgets in birds and mammals - ecological implications. *Trends in Ecology & Evolution* **7**, 384-388 (1992).

12 Weibel, E. R., Taylor, C. R. & Hoppeler, H. The concept of symmorphosis - a testable hypothesis of structure-function relationship. *Proceedings of the National Academy of Sciences of the United States of America* **88**, 10357-10361 (1991).

13 Kersten, M. & Visser, W. The rate of food processing in the Oystercatcher: Food intake and energy expenditure constrained by a digestive bottleneck. *Functional Ecology* **10**, 440-448 (1996).

14 Essington, T. E., Hodgson, J. R. & Kitchell, J. F. Role of satiation in the functional response of a piscivore, largemouth bass (*Micropterus salmoides*). *Canadian Journal of Fisheries and Aquatic Sciences* **57**, 548-556 (2000).
15 Holling, C. S. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *Canadian Entomologist* **91** (1959).
16 Kitchell, J. F., Stewart, D. J. & Weininger, D. Applications of a bioenergetics model to yellow perch (*perca-flavescens*) and walleye (*stizostedion-vitreum-vitreum*). *Journal of the Fisheries Research Board of Canada* **34**, 1922-1935 (1977).
17 Fish Bioenergetics 3.0 (University of Wisconsin Sea Grant Institute, Madison, Wisconsin, 1997).
18 Elliott, J. M. & Persson, L. Estimation of daily rates of food-consumption for fish. *Journal of Animal Ecology* **47**, 977-991 (1978).
19 Kitchell, J.F., *et al*. Predator-prey dynamics in an ecosystem context. *Journal of Fish Biology*. **45**, 209-226 (1994).
20 Secor, S. M., Stein, E. D. & Diamond, J. Rapid up-regulation of snake intestine in response to feeding - a new model of intestinal adaptation. *American Journal of Physiology* **266**, G695-G705 (1994).
21 Breck, J. E. Foraging theory and piscivorous fish - are forage fish just big zooplankton. *Transactions of the American Fisheries Society* **122**, 902-911 (1993).
22 DeAngelis, D. L. a. G., L.J. *Individual-based models and approaches in ecology. Populations, communities, and ecosystems*. (Chapman and Hall, 1992).
23 Huey, R. B., Pianka, E. R. & Vitt, L. J. How often do lizards "run on empty"? *Ecology* **82**, 1-7 (2001).
24 Arrington, D. A., Winemiller, K. O., Loftus, W. F. & Akin, S. How often do fishes "run on empty"? *Ecology* **83**, 2145-2151 (2002).
25 Jeschke, J. M. When carnivores are "full and lazy". *Oecologia* **152**, 357-364, doi:10.1007/s00442-006-0654-2 (2007).
26 Brodin, A. & Clark, C. Energy storage and expenditure. In: *Foraging,* eds. Stephen, D.S., Brown, J.S., & Ydenberg, R.C. (University of Chicago Press, 2007).
27 Hofmann, R. R. Evolutionary steps of ecophysiological adaptation and diversification of ruminants - a comparative view of their digestive-system. *Oecologia* **78**, 443-457 (1989).
28 Schindler, D. E. & Eby, L. A. Stoichiometry of fishes and their prey: Implications for nutrient recycling. *Ecology* **78**, 1816-1831 (1997).
29 Yang, L. H., Bastow, J. L., Spence, K. O. & Wright, A. N. What can we learn from resource pulses? *Ecology* **89**, 621-634 (2008).
30 McWilliams, S. R. & Karasov, W. H. Phenotypic flexibility in digestive system structure and function in migratory birds and its ecological significance. *Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology* **128**, 579-593 (2001).

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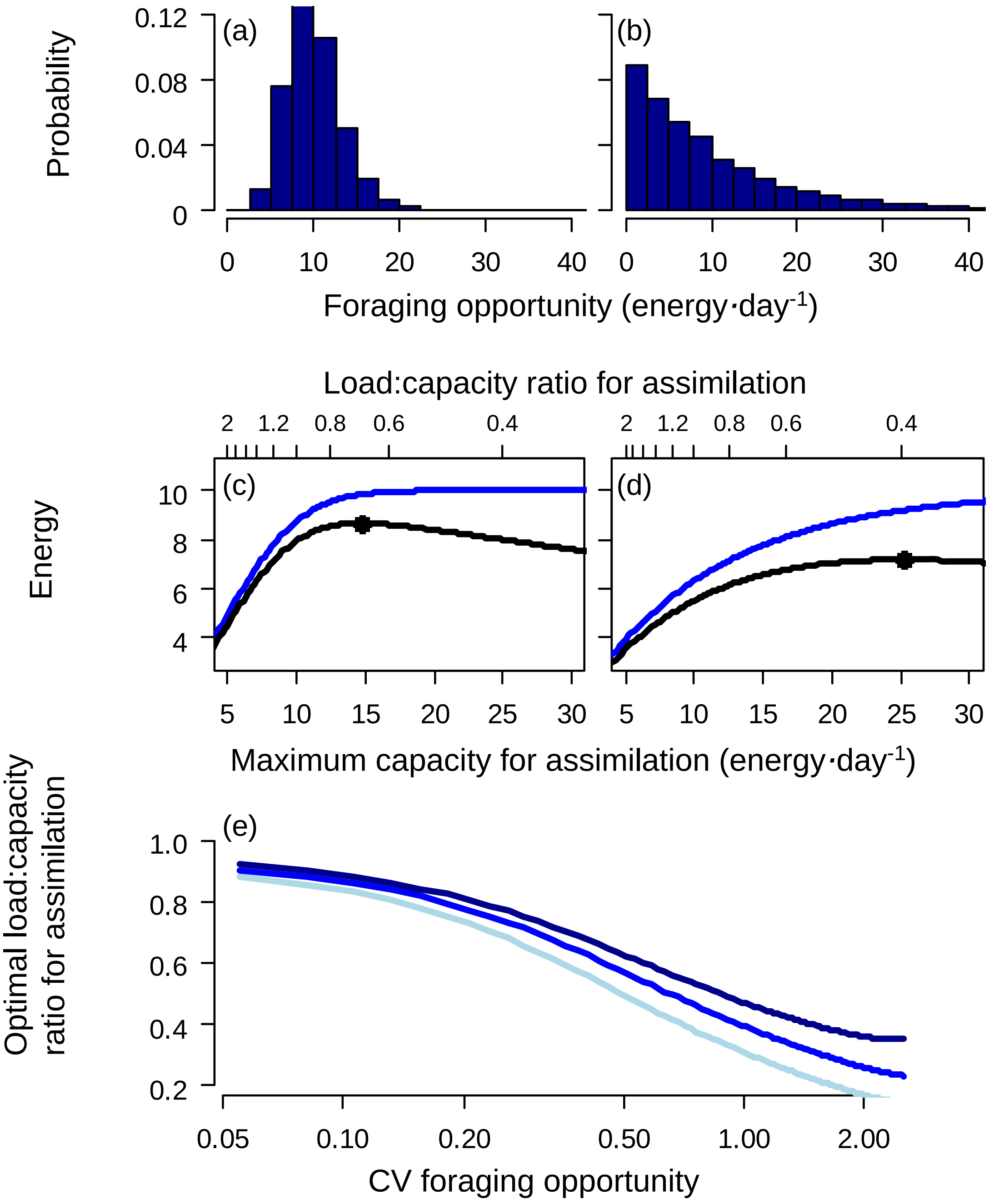
(a)
(b)
Probability
0.12
0.08
0.04
0
0
10
20
30
40
Foraging opportunity (energy·day^{-1})
Load:capacity ratio for assimilation
2
1.2
0.8
0.6
0.4
(c)
(d)
Energy
10
8
6
4
5
10
15
20
25
30
Maximum capacity for assimilation (energy·day^{-1})
(e)
Optimal load:capacity ratio for assimilation
1.0
0.8
0.6
0.4
0.2
0.05
0.10
0.20
0.50
1.00
2.00
CV foraging opportunity

Figure 1. Results from a simulation model exploring the energetic profitability of excess capacity for assimilation (i.e. digestion and absorption) as a function of the daily variation in foraging opportunity. Top row: gamma distributions characterizing two scenarios of ecological heterogeneity that both yield an average of 10 energy units per day in foraging opportunity: (a) variance in daily foraging opportunity is equal to the mean, as from a Poisson distribution (CV=32%, θ=1, k=10). (b) Foraging opportunities are highly right-skewed and exhibit 10 times more variance than a Poisson distribution with similar mean (CV = 100%, θ=10, k=1). Middle Row: a cost-benefit analysis of excess assimilative capacity under the two scenarios of ecological heterogeneity [(c) and (d), panels correspond to distribution displayed above]. Lines represent gross and net energetic gains (blue and black, resp.) resulting from different levels of assimilative capacity (i.e. maximum daily consumption rate). The upper x-axis measures excess capacity in terms of the load:capacity ratio (the mean daily consumption rate relative to the maximum rate). Filled circle on graphs shows where the energetically optimal digestive capacity occurs. Results shown are from the medium cost scenario (see supplementary material for full description). (e) Model results showing the energetically optimal load:capacity ratio as a function of the CV in daily foraging opportunity. Curves depict different cost scenarios (lt. blue: low, blue: medium, dk. blue: high, see supplementary material for full description).

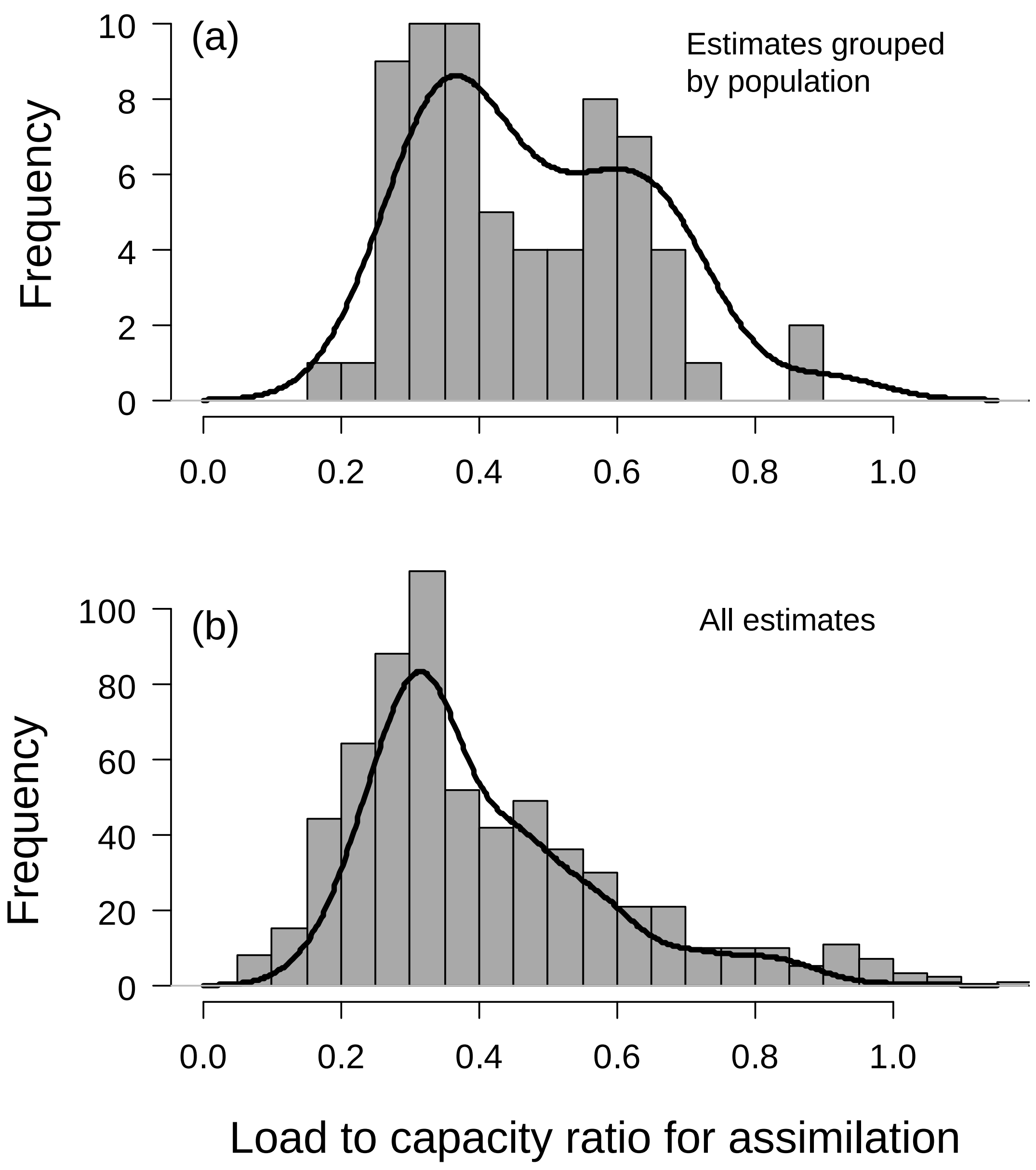
(a)
Estimates grouped by population
Frequency
0
2
4
6
8
10
0.0
0.2
0.4
0.6
0.8
1.0
(b)
All estimates
Frequency
0
20
40
60
80
100
0.0
0.2
0.4
0.6
0.8
1.0
Load to capacity ratio for assimilation

Figure 2. Histograms showing bioenergetics estimates of integrated consumption rates in wild piscine predators, expressed as the assimilative load:capacity ratio (average daily consumption rate divided by physiological maximum). Panel (a): estimates grouped by unique combinations of species and publication (*n*=66). Panel (b): all estimates (*n*=639). Lines show kernel density estimate of each distribution.

Methods Summary

To characterize the assimilative load:capacity ratios of piscine predators, we compiled data from bioenergetics analyses that express integrated consumption rates relative to the physiological maximum. These models[16,17] use field measurements of growth at monthly to annual timescales to reconstruct consumption rates, based on the energy budget:

(7) $G = C - (R+W+SDA)$

Where G is growth, C is food consumption, R is active metabolism, W is waste (feces and urine), and SDA is specific dynamic action (the cost of digestion). Empirically derived, species-specific functions model the effects of water temperature and body mass on respiration and the maximum daily consumption rate ($Cmax$). Additional functions model waste and SDA as taxes on consumption. To incorporate thermal and allometric constraints on C, the parameter p scales the actual consumption rate relative to the maximum consumption rate according to $p = C/Cmax$. Thus, equation 7 becomes:

(8) $G = p \cdot Cmax - (R+W+SDA)$

Based on observed growth, diet composition, predator and prey energy densities, and the temperature regime experienced by a fish for the time interval over which growth is estimated, the model solves for the value of p that produces the value of G observed in the field. Because $Cmax$ is determined by rates of food-processing[18], p represents the load:capacity ratio for assimilation—the process that includes both the break down of food macromolecules and the transportation of nutrients across the gut wall.

For our meta-analysis of p estimates, we searched *Web of Science* and *Google Scholar* for all publications (n=345) citing the bioenergetics framework outlined above[16,17]. We compiled data from all publications (42 journal articles and 4 theses) that studied predators *in situ* and reported the parameter p. The meta-data and source publications are provided in table S1.

Methods

Description of the fish bioenergetics model (FBEM) used to estimate assimilative load:capacity ratios:

The FBEM[16,17] is an energy balance approach to bioenergetics that provides an adaptable modeling framework, which has been applied to a wide variety of species and ecosystems. The model balances an energy budget where inputs must equal outputs, specifically:

(7) $C = G + R + W + SDA$

Where C is food consumption, G is growth, R is active metabolism, W is waste (feces and urine), and SDA is specific dynamic action (the cost of digestion). The FBEM provides functions that model the effects of water temperature and body mass on respiration and the maximum daily consumption rate (*Cmax*). These functions are parameterized for individual species through controlled laboratory experiments. To formulate the respiration functions, oxygen consumption is measured in experiments that manipulate body size and water temperature. In addition, an activity multiplier is calculated to relate basal and active metabolism. To formulate the *Cmax* functions, daily consumption rates are measured in *ad libitum* feeding experiments that manipulate temperature and body size. Additional functions model waste and SDA as taxes on consumption. A full description of these functions is available in the Bioenergetics 3.0 software manual available though the UW-Madison Center for Limnology and the Wisconsin Sea Grant Institute.

Researchers typically use the FBEM to estimate consumption rates based on the observed growth rates of fishes in the field. This is done by rearranging the original terms in the energy budget so that growth represents surplus energy after gains from consumption are paid to energetic costs:

(8) $G = C-(R+W+SDA)$

Growth is measured directly over some relatively long time interval (e.g., monthly to annual growth increments) and the model is used to estimate the consumption rate C required to satisfy equation (8) to produce the observed growth increment. To incorporate thermal and allometric constraints on C, the parameter p scales the actual consumption rate relative to the maximum consumption rate according to $p = C/Cmax$. Thus, equation 8 becomes:

(9) $G = p \cdot Cmax-(R+W+SDA)$

Based on observed growth, diet composition, predator and prey energy densities, and the temperature regime experienced by a fish for the time interval over which growth is estimated, the model solves for the value of p that produces the value of G observed in the field. The model is implemented at a daily time step and linearly interpolates between observations of temperature, diet composition and energy density. Because growth of fishes in indeterminate, the value of p is a sensitive but informative integrated parameter that reflects the realized consumption rate relative to the physiological maximum rate that an individual fish is capable of, based on its metabolic parameters, its body size, its energy density and the energy density of its prey, and water temperature. Because *Cmax* is determined by rates of food-processing[18] p represents the load:capacity ratio for assimilation—the process that includes both the break down of food macromolecules and the transportation of nutrients across the gut wall. Consumption estimates from the FBEM have been independently corroborated by intensive field-based methods[31,32].

For our meta-analysis of p estimates, we searched *Web of Science* and *Google Scholar* for all publications (n=345) citing the bioenergetics framework outlined above[16,17]. We compiled data from all publications that studied predators *in situ* and reported the parameter p (42 journal articles and 4 theses). The meta-data and source publications are provided in table S1.

Additional description of our numerical model simulating trade-offs associated with digestive capacity:

We used the gamma distribution to simulate variation in daily foraging opportunity because it can generate a diversity of biologically realistic shapes, ranging from narrow and Gaussian to extremely right-skewed, representing an environment where prey encounters are extremely patchy. The gamma distribution has two parameters: k and θ, which relate to the mean and variance of the distribution as follows:

(10) $\text{mean} = k \cdot \theta$

$\text{variance} = k \cdot \theta^2$

Rearranging equation (10) yields:

(11) $k = \text{mean}^2/\text{variance}$

$\theta = \text{variance}/\text{mean}$

In order to examine the effect of variability in foraging opportunity on the energetic profitability of excess assimilative capacity, we varied θ and k, to generate gamma distributions with an equal mean, but different levels of variation. This simulates ecosystems that have an equal amount of prey available to predators, but different levels of variation in the temporal patterning of daily predator-prey encounters.

To provide biologically interpretable results, we used the coefficient of variation [CV: (s.d./mean)·100] to describe variation in the gamma distribution. Unlike other metrics of variation (e.g., the variance to mean ratio) the relationship between the CV and shape of the gamma distribution scales isometrically with the mean of the distribution (e.g., if the CV is held constant, changing the mean does not affect the skew of the distribution). Therefore, we could explore all ecologically relevant shapes of the gamma distribution by changing the CV of the distribution (range: 0.1% to 500%) while keeping the mean fixed at an arbitrary value. Figure S1 shows a subset of the gamma distributions that were generated in our simulations to illustrate the diversity of shapes that we considered.

The relationship between the maintenance cost and assimilative capacity of the gut (*Rgut* and *Cmax*) is poorly documented. For the sake of parsimony, and because empirical data suggest assimilative capacity in fish is related the surface area of the gut[33], we modeled a linear relationship between *Cmax* and *Rgut*, such that a proportional change to *Cmax* produces the same proportional change in *Rgut* (e.g., doubling *Cmax* would double *Rgut*). The relationship between *Cmax* and total metabolic cost, *M,* depends on the ratios of *Rgut*:*M* and *M*:*Cmax.* Under the assumed linear relationship, the slope (*r*) of *M* as a function of *Cmax* is:

$$r = {}^{R_{gut}}\!\big/_{R_{tot}} \bullet {}^{R_{tot}}\!\big/_{C_{\max}} \tag{6}$$

We assumed one-third of total daily respiration goes to maintaining digestive capacity, as this is the approximate proportion of total cardiac output delivered to an empty gut[34]. The empirically derived functions in the FBEM[17] suggest energetic losses due to respiration typically represent 1/3 to 1/9 of *Cmax* in fishes. Given these estimations, *r* ranges from 0.04 to 0.11. Since the y-intercept of a linear cost function (here, the cost of metabolism not associated with the gut) does not affect the optimal value for profit maximization, we modeled total metabolic cost, *M*, as a constant fraction, *r*, of *Cmax*, and included three cost scenarios: low (*r*=4%), medium (*r*=8%) and high (*r*=12%). We did not consider specific dynamic action or excretion in our cost analysis, because we assumed these were taxes on consumption that do not represent physiological maintenance.

References

31 Rice, J. A. & Cochran, P. A. Independent evaluation of a bioenergetics model for largemouth bass. *Ecology* **65**, 732-739 (1984).

32 Beauchamp, D. A., Stewart, D. J. & Thomas, G. L. corroboration of a bioenergetics model for sockeye salmon. *Transactions of the American Fisheries Society* **118**, 597-607 (1989).

33 Stevens, E. D. & Devlin, R. H. Intestinal morphology in growth hormone transgenic coho salmon. *Journal of Fish Biology* **56**, 191-195 (2000).

34 Farrell, A. P. *et al.* Gut blood flow in fish during exercise and severe hypercapnia. *Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology* **128**, 551-563 (2001).

Chapter 2: Thermal heterogeneity mediates the effects of pulsed subsidies across a landscape

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Abstract

Spatial and temporal heterogeneity interact to make the foraging rates of individuals more variable than expected from models assuming that spatial and temporal dimensions of habitat conditions operate independently. For example, trophic resource pulses produce temporal patches of prey superabundance, yet little is known about how spatial heterogeneity in habitat conditions mediates the ability of consumers to exploit these high quality foraging opportunities. We studied how spatial variation in water temperature regulates the potential for juvenile coho salmon to exploit a seasonal pulsed subsidy of eggs produced by anadromous sockeye salmon. Streams within the Wood River watershed (SW Alaska) ranged in mean summer temperature from 3.6 to 14.5°C. Growth of juvenile coho prior to the arrival of the seasonal egg subsidy was positively related to water temperature among streams. An *in situ* experiment combined with field samples of diets revealed a size threshold for egg consumption; only individuals longer than ~70 mm could consume eggs due to gape limitation of smaller individuals. A bioenergetics simulation demonstrated that water temperature regulated whether age-0 coho salmon could grow large enough to exceed the size threshold for egg consumption. Coho salmon that consumed eggs had energy rations that were 5 times higher than fish that did not consume eggs, resulting in a positive feedback of water temperature on their integrated seasonal growth. Across this landscape, heterogeneity in water temperature mediates individual- and population-level responses to seasonally available resource pulses. Our study illustrates that ecological

mechanisms, such as size based foraging asymmetries, can magnify the effects of climate change compared to predictions based on physiology alone.

Introduction

Many consumers are faced with the challenge of capitalizing on temporally variable prey resources, which may be in excess of physiological capacity during some time periods and below levels needed for maintenance energy demands during others (Bustard 1967, Arrington et al. 2002). To achieve positive energy balance over long periods of time, many individuals must mitigate bouts of negative energy balance (e.g., winter, reproduction, migration) by storing energy and growing during periods where positive energy balance is possible--for instance, during periods when food is abundant.

Consumers facing high temporal variation in prey availability can be further constrained by spatial variation in habitat conditions. For example, heterogeneity in the physical structure of habitat can affect foraging success as much as prey availability (Hopcraft et al. 2005, Kauffman et al. 2007). A continuing challenge for ecologists is to understand how heterogeneity in space and time combine to affect the foraging rates of individuals. At present there remains little understanding of how spatial heterogeneity in specific habitat conditions affects the ability of consumers to capitalize on temporally varying prey resources. Here we show that spatial variation in water temperature regulates the potential for consumers to exploit a pulsed subsidy.

Pulsed subsidies occur when spatial export of material from donor ecosystems generates ephemeral resource superabundance in recipient ecosystems (Polis et al. 1997, Yang et al. 2008). Pulses of food can produce the potential for extreme growth and energy storage in consumers, but only if individuals can effectively exploit the pulsed food item. To exploit a pulsed subsidy, individuals often need to exhibit adaptive behavior by perceiving the new resource, learning to consume it, and moving to capitalize on spatially patchy feeding opportunities (Yang et al. 2008). Importantly, individuals must be morphologically able to capture and consume the novel food item. Morphological constraints can hinder consumption, for example, if the size of a food item exceeds the jaw gape or throat diameter of a consumer (Lawrence 1958, Wheelwright 1985). Such physical constraints create size-based foraging asymmetries, where larger individuals obtain more resources because they can consume a wider spectrum of prey size (Werner and Gilliam 1984). When prey vary in size, this is likely to create a roughly linear relationship between consumer size and potential consumption. However, if prey size is relatively uniform, as with many pulsed food items (e.g., gametes; Clifton 1997, seeds; Kelly 1994, larvae; Ruggerone 1992) there is the potential for size-based foraging thresholds, where the relationship between consumer size and potential consumption is sigmoidal. If these relationships occur during critical periods of energy acquisition, such as pulsed subsidies, small differences in body size may have disproportionate effects on fitness.

For poikilothermic consumers, ambient temperature can affect the body size of individuals by regulating physiological growth potential. As temperature increases the internal handling time for prey decreases (Elliot and Persson 1978), and the maximum consumption rate (Cmax) increases. Metabolic costs also increase with temperature, but at the cooler end of a species' thermal range, warming increases Cmax faster than metabolic costs, so the scope for growth increases with temperature (Hansen et al. 1997). Therefore, when food is not limiting, fish can achieve a larger body size in warmer water. We hypothesized that spatial heterogeneity in temperature could mediate the effects of pulsed subsidies when size-based foraging thresholds existed. We tested this hypothesis studying the pulsed marine subsidies that occur when anadromous semelparous Pacific salmon (*Oncorhynchus* spp.) spawn in streams, providing high quality resources (e.g., eggs and carcass flesh, Schindler et al. 2003) to consumers. Juvenile coho salmon (*O. kisutch*) are opportunistic predators that rear in a wide variety of streams with contrasting thermal regimes and exploit trophic subsidies provided by other salmon species (Bilby et al. 1998, Reichert et al. 2008). Our goal was to determine how the thermal variation among streams within the same watershed influenced the ability of coho salmon to capitalize on pulsed subsidies provided by sockeye salmon (*O. nerka*).

Across northwestern North America, coho salmon co-occur with Pacific salmon species that spawn in streams, but rear in estuaries or lakes. These species, including pink salmon (*O. gorbuscha*), chum salmon (*O. keta*), and sockeye salmon, often spawn in high densities (Quinn 2005, Moore et al. 2008). During spawning, salmon eggs subsidize aquatic food webs as females are killed by predators before they complete spawning (Gende et al. 2004), fail to bury all of their eggs in the benthos (Briggs 1953), or dig up existing nests (McNeil 1964). Eggs are 2-3 times as energy dense as benthic invertebrates, and can be extremely abundant (Moore et al. 2008). This ephemeral food source, often lasting 2-6 weeks, can account for the majority of summer growth in resident fish (Scheuerell et al. 2007, Moore et al. 2008). However, salmon eggs are large and relatively uniform in size (Quinn 2005), so they can exceed the gape size of smaller fish (Foote and Brown 1998).

If gape-size limits egg consumption, growth conditions prior to sockeye salmon spawning should strongly influence whether juvenile coho salmon can exploit seasonal pulses of eggs. Because growth is temperature-dependent, we hypothesized that spatial heterogeneity in temperature could alter the effects of sockeye salmon egg subsidies across a landscape. Specifically, we predicted that in cold streams, the maximum growth potential would be too low to allow individuals to grow large enough to exceed the size threshold for egg consumption. To test this hypothesis, we (1) quantified how among-stream temperature variation affects the potential size of an age-0 coho salmon during the season when the pulsed subsidy is available for consumption, (2) experimentally determined how body size affects the ability of juvenile coho salmon to eat eggs, and (3) compared our model predictions to observed data on coho salmon size distributions and diets. Our results demonstrate that landscape thermal heterogeneity translates into differential ability of coho salmon populations to exploit seasonally pulsed subsidies.

Materials and Methods

Study system

This study was conducted in a 1600 km^2 region of the Wood River watershed in southwestern Alaska, USA. The streams in our analyses included one tributary of the Wood River, eight tributaries of Lake Aleknagik, and four tributaries of Lake Nerka. These streams flow through glaciated valleys, are low gradient (0.5-1%), range in bank full width from 7-15 m (Marriot 1964), and are <50 m above sea level. Coho salmon comprise a small portion of the system's adult salmon returns, but their juveniles can be numerically dominant in streams (*Armstrong unpublished data*) because more numerous salmon species emigrate from streams soon after emerging from the gravel. The sockeye salmon escapement (run size after commercial fishing) to the Wood River system has averaged 1.1 million over the last 50 years (Baker et al. 2006). The timing of sockeye spawning in the Wood River system varies, starting between mid-July and mid-August and ending within 2- 6 weeks (Marriot 1964, Hodgson and Quinn 2002). Sockeye salmon egg size varies among spawning habitat types (stream, river, or lake shore: Quinn et al. 1995), but most of the eggs spawned in streams fall within a relatively narrow size range. In 8 Lake Aleknagik tributaries, the mean and standard deviation of egg diameter were

5.75 mm and 0.34 mm, respectively, for 458 females (*T. Quinn unpublished data*). Sockeye salmon spawn in streams and lakes. Juveniles typically rear in lakes for 1 or 2 years before spending 1,2, or 3 years in the ocean and returning during summer months to spawn (Quinn 2005).

Coho salmon typically rear in streams for their first 1 or 2 years of life (Quinn 2005). In spring they then migrate to sea and return the following or subsequent fall to spawn. Eggs incubate in the benthos over the winter and offspring emerge between late winter and summer, depending on latitude. Growth opportunities during the first summer can determine subsequent fitness because over-winter survival and marine survival are size-dependent (Quinn and Petersen 1996, Holtby et al. 1990, respectively).

Water temperature

To quantify thermal variation among streams within our system, we placed iButton temperature loggers (Dallas Semiconductor, Dallas, Texas, USA) in the main channel of 13 streams in reaches where sockeye spawn. In 2007 and 2008 the loggers ran from June through early September, measuring temperature to the nearest 0.125°C in 3 h intervals, which we converted to mean daily temperatures. The accuracy of the temperature loggers was within +/- 1° C.

Bioenergetics model

We used a modified version of the Wisconsin Bioenergetics model (Hansen et al. 1997) to estimate the size of an age-0 coho salmon at the date of peak sockeye salmon spawning based on three ecological variables: water temperature, emergence date in the spring, and potential ration. Potential ration represented the amount of food available to a fish in 1 d (standardized by fish mass) and was temperature-independent in our simulations. Temperature influences Cmax, such that consumption is thermally constrained at cool temperatures where the potential ration > Cmax. The Wisconsin model balances an energy budget where growth is equal to consumption minus the sum of respiration and excretion. We used the physiological parameters for coho salmon from Stewart and Ibarra (1991). The energy density of prey was calculated as the mean energy density from observed juvenile coho diets that did not contain eggs (n = 522). These rations, dominated by larval benthic invertebrates, had a mean energy density of 3.50 kJ/g wet mass (std. dev. = 1.02 kJ/g).

Simulations were initialized with 34 mm fish (the size at emergence) and simulated growth under 6 thermal regimes spanning variation observed within our system (mean daily temperature = 3-13°C in 2°C increments). For each thermal regime we computed the size on 15 August across a grid of emergence date and potential ration values that encompassed the variation estimated to occur in our system. Emergence date ranged according to the dates we have observed recently emerged fish (25 May to 15 July), and the potential ration ranged from 0 g/g/d. (starvation) to 0.3 g/g/d (Cmax for a 1 g fish with no thermal constraints on consumption).

Gape limit experiment

To determine how body size affects the ability of juvenile coho salmon to eat sockeye salmon eggs, we performed an *in situ* feeding experiment in July, 2008. Salmon eggs, hypotonic to fresh water, rapidly absorb water after being released from the female's body cavity, becoming turgid (water-hardened) within 1 h (Danner 2008). We collected eggs from mature sockeye salmon females and hardened a subset of eggs by soaking them in water for 1h. The experimental arena, a 1.25 m x 0.75 m x 0.75 m rectangular enclosure with nylon screen walls, was secured in slow-moving portions of a stream. We captured juvenile coho salmon with nets, transferred a single individual to the enclosure, and allowed 180 s for acclimation. In each trial we delivered individual eggs in front of the fish until we observed a feeding response. We released water-hardened eggs first and switched to fresh eggs after the first foraging attempt on hard eggs. We evaluated foraging success as a binary response, where partial or complete consumption of the egg was scored 1, and failure was scored 0. Fish were scored based on their first foraging attempt for each egg condition and were only scored if they attempted to eat an egg. After each trial we measured the fish's fork length, the distance from the nose to the tail fork, to the nearest 1 mm. We tested 93 fish ranging from 42-105 mm long. For both egg conditions, we analyzed the effect of body length on foraging success with logistic regression. We considered the gape-size limit for egg consumption to occur at the fork length where the predicted probability of foraging success equaled 0.5.

Field data

We randomly sampled fish throughout each of our study streams to characterize the seasonal changes in their diets and size distributions. Fish were captured with a stick seine, anesthetized in a 50 ppm solution of MS-222 (tricane methane sulfonate), measured to the nearest 1 mm fork length, and released. A random subset of these fish was weighed and sampled for diet by gastric lavage (individuals > 60 mm) or stomach extraction (individuals <= 60 mm). In 2007 we sampled Whitefish, Bear, and Yako creeks approximately every two weeks from June to mid-September yielding 6-8 sampling events at each stream. In 2008 we sampled monthly in Silver Salmon Creek from June to August, yielding three sampling events. We inferred age structure from length-frequency distributions at discrete time periods and direct aging of individuals from scale annuli (Appendix A). We compared size distributions among streams in mid-August, when sockeye salmon spawning is near peak levels and egg abundance was predicted to be highest, by using multiple two-sample Kolmogorov-Smirnov (KS) tests in R (R development core team 2008) and assessing p-values with a Bonferroni corrected alpha-value.

Diet Analysis

For each diet, prey items were sorted by taxonomic order, blot-dried, and weighed to 0.0001 grams. Some large diets items were counted and measured in the field, and then converted to wet weight based on length-weight regressions generated from preserved prey items. Fish diets were converted to mass-specific instantaneous rations by summing the products of each prey taxa wet weight and energy density (obtained from Cummins and Wuycheck 1971 or Hendry and Berg 1999) and dividing by fish weight. We analyzed instantaneous rations by pooling individuals into three groups: fish sampled prior to sockeye spawning (n = 182), fish sampled during sockeye salmon spawning that had sockeye eggs in their guts (n = 110), and fish sampled during sockeye salmon spawning that had no sockeye eggs in their guts (n = 113). We excluded samples from individuals with empty stomachs (n = 9). Diet data were right-skewed and showed unequal variance among groups, so non-parametric statistical analyses were used. We tested for differences among groups in mean instantaneous ration using a Kruskal Wallis test, followed by non-parametric multiple comparison in R (R development core team 2008).

Estimating bioenergetics parameters for observed coho salmon populations

For the coho salmon population in each focal stream we estimated emergence date by fitting a curve to modal fork length plotted through time and hindcasting to estimate the date when fish were 34 mm, the typical size at emergence. We converted fork length to weight from the observed length-weight regression (r^2=0.98) and inferred growth as the change in modal weight between sampling events. Using the bioenergetics model, we then calculated the level of consumption (proportion of Cmax) that would produce the inferred growth during a sampling interval, given the observed temperature and prey energy density. To explore how the effects of pulsed subsidies varied among coho salmon populations we compared the observed body size in September to the predicted body size had no eggs had been available. For each population, we started with the modal body weight prior to the observed onset of sockeye spawning and simulated growth until 7 September using the estimated consumption level during the two sampling intervals preceding sockeye salmon spawning, the non-egg prey energy density, and the observed temperature during the simulated time period.

Results

Temperature heterogeneity among streams

The mean temperature from June through September varied more than 10°C among the 13 streams in our study, ranging from 3.6 °C in Mission Creek, to 14.5 °C in Lynx Creek (Fig.1a). The streams where we sampled coho salmon encompassed much of this range in temperature. The mean daily temperature during the growth period prior to the sockeye salmon egg subsidy was 5.8°C in Yako, 6.6°C in Bear, 12.1°C in Silver Salmon, and 14.6°C in Whitefish creeks (Fig. 1b).

Water temperature and coho salmon growth prior to the egg subsidy

The range of temperatures observed in our system produced very different growth potentials for coho salmon prior to the sockeye salmon egg subsidy. Growth was highly sensitive to potential ration size, but asymptoted when the potential ration exceeded Cmax. Since emergence date determined the duration of the growth period, its effect on the predicted fish size at 15 Aug was proportional to the growth rate during that period. Water temperature, by governing Cmax, determined where growth rates asymptoted with increasing potential ration, and thus mediated the maximum body size that fish could achieve prior to the pulsed subsidy

(Fig. 2). For example, the predicted body size for fish feeding at maximum consumption and emerging on 25 May ranged from 60 mm at 4.5°C to 130 mm at 12°C.

The effect of body size on potential egg consumption

The feeding experiment demonstrated a size-based foraging asymmetry in juvenile coho salmon fed water-hardened sockeye salmon eggs. Larger individuals (range: 64-105 mm) could swallow eggs whole, whereas smaller individuals (range: 42-72 mm) could not, creating a sharp contrast in potential consumption (Fig. 3b). A logistic regression showed that size was a significant factor ($\beta = 0.3633$, $p = 0.003$, df = 70) in determining whether a coho salmon could consume a hardened sockeye salmon egg (Fig. 3b). The predicted probability of being able to eat an egg reached 50% at a fork length of 70 mm. Smaller individuals (>43 mm fork length) were able to consume fresh sockeye salmon eggs (Fig. 3a), because they could break the external membrane and consume a portion of the contents. The smallest individuals in our study (42-43 mm) were unable to break fresh eggs, but we found very few individuals this small during mid-summer, so this size-based trend in fresh egg consumption was not statistically significant.

Patterns in egg consumption in streams confirmed the experimental results for water-hardened eggs (Fig. 3c). Body size affected whether individuals had eggs in their diets ($\beta = 0.0663$, $p < 0.001$, df = 132), and the smallest fish that consumed eggs was 67 mm long. Eggs were never observed in the diets of fish in the size range capable of eating fresh eggs but not hard eggs (43-64 mm, Fig. 3c). When sockeye salmon were spawning in streams, coho salmon with eggs in their diet had instantaneous rations that were >5x higher (0.53 ± 0.29 kJ/g [mean ± SD]) than those with only invertebrates in their diets (0.08 ± 0.08 kJ/g), or those sampled prior to the availability of eggs (0.10 ± 0.18 kJ/g; Kruskal-Wallis: $p < 0\ .001$, non-parametric multiple comparison: $p < 0.001$; Fig. 4).

Water temperature and the potential for age-0 coho to exploit egg subsidies

Model simulations showed that much of the variation in emergence date, food availability, and water temperature estimated to occur in our system would not combine to provide adequate growth for age-0 coho salmon to eat eggs during peak sockeye spawning (Fig. 2, non-shaded regions). Early emergence and high potential rations contributed to larger body size at 15 August, but whether this size exceeded 70 mm depended most strongly on water temperature. In the coldest streams in our system (< 5°C) not even early-emerging fish feeding at their physiological maximum rate could grow large enough to exceed the size threshold to eat eggs. As simulated water temperature increased from 5°C to 13°C, progressively later emergence dates were required to exceed the size threshold for egg consumption because fish could utilize higher potential rations (Fig. 2).The estimated modal emergence date of the coho salmon populations in our study was 10 July in Yako and Bear creeks, 15 June in Silver Salmon Creek, and 28 May in Whitefish Creek. The consumption level (proportion of Cmax) during the entire period prior to the pulsed subsidy, and the range of estimated consumption levels during 2 wk intervals within this period, respectively, was 0.5-0.9, 0.7 in Yako Creek, 0.4-0.7, 0.6 in Bear Creek, 0.4-0.6, 0.5 in Silver Salmon Creek, and 0.3-1, 0.6 in Whitefish Creek.

Variation in body size among populations

The size structure of juvenile coho salmon varied significantly among the four streams during the mid-August period of peak sockeye salmon spawning (KS test: $p<0.001$ in all comparisons, Bonferroni corrected $\alpha=0.008$). Each stream exhibited a bimodal size distribution with a large number of smaller age-0 individuals and a smaller number of larger age-1 individuals (Fig 5a, Appendix A). The percentage of individuals exceeding the gape-size limit to eat eggs in mid-August was 18% in Yako, 22% in Bear, 35% in Silver Salmon, and 77% in

Whitefish (in increasing order of water temperature). Size distributions monitored through time combined with direct aging of individuals (Appendix A) showed differing patterns of potential egg consumption among cohorts within each stream at mid-August (Fig. 5a). In the warmer streams (Silver Salmon and Whitefish) a substantial proportion of the age-0 cohort grew large enough to consume eggs when they were available, while in the cooler streams (Yako and Bear) the fish that could eat eggs were almost entirely age-1.

Growth resulting from egg subsidies

In Whitefish Creek the observed modal weight of coho salmon after the egg subsidy was 15.2 g, >2x the weight expected from pre-subsidy foraging conditions (6.2 g, Fig. 5b). In Bear and Yako creeks, the observed modal weight after the egg subsidy (1.6 g and 1.9 g, respectively) was less than that expected from pre-subsidy foraging conditions (2.1 g for both, Fig. 5b). This pattern was not due to variation among streams in egg abundance, as Bear and Yako creeks had >3x more spawning sockeye salmon than Whitefish Creek (*Armstrong unpublished data*).

Discussion

We documented a 10°C range in mean summer water temperature among streams within a single watershed that support sockeye salmon spawning (Fig. 1). The temperatures in cooler streams constrained the potential for post-emergence growth in age-0 coho salmon, restricting their maximum size during a seasonal pulse of sockeye salmon eggs (Fig. 2, Fig. 5). Because gape-size prevented smaller individuals from consuming eggs (Fig. 3), cold temperatures indirectly prevented smaller fish from exploiting egg subsidies, severely reducing their growth potential (Fig. 4, Fig. 5). Thus landscape heterogeneity in water temperature mediated the potential for consumers to exploit seasonal resource pulses.

Smaller individuals (43-64 mm) could consume fresh eggs in our feeding experiment, but were not observed to do so in the wild (Fig. 3a,c.). Moore et al. (2008) showed that most eggs enter the drift when female salmon dig up previously buried eggs, which are water-hardened. In addition, juvenile coho salmon rarely reside close enough to spawning sockeye salmon to eat any fresh eggs before they harden in the drift (*Armstrong unpublished data*). Our experimental data (Fig. 3a,b) and observational data (Fig. 3c, Fig. 4) provide strong evidence that gape limits produced a sharp size-based foraging asymmetry, preventing smaller individuals from capitalizing on a pulse of energy rich food. Previous studies have shown that morphological constraints drive individual- and population-level variation in resource use (e.g., ontogenetic shifts to piscivory in bass: Johnson 1996, Post et al. 2003). We studied a prey item that is relatively uniform in size and available for a brief, but predictable, period each year. A gape-size limit for such a food item creates a threshold relationship between body size and potential consumption (Fig. 3), such that smaller individuals do not merely have to wait longer to exploit a resource, but instead miss the opportunity entirely. Post et al. (2003) suggested that investigating intrinsic properties of the individual will reveal how some individuals can grow large enough to exploit resources while others do not. Here we showed that an extrinsic factor, water temperature, sets the bounds in which intrinsic properties (emergence date and foraging behavior) can influence individual body size. In particular, we found an interaction effect, where the effect of emergence date and foraging behavior on resource use depends on water temperature (Fig. 2).

Many streams in our system have mean daily temperatures in the 6-8°C range during the period prior to sockeye salmon spawning (Fig. 1). In these streams individuals must emerge early in order to exploit eggs, because thermal constraints on consumption reduce the maximum potential growth rate, increasing the minimum time required to reach the size threshold for egg consumption. The field observations of coho salmon in Bear and Yako creeks support this conclusion, as the vast majority of individuals in these cool streams emerged late, did not reach the size threshold to consume eggs, and did not experience increased growth rates during the pulsed subsidy (Fig. 5). With warmer water temperatures (8-15°C) potential growth rates increase and individuals with later emergence dates can grow large enough to consume eggs, provided that sufficient food is available prior to the subsidy. The size distributions of coho salmon in Whitefish and Silver Salmon creeks confirm the hypothesis that in warmer streams, a greater proportion of individuals grow large enough to exploit eggs (Fig. 5a), producing a positive feedback in growth. After the egg subsidy, the fall body size of coho salmon in Whitefish Creek exceeded that expected from pre-subsidy foraging conditions by >2x (Fig. 5b). In combination, these results show that landscape variation in water temperature mediates the effects of pulsed sockeye salmon subsidies on juvenile coho salmon individuals and populations.

While our growth simulations explored the physiological effects of water temperature, ecological effects of water temperature also influence the size of coho salmon during pulsed egg subsidies. Warmer streams may exhibit higher *in situ* production (Holtby 1988), providing higher potential rations that could increase growth if they exceed increases in metabolic demand. Water temperature is also likely to affect the duration of the growth period prior to the pulsed subsidy.. In our study streams the emergence date of coho salmon was negatively correlated with water temperature ($p<0.01$), such that fish emerged 5 d earlier for each 1° C increase in water temperature. In addition, the onset of sockeye salmon spawning occurs later in warmer streams (Hodgson and Quinn 2002) because incubation rates are faster. Thus warmer streams have pre-subsidy growth periods that start sooner, and end later. The combined physiological and ecological effects of water temperature likely produce stronger feedbacks in coho salmon growth than our model results suggest.

Increased summer growth in coho salmon individuals may increase population productivity, because the juvenile life stage is thought to be a population bottleneck for coho salmon (Scarnecchia 1981). Fall body size has been shown to correlate positively with over-winter survival (Holtby 1988, Quinn and Petersen 1996) and negatively with age at seaward migration (Holtby 1988, Holtby et al. 1990). Reducing the mean smolt age of a population should reduce juvenile mortality in streams, because emigration of age-1 individuals reduces competition for food and over-wintering habitat. Food limitation in streams can determine the carrying capacity for populations of coho salmon and other salmonids (Dill et al. 1981, Scrivener et al. 1984). In coastal streams along the Pacific Rim, salmon egg subsidies can dramatically increase food availability and are hypothesized to increase the carrying capacity for resident fishes (Schindler et al. 2003). Our research suggests that water temperature mediates whether subsidy-induced increases to the carrying capacity of streams are realized by juvenile salmonids.

The temperature-dependence of fish growth is well studied, and many have described how it varies across landscapes (e.g., spatially explicit bioenergetics models: Brandt et al. 1992). The novelty of our study was that we (1) connected landscape variation in growth potential to size-based mechanisms affecting individual foraging success and (2) show how this spatial heterogeneity in foraging potential interacts with temporal heterogeneity in food abundance to drive individual- and population-level variation in seasonal growth potential. In the cool water temperatures found in high-latitude streams (3-15° C), the maximum growth rate of coho salmon increases with temperature (Brett 1995). We showed that increases in body size drive a sigmoidal increase in the potential for juvenile coho salmon to exploit salmon egg subsidies.

These two mechanisms combined can drive strong non-linear responses to thermal variation, because small increases in water temperature can push coho salmon individuals past the size threshold to exploit seasonal resource superabundance, greatly increasing their summer growth potential. Alaska is one of the most rapidly warming regions on the planet and is predicted to warm by 2-4°C in the next 50 years (Schindler and Rogers *in press*). Our results suggest that small changes in temperature can produce an ecologically-driven positive feedback in the growth of juvenile coho salmon. This emphasizes that ecological mechanisms can magnify the direct effects of climate change on organisms, such that responses to warming exceed those predicted by physiological models alone (McDonald et al. 1996, Van Winkle 1997).

The magnitude of thermal heterogeneity we have documented has important implications for models predicting large-scale effects of global climate change. For example, recent work predicts that global warming will cause dramatic faunal range shifts in regions that include our study area (Lawler et al. 2009). The models producing these predictions and others use spatial grain sizes of 2500 km^2 and larger. We demonstrated that mean summer water temperature can vary by 10° C among streams within the same watershed. Coarse-scale climate change models would eliminate this spatial variation in thermal conditions by generating grid cells representing the mean temperatures of different landscapes. Alarmingly, the spatial variation in temperature lost by homogenizing landscapes can be greater in magnitude than the temporal change in temperature that climate change models aim to understand. Our study demonstrates the importance of linking spatial and temporal patterns of variation and highlights the need to improve our understanding of the scale-dependencies of ecological responses to changing climate.

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References

Arrington, D. A., K. O. Winemiller, W. F. Loftus, and S. Akin. 2002. How often do fishes "run on empty"? Ecology **83**:2145-2151.

Baker, T. T., L. F. Fair, R. A. Clark, and J. J. Hasbrouck. 2006. Review of salmon escapement goals in Bristol Bay, 2006. Alaska Department of Fish and Game, Fisheries Manuscript Number 06-05, Anchorage, Alaska, USA.

Bilby, R. E., B. R. Fransen, P. A. Bisson, and J. K. Walter. 1998. Response of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus mykiss*) to the addition of salmon carcasses to two streams in southwestern Washington, USA. Canadian Journal of Fisheries and Aquatic Sciences **55**:1909-1918.

Brandt, S.B., D.M. Mason, and E.V. Patrick. 1992. Spatially-explicit models of fish growth. Fisheries **17**:23-35

Brett, J. R. 1995. Energetics. UBC Press, Vancouver, British Columbia, Canada.

Briggs, J. C. 1953. The behavior and reproduction of salmonid fishes in a small coastal stream. California. Department of Fish and Game. Fish Bulletin **94**.

Bustard, H. R. 1967. Gekkonid lizards adapt fat storage to desert environments. Science **158**:1197-1198.

Clifton, K. E. 1997. Mass spawning by green algae on coral reefs. Science **275**:1116-1118.

Cummins K.W. and J.C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. Mitteilungen der Internationale Vereinigung fu¨ r Theoretische und Angewandte Limnologie, **18**: 1–158.

Danner, G. R. 2008. Salmonid embryo development and pathology. American Fisheries Society Symposium **65**:37-58.

Dill, L. M., R. C. Ydenberg, and A. H. G. Fraser. 1981. Food abundance and territory size in juvenile coho salmon (*Oncorhynchus kisutch*). Can. J. Zool. **59**:1801-1809.

Elliot, J.M. and L. Persson. 1978. The estimation of daily rates of food consumption for fish. The journal of animal ecology **47**: 977-991.

Foote, C. J. and G. S. Brown. 1998. Ecological relationship between freshwater sculpins (genus *Cottus*) and beach-spawning sockeye salmon (*Oncorhynchus nerka*) in Iliamna Lake, Alaska. Canadian Journal of Fisheries and Aquatic Sciences **55**:1524-1533.

Gende, S. M., Quinn, T. P., Hilborn, R., Hendry, A. P., and B. Dickerson. 2004. Brown bears selectively kill salmon with higher energy content but only in habitats that facilitate choice. Oikos **104**: 518-528.

Hanson P.C., T.B. Johnson, D.E. Schindler and J.F. Kitchell. 1997. Fish Bioenergetics 3.0. University of Wisconsin Sea Grant Institute, Madison, WI.

Hendry, A. P. and O. K. Berg. 1999. Secondary sexual characters, energy use, senescence, and the cost of reproduction in sockeye salmon. Canadian Journal of Zoology-Revue Canadienne De Zoologie **77**:1663-1675.

Hodgson, S. and T. P. Quinn. 2002. The timing of adult sockeye salmon migration into fresh water: adaptations by populations to prevailing thermal regimes. Canadian Journal of Zoology-Revue Canadienne De Zoologie **80**:542-555.

Holtby, L. B. 1988. Effects of logging on stream temperatures in Carnation Creek, British Columbia, and associated impacts on the coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences **45**:502-515.

Holtby, L. B., B. C. Andersen, and R. K. Kadowaki. 1990. Importance of smolt size and early ocean growth to interannual variability in marine survival of coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences **47**:2181-2194.

Hopcraft, J. G. C., A. R. E. Sinclair, and C. Packer. 2005. Planning for success: Serengeti lions seek prey accessibility rather than abundance. Journal of Animal Ecology **74**:559-566.

Johnson, J. M. and D. M. Post. 1996. Morphological constraints on intracohort cannibalism in age-0 largemouth bass. Transactions of the American Fisheries Society **125**:809-812.

Kauffman, M. J., N. Varley, D. W. Smith, D. R. Stahler, D. R. MacNulty, and M. S. Boyce. 2007. Landscape heterogeneity shapes predation in a newly restored predator-prey system. Ecology Letters **10**:690-700.

Kelly, D. 1994. The evolutionary ecology of mast seeding. Trends in Ecology & Evolution **9**:465-470.

Lawler, J.J, S.L. Shafer, D. White, P. Kareiva, E.P. Maurer, A.R. Blaustein, and P.J. Bartlein. 2009. Projected climate-induced faunal change in the Western hemisphere. Ecology **90**:588-597.

Lawrence, J.M. 1958. Estimated sizes of various forage fishes largemouth bass can swallow. In: *Proc. Annu. Conf. Southeast. Assoc. Game Fish Comm.* **11**:220–225.

MacDonald, M.E, A.E. Hershey, and M.C. Miller. 1996. Global warming impacts on lake trout in Arctic lakes. Limnology and Oceanography **41**:1102-1108.

Marriott, R.A. 1964. Stream catalog of the Wood River lake system, Bristol Bay, Alaska. U.S. Fish Wildl. Serv. Sp. Sci. Rept. - Fisheries No. 494.

McNeil, W.J. 1964. Redd superimposition and egg capacity of pink salmon spawning beds. Journal of Fisheries Research Board of Canada 21: 1385-1396.

Moore, J. ., D. E. Schindler, and C. P. Ruff. 2008. Habitat saturation drives thresholds in stream subsidies. Ecology **89**:306-312.

Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: The dynamics of spatially subsidized food webs. Annual Review of Ecology and Systematics **28**:289-316.

Post, D.M. 2003. Individual variation in the timing of ontogenetic niche shifts in largemouth bass. Ecology **84**:1298-310

Quinn, T. P. 2005. The behavior and ecology of Pacific salmon and trout. University of Washington Press, Seattle, Washington, U.S.A.

Quinn, T. P., A. P. Hendry, and L. A. Wetzel. 1995. The influence of life history trade-offs and the size of incubation gravels on egg size variation in sockeye salmon (*Oncorhynchus nerka*). Oikos **74**:425-438.

Quinn, T. P. and N. P. Peterson. 1996. The influence of habitat complexity and fish sire on over-winter survival and growth of individually marked juvenile coho salmon (*Oncorhynchus kisutch*) in Big Beef creek, Washington. Canadian Journal of Fisheries and Aquatic Sciences **53**:1555-1564.

Reichert, W. L., C. M. Greene, and R. E. Bilby. 2008. Seasonal variations in stable isotope ratios of juvenile coho salmon (*Oncorhynchus kisutch*) from western Washington rivers. Canadian Journal of Fisheries and Aquatic Sciences **65**:681-690.

Ruggerone, G.T. 1992. Predation on sockeye salmon fry by juvenile coho salmon in the Chignik Lakes, Alaska: Implications for salmon management. North American Journal of Fisheries Management **12**:87-102

Scarnecchia, D.L. 1981. Effect of streamflow and upwelling on yield of wild coho salmon (*Oncorhynchus kisutch*) in Oregon. Canadian Journal of Fisheries and Aquatic Sciences **38**:471-475.

Scheuerell, M. D., J. W. Moore, D. E. Schindler, and C. J. Harvey. 2007. Varying effects of anadromous sockeye salmon on the trophic ecology of two species of resident salmonids in southwest Alaska. Freshwater Biology **52**:1944-1956.

Schindler, D. E., M. D. Scheuerell, J. W. Moore, S. M. Gende, T. B. Francis, and W. J. Palen. 2003. Pacific salmon and the ecology of coastal ecosystems. Frontiers in Ecology and the Environment **1**:31-37.

Schindler, D.E., and L.A. Rogers. *In press*. Responses of Pacific salmon populations to climate variation in freshwater ecosystems. American Fisheries Society Symposium **70**.

Scrivener, J. C., and B. C. Andersen. 1984. Logging impacts and some mechanisms that determine the size of spring and summer populations of coho salmon fry

(*Oncorhynchus kisutch*) in Carnation Creek, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences **41**:1097-1105.

Stewart, D. J. and M. Ibarra. 1991a. Predation and production by salmonine fishes in Lake Michigan, 1978-88. Canadian Journal of Fisheries and Aquatic Sciences **48**:909-922.

Werner, E. E. and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size structured populations. Annual Review of Ecology and Systematics **15**:393-425.

Wheelwright, N. T. 1985. Fruit size, gape width, and the diets of fruit eating birds. Ecology **66**:808-818.

Van Winkle, W., K. A. Rose, B. J. Shuter, B. I. Jager, and B. D. Holcomb. 1997. Effects of climatic temperature change on growth, survival, and reproduction of rainbow trout: predictions from a simulation model. Canadian Journal of Fisheries and Aquatic Sciences **54**:2526-2542.

Yang, L. H., J. L. Bastow, K. O. Spence, and A. N Wright. 2008. What can we learn from resource pulses? Ecology **89**:621-34

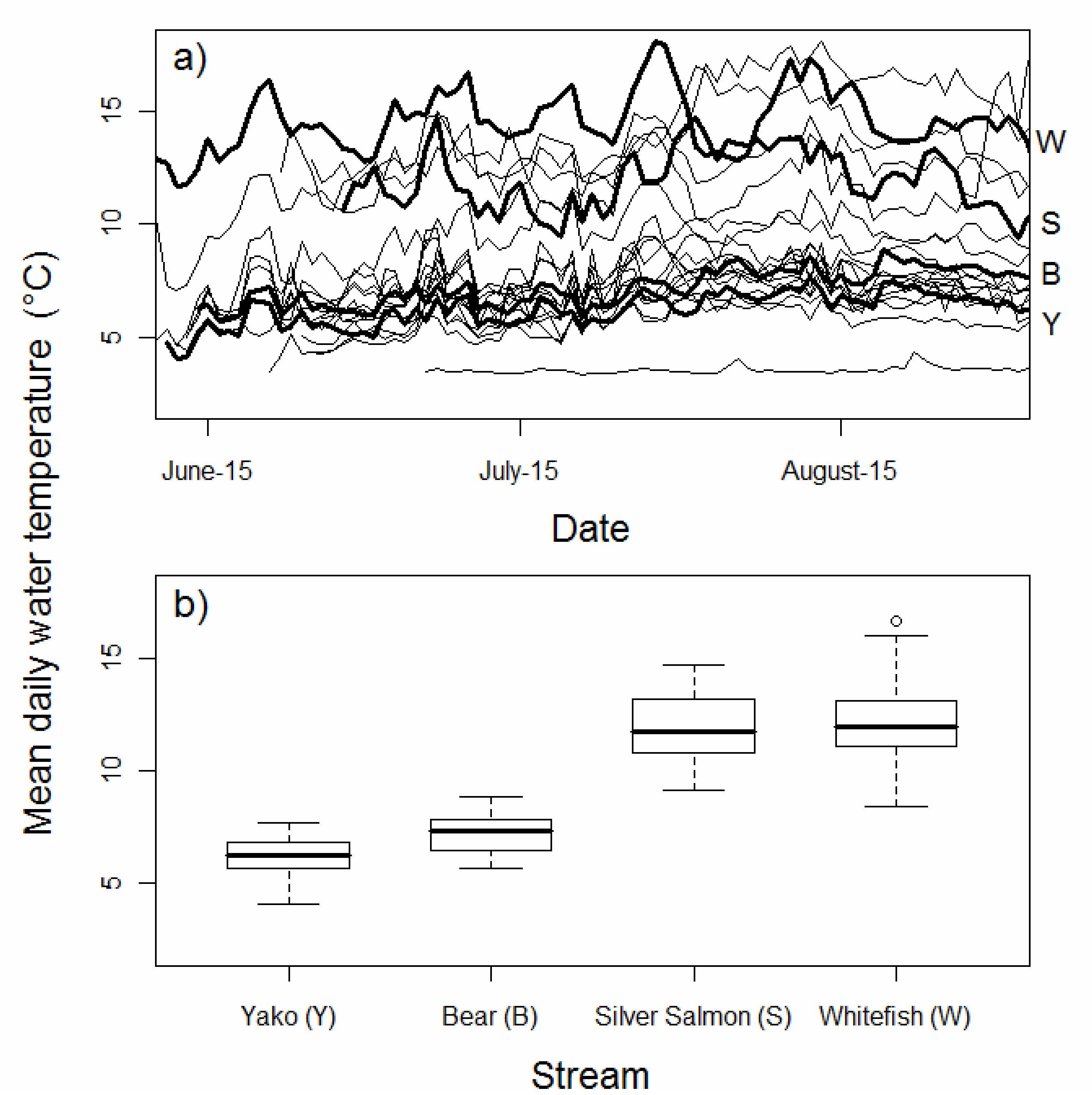

Figure 2.1 (a) Summer temperature profiles for 13 streams of the Wood River system monitored in 2007 and 2008. Each line shows the mean daily temperature during the summer months for a single stream in a single year. Bold lines represent stream/year combinations in which we studied coho salmon populations: Whitefish Ck. 2007 (W), Silver salmon Ck. 2008 (S), Bear Ck. 2007 (B), and Yako Ck. 2007 (Y). (b) Box plots of mean daily temperature for the four streams in which we studied coho salmon populations. Outliers are shown as circles.

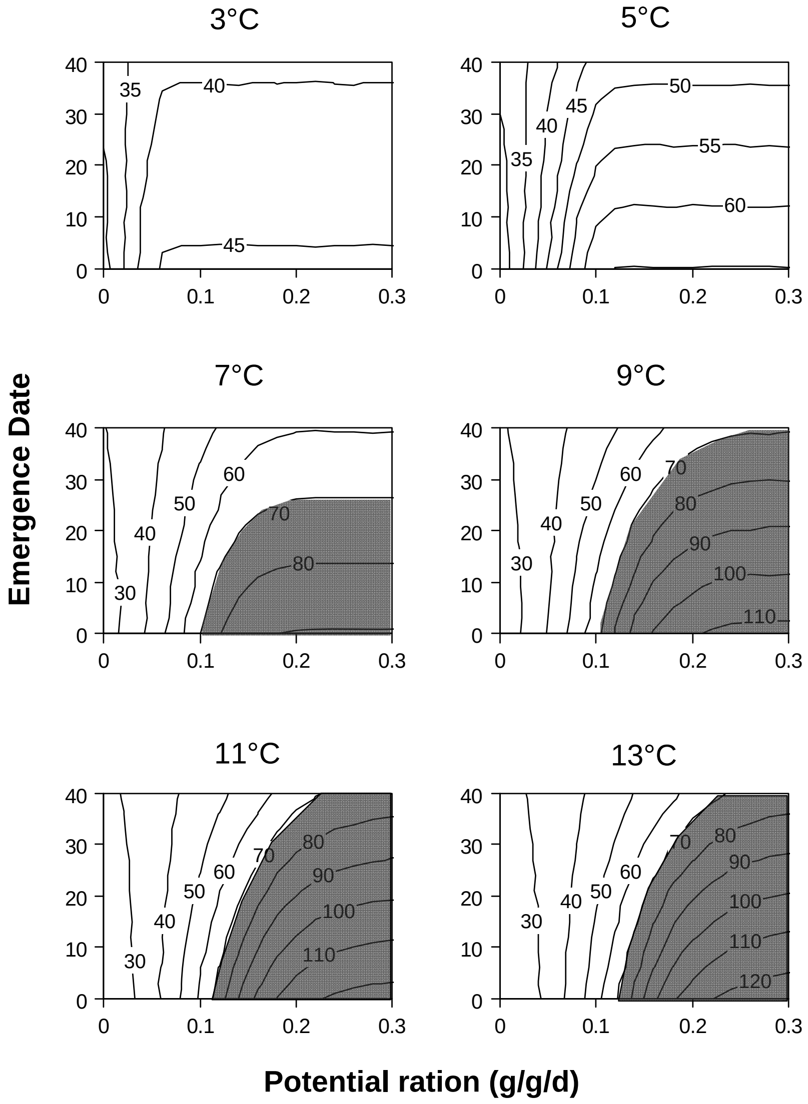

Figure 2.2 The results of bioenergetics simulations predicting the size of age-0 coho salmon on 15 August (the approximate date of peak egg abundance) in streams with different thermal regimes. Each panel shows contours of fork length (mm) that result from different combinations of emergence date (days after 25 May) and food availability (potential ration: g food/g fish/d). Panels differ by the mean daily water temperature used in simulations, which is shown above each panel in ° C. Regions of predicted growth that exceed the gape-size limit to eat water-hardened sockeye eggs (70 mm, Fig.3b) are shaded. The prey energy density used in simulations, 3.50 kJ/g wet mass, was the mean energy density of coho diet samples not containing eggs (sd=1.02, n=522).

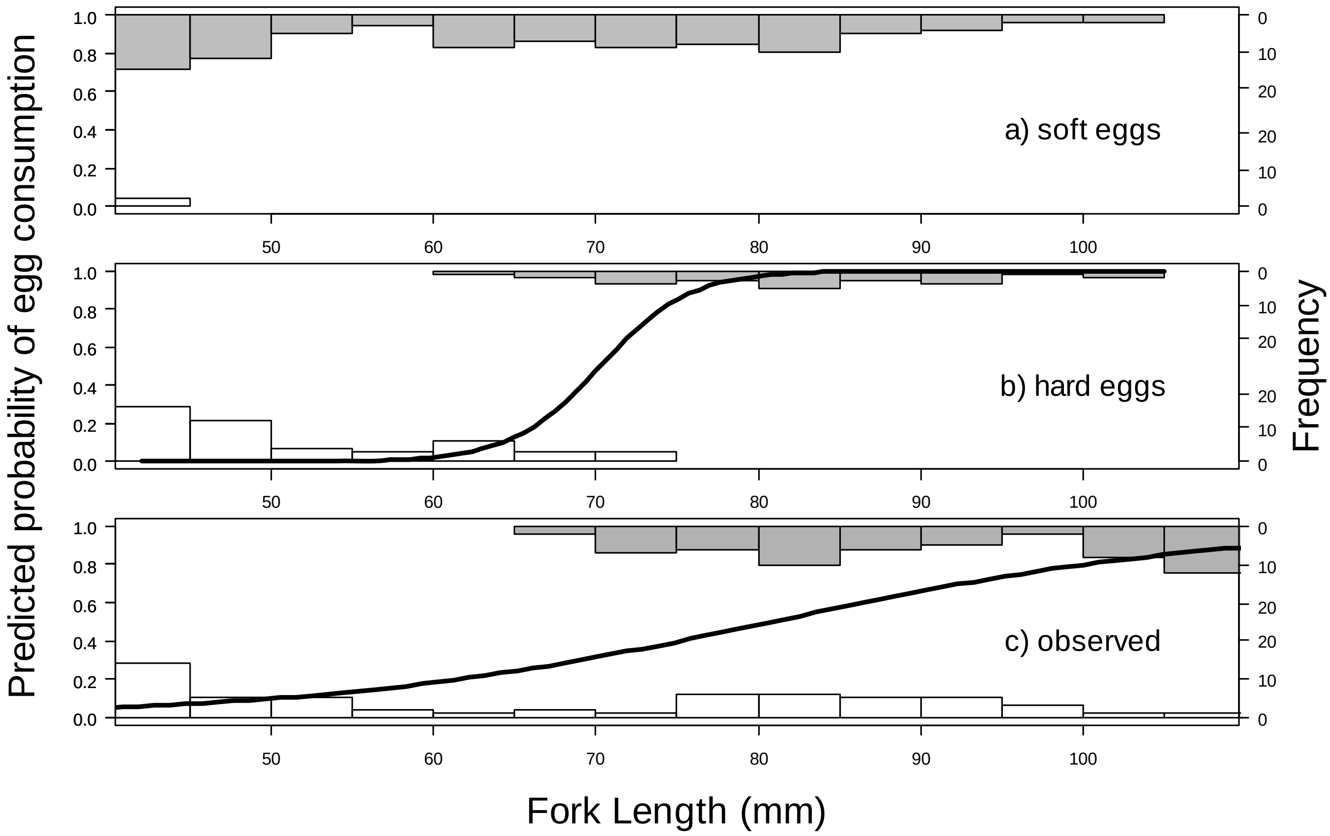

Figure 2.3 Graphs of fork length vs. the occurrence of egg consumption from juvenile coho salmon fed fresh- and water-hardened sockeye salmon eggs *in situ* (a & b, respectively) and from observed stomach contents in natural populations (c). A fitted logistic regression shows the predicted probability of egg consumption (left y-axis) as fork length increases (a: n.s., b: $p<0.01$. c: $p<0.001$). The right y-axis axis shows the frequency of individuals in each 5 mm size bin that did (top histogram, shaded) or did not (bottom histogram, non-shaded) consume eggs.

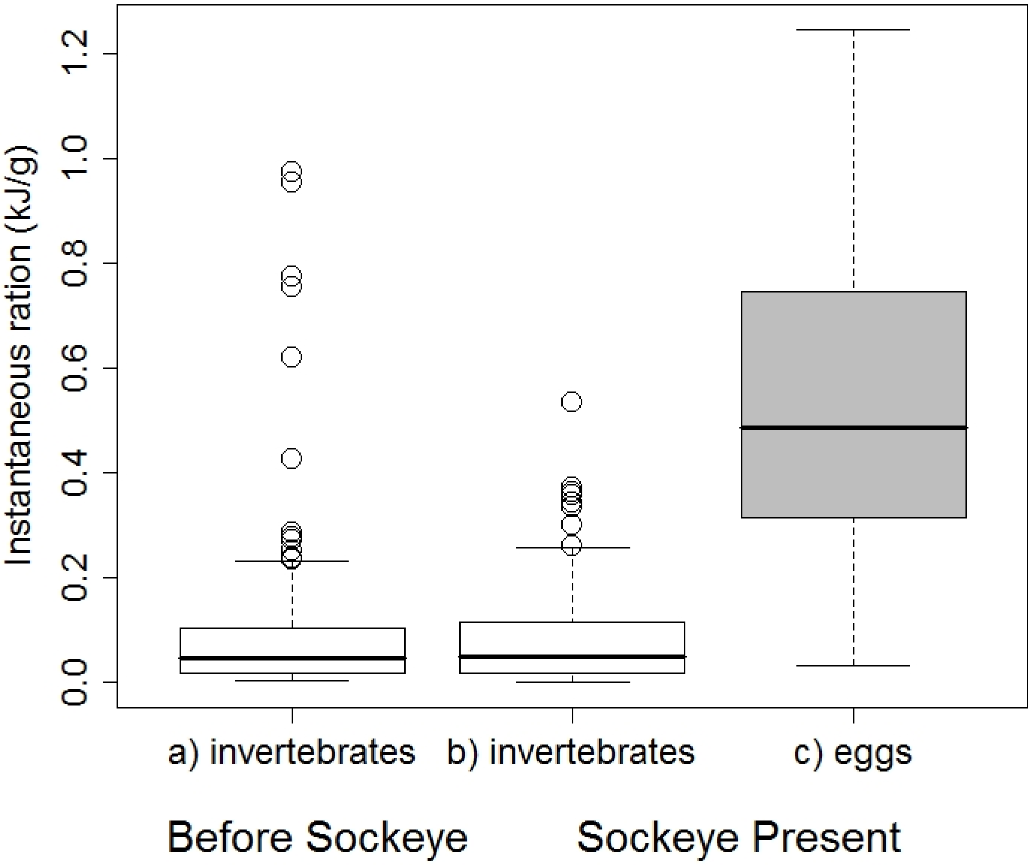

Figure 2.4 Box plots of instantaneous ration (total energy of diet contents divided by fish mass) for juvenile coho salmon in three groups: (a) fish sampled prior to sockeye salmon spawning, when invertebrates were the dominant food item (n=182), (b) fish sampled during sockeye spawning that had no eggs in their stomach (n=110), and (c) fish sampled during sockeye spawning that eggs in their stomach (n=113, shaded). Fish that did not eat eggs had diets comprised of invertebrates. Shades denote statistically significant differences in instantaneous ration among groups (Kruskal Wallis test, p<0.001). Fish with empty stomachs (n=9) were excluded from the analysis, though they did not affect results. Outliers are shown as circles.

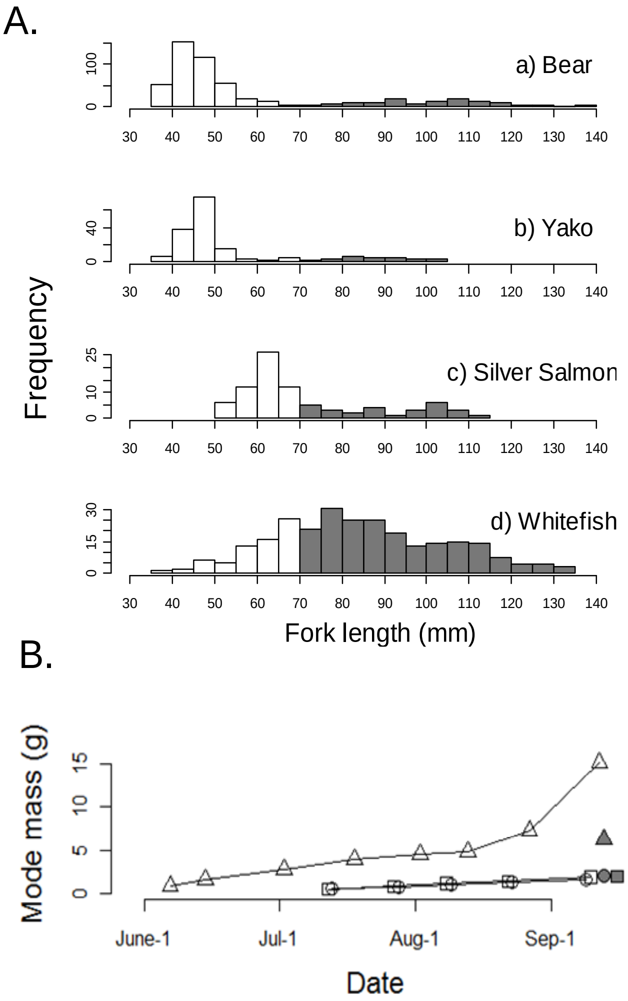

Figure 2.5 (A) Size distributions of juvenile coho salmon in four streams sampled during mid-August, when sockeye salmon eggs were most abundant. Panels are labeled by stream. Size bins with >50% predicted probability of being able to eat water-hardened sockeye salmon eggs (fork length>70 mm, Fig. 3b) are shaded grey. Note differing scale in y-axes. (B) The modal coho salmon body mass through the summer in three streams: Whitefish Ck. (triangles), Bear Ck. (circles), and Yako Ck. (squares). Shaded symbols at right show the predicted coho salmon body mass at 7 September in the absence of sockeye salmon subsidies, based on bioenergetics simulations. The symbols for Bear and Yako overlap, due to similar patterns of growth in both streams.

Chapter 3: Diel horizontal migration in streams: juvenile fish exploit spatial heterogeneity in thermal and trophic resources

This chapter was under revision at *Ecology* when this dissertation was submitted.

Abstract:

Vertical heterogeneity in the physical characteristics of lakes and oceans is ecologically salient and exploited by a wide range of taxa through diel vertical migration to enhance their growth and survival. Whether analogous behaviors exploit longitudinal habitat heterogeneity in streams is largely unknown. Here we document cyclic horizontal movements at daily time scales in a stream-dwelling fish. Juvenile coho salmon made feeding forays into cold habitats with abundant food, and then moved long distances (350-1300 m) to warmer habitats to accelerate metabolism and increase their assimilative capacity. This behavioral thermoregulation enabled fish to mitigate trade-offs between trophic and thermal resources by exploiting thermal heterogeneity. Fish that exploited thermal heterogeneity grew at substantially faster rates than individuals that assumed other behaviors. Our results provide empirical support for the importance of thermal diversity in lotic systems, and emphasize the importance of considering interactions between animal behavior and habitat heterogeneity when restoring ecosystems.

Introduction:

Habitat homogenization has been one of the most prevalent transformations that humans have caused to the Earth. Activities such as agriculture (Benton et al. 2003), industrial fishing (Thrush and Dayton 2002), and urbanization (McKinney 2006) can directly homogenize physical templates, while the suppression of disturbance regimes (Poff et al. 2007) and the functional extirpation of ecosystem engineers (Owen-Smith 2005) can dampen the underlying processes that maintain and generate habitat heterogeneity. Habitat homogenization can reduce biodiversity by eliminating the niches of native species or facilitating colonization by invasive species (Rahel 2002). Habitat homogenization may also threaten intra-specific diversity by reducing local adaptation and genetic variation among populations or phenotypic variation within populations (Watters et al. 2003). While habitat homogenization clearly affects biological diversity, less is known about how it affects biological productivity, for example by influencing the growth and survival of individuals (Wang et al. 2006, Ruff et al. 2011).

Individuals can exploit habitat heterogeneity by moving among habitats at a variety of spatial and temporal scales that enable them to capitalize on the benefits of disparate habitats. Many animals exhibit movements that generate cyclic patterns of habitat use, such as central place foraging (Orians and Pearson 1979), retreat behavior (Huey 1991), and diel vertical migration (Narver 1970, Wurtsbaugh and Neverman 1988, Scheuerell and Schindler 2003). Diel vertical migration (DVM) is ubiquitous in aquatic ecosystems and performed by organisms ranging from plankton in small ponds (Gilbert and Hampton 2001) to sharks in the open ocean (Campana et al. 2011). DVM behavior may have broader ecological effects, such as mediating food web structure and nutrient cycling (Schindler et al. 1993), or interacting with landscape features to determine the spatial distribution of commercially important predators (Genin 2004). Given the importance of DVM to our understanding of marine and lentic aquatic systems, there is surprisingly little known about how organisms in lotic systems (i.e., streams and rivers) use daily movements to exploit habitat heterogeneity (Hohausova et al. 2003, Muhlfeld et al. 2003). This dearth of knowledge is problematic because stream habitats are some of the most threatened on the planet and subject to widespread homogenization and fragmentation (Rahel 2002, Poff et al. 2007). Society is investing substantial resources to restore physical attributes of stream habitat, yet these efforts frequently fail to generate substantial biological responses (Palmer et al. 2009, Beechie et al. 2010), suggesting that critical habitat characteristics remain impaired following most restoration efforts.

Perhaps the most biologically important aspect of aquatic ecosystems is water temperature (Magnuson 1979). A basic paradigm of hydrology is that streams gradually warm as they flow downstream and equilibrate to air temperature (Vannote et al. 1980). However, as improvements in technology increase the ability of researchers to measure water temperature, there is increasing recognition that nested within these coarse-scale patterns there exists finer-scale thermal heterogeneity that may be ecologically important (Torgersen et al. 1999, Armstrong et al. 2010, Ruff et al. 2011). Many studies have shown that fish can exploit thermal heterogeneity to cope with heat stress. For example, during hot or dry periods, organisms move to habitat types that are weakly coupled to regional climate, such as catfish burrows (Glodek 1978), deep pools (Torgersen et al. 1999), and groundwater seeps (Torgersen et al. 1999, Breau et al. 2011). However, there is virtually no knowledge of how stream dwelling organisms exploit thermal heterogeneity under non-stressful conditions. An important question is whether organisms in streams exploit thermal heterogeneity not merely to survive, but also to thrive. Here we investigate whether stream dwelling fish can exploit spatial heterogeneity in water temperature to increase their digestive and growth capacity during a resource pulse.

Foraging opportunities for fish are patchy in time (Armstrong and Schindler 2011), and individuals may achieve the majority of growth and energy storage while gorging during resource pulses (Junk 1985, Denton et al. 2010). Water temperature sets the maximum rates for digestion and absorption (i.e., assimilation) and can limit the extent to which consumers benefit from resource pulses in aquatic ecosystems (Brett 1971, Elliot and Persson 1978). If prey are abundant in areas with suboptimal temperatures, fish may exploit thermal heterogeneity by selecting different habitats for foraging and assimilation. For example, larval sculpins in a thermally stratified lake fed during the day in cool waters below the thermocline, and ascended to warmer waters during the night, which provided over 3-x faster rates of assimilation (Wurtsbaugh and Neverman 1988). In laboratory experiments, fish have been shown to select warmer habitat after being fed larger meals (Mac 1985). The energetic benefits conferred by these examples of post-feeding thermotaxis are supported by empirically derived physiological models (Elliot and Persson 1978). Despite increasing recognition that the energy budgets of fish are constrained by rates of assimilation, and a strong mechanistic understanding of how fish can manipulate assimilative capacity through cyclic use of thermal habitat, there is virtually no evidence of fish in lotic systems exploiting thermal heterogeneity to increase growth (but see Hohausova et al. 2003). Here we provide new evidence of lotic consumers exhibiting behavioral thermoregulation to increase their assimilative capacity. Specifically, we explore the foraging behavior of juvenile coho salmon (*Oncorhynchus kisutch*) in a thermally heterogeneous stream with a seasonal resource pulse.

Coho salmon occur through much of the Pacific Rim and often rear in streams where additional species of Pacific salmon (*Oncorhynchus* spp.) spawn and generate resource pulses as energy-rich eggs become available to consumers. The assimilative capacity of coho salmon exhibits a dome-shaped relationship with water temperature, increasing rapidly from 5-10°C and peaking around 15°C (Brett 1971, Stewart and Ibarra 1991). When Pacific salmon spawn in summer and fall, spatial variation in water temperature may be high in magnitude (>5°C) both within and among streams (Armstrong et al. 2010, Ruff et al. 2011). This thermal heterogeneity provides the potential for coho salmon to regulate their assimilative capacity through movement.

In many instances, salmonid spawning habitat is spatially associated with cold upwelling groundwater (Lorenz and Filer 1989, Baxter and Hauer 2000) which can produce energetic trade-offs for stream-dwelling fishes that feed on the embryos of conspecifics or of other species, where prey productivity and assimilative capacity are inversely related across space. We sought to quantify such trade-offs and explore whether coho salmon could increase their energy intake by exploiting the thermal heterogeneity across a riverscape. The objectives of this study were to (1) map spatial patterns of spawning salmon density and water temperature to characterize trade-offs between trophic and thermal resources, (2) monitor the foraging behavior of juvenile coho salmon to describe how they exploit thermal heterogeneity within individual streams, (3) measure stomach capacity and thermal effects on assimilation rates to assess the physiological underpinnings of potential thermoregulatory strategies, and (4) test whether behavioral strategies that exploit horizontal thermal heterogeneity confer increased growth rates.

Methods:

Study system

This research was conducted in the Wood River watershed, which consists of five large interconnected lakes that drain into Bristol Bay, SW Alaska, USA. Our focal system is Bear Creek, a 4-km-long tributary of Lake Aleknagik. From its headwaters, Bear Creek travels roughly 2.5 km through beaver-meadow-complex habitat where it is 1-3 m wide. In the final 1.5 km before the stream enters Lake Aleknagik, groundwater springs augment the flow and the stream increase in width to 4-8 m. Coho salmon rear in Bear Creek for 2 or 3 years and do not grow large enough to consume salmon eggs until their second year of life (Armstrong et al. 2010). Sockeye salmon spawn annually in Bear Creek from late-July to mid-August. After spawning, eggs may be available to consumers if they are poorly buried or exposed by scour from high flows. Sculpins (*Cottus* spp.) and juvenile char (*Salvelinus* spp. < 200 mm) are the only other fishes consistently present in the stream. Piscivorous fishes including adult char (*Salvelinus* spp. >200 mm) and Northern pike (*Esox lucius*) are abundant in Lake Aleknagik, and can occur in high densities near the mouth of Bear Creek, but they have not been observed more than 100 m upstream. River otters (*Lontra canadensis*) are present and likely prey on juvenile coho salmon.

Quantifying spatial and temporal patterns in water temperature

We recorded time-series of thalweg (i.e. main channel) water temperature at point locations upstream and downstream of the groundwater springs using calibrated i-Button temperature data loggers (Dallas Semiconductor, Dallas, Texas, USA) that recorded temperature at 90-minute intervals (± 1°C). In 2007, we deployed 3 temperature data loggers, and in 2008 we deployed 5. To quantify the temperature available to juvenile coho salmon during the period over which they could potentially consume sockeye salmon eggs, we calculated the average temperature when sockeye salmon were actively spawning in the stream (21 July -21 August). We generated a high-resolution (1 m), spatially continuous map of water temperature in the entire study reach of Bear Creek on 4 August 2008 as outlined by Ruff et al. (2011).

Quantifying spatial and temporal patterns of sockeye salmon abundance

From 2005-2008, we visually enumerated and mapped the spatial distribution of spawning sockeye salmon in Bear Creek at a resolution of 200 m stream reaches. There were 3 counting events per year. In 2007 and 2008, we performed supplementary presence/absence surveys to confirm the upstream extent of spawning sockeye salmon.

Field monitoring of coho salmon foraging behavior

We monitored the spatial distribution, diet, growth, and in-stream movement of age-1 and age-2 coho salmon (> ~65 mm fork length) throughout the summer. Our sampling events spanned from late June to early September, at bi-weekly intervals in 2007 (*n* = 6) and approximately 10-d intervals in 2008 (*n* = 8) centered around the peak of sockeye salmon spawning that occurred from 1 August to 19 August. During each event, we visually surveyed and sampled all pools and off-channel habitat in the lower 2000 m of the stream and opportunistically surveyed habitats further upstream when time permitted. A researcher in a dry suit and snorkel gear visually surveyed each habitat unit, and if juvenile coho salmon were present, the researcher herded the fish into a seine net. Fish were measured to the nearest 1 mm fork length and released. A random subset of these fish was weighed and sampled for diet by gastric lavage. In 2008, we tagged fish greater than 60 mm fork length with passive integrative transponder (PIT) tags and scanned all captured fish with a hand-held PIT tag reader to detect recaptures. Between 26 June and 21 August, we tagged 405 individuals ranging in fork length from 60-115 mm and weighing 2.4-19.2 g.

Monitoring fish movement

In 2008, we installed stationary antenna arrays equipped with PIT tag readers that recorded individual fish ID and a timestamp when tagged fish swam past the antenna (Bond et al. 2000). Each antenna spanned the entire stream and was placed in shallow riffle habitat (< 20 cm depth) where the detection range extended beyond the water surface. We installed two sites, each equipped with paired antennas that identified the direction of fish movement based on the sequence of detections. One site was located 930 m upstream from Lake Aleknagik, near the upper limit of spawning sockeye salmon. The second site was located 1360 m upstream, immediately downstream of a groundwater seep entering the stream channel. Thus, the antenna sites divided the stream into three regions: a cold downstream region with abundant sockeye salmon (region *I:* 0-930 m), a cold middle region with few if any sockeye salmon (region *II*: 930-1360 m), and a warm upstream region where spawning sockeye salmon were absent (region *III*: 1360 m +). The lower antenna site collected data from 29-July to 19-August, and the upper antenna site collected data from 31-July to 4-August and 9-August to 19-August. The non-functioning periods during which no data were collected were caused by brown bears (*Ursus arctos*) damaging the antennas. We estimated detection efficiency as follows: the total number of detections was the sum of serial detections between two different antennas for an individual tag (n = 1536). Positive detections were classified as serial detections between adjacent antennas (n = 1463), whereas missed detections were serial detections between non-adjacent antennas (e.g. those separated by another antenna) (n = 63). Positive detections represented 96% of the total number of detections.

Analyzing movement data

For each tagged fish that was detected on an antenna, we identified transitions among the three regions (*I*, *II*, and *III*) of stream based on serial detections at the antenna sites bordering the regions. The possible upstream transitions were *I-II* and *II-III*, and the downstream transitions were *III-II* and *II-I*. We were interested in whether individuals made diel horizontal movements (DHM) between region *III* and region *I*, exhibiting a sequence of transitions as follows: *III-II*, *II-I*, *I-II*, *II-III* in a period of less than 24 hours. During the period when only the lower antenna site was functional, we considered a DM to occur if an individual was recaptured in *region III* in between successive *I-II*, *II-I* transitions spanning a period of less than 72 hours. To characterize the timing of diel movements, we filtered the data for transitions that represented diel movement sequences, pooled the data across individuals, and calculated the modal times of day when fish exhibited the 4 transitions comprising a DHM. We calculated the mode from kernel density estimates based on the circular distributions of time of day, and selected the bandwidth following the methods outlined in Hall et al. (1987) implemented through the *Circular* package in R (R Development Core Team 2012).

Growth rate estimation

We identified four movement strategies: *downstream non-movers*, *upstream non-movers*, *diel movers*, and *unassigned movers*. *Downstream non-mover* was applied to individuals that were tagged and recaptured in region *I* or *II* but not detected moving upstream into region *III*. *Upstream non-movers* were fish that were tagged and recaptured in region *III* but not detected moving into region *II*. *Diel mover* individuals were those that made at least one DHM. Individuals that did not exhibit diel movement but were detected or recaptured between region *III* and region *I* or *II* were considered *unassigned movers*. We calculated instantaneous growth of recaptured individuals if the time interval between recaptures spanned the period when sockeye salmon were spawning (21 July to 20 August) and was at least 7 days long. We calculated growth, G, as

(1) $G = \ln(mass_F) - \ln(mass_I) / t$

where $mass_F$ is the mass at final capture, $mass_I$ is the mass at initial capture, and t is the number of days elapsed between captures. We used linear mixed effects models to model growth using the *nlme* library in R (R Development Core Team 2012). Our response variable was growth rate from eq. 1, and our candidate models included strategy and body size as fixed effects. Because some individuals were recaptured multiple times, we included individual ID as a random effect. The full model was

(2) $G_i = \beta_0 + \tau_0 + \beta_1 X_{\mathrm{i},} + n_i + \tau_1 X_i + \varepsilon_{\mathrm{i}}$

where G_i is the growth of individual i, β_0 is the intercept, τ_0 is an adjustment to the intercept due to the fixed effect of strategy on growth, β_1 is a coefficient (i.e., slope) describing the fixed effect of the natural logarithm of body mass, X_i, on growth, n_i is the random effect of individual, τ_1 is the adjustment to slope due to strategy, and ε_i is error.

We compared four candidate models nested within the full model by setting different parameters (τ_0 , τ_1) to zero and selecting the best model using Akaike's information criterion adjusted for small samples size (AICc; Burnham and Anderson 2002)

Quantifying stomach capacity and gastric evacuation rates

We performed an *in situ* experiment to measure coho salmon stomach capacity and rates of gastric evacuation of stomach contents. The experiment occurred in Whitefish Creek, which is located 6 km from Bear Creek, exhibits thermal heterogeneity, and has an abundance of juvenile coho salmon that exploit sockeye salmon eggs. We found a stream reach in which no spawning salmon were present, and we experimentally added fresh eggs from 3 adult sockeye salmon (~9000 eggs total). For a period of 10 minutes, we added eggs into two pools with high densities of coho salmon and where we could confirm that they were actively feeding on the eggs we fed them. We waited an additional 10 minutes, at which point most individuals were no longer feeding (i.e., satiated). We then seined each pool and randomly assigned fish to two 20-L holding tanks. The tanks were placed on either side of a naturally occurring thermal gradient (a tributary junction) and allowed 90 minutes to acclimate to ambient temperatures. We randomly transferred fish from the holding tanks into 8 conical Gee minnow traps (44 X 23 cm), placing 6 individuals in each trap. We placed 4 traps in low-velocity areas of the tributary plume and 4 traps in low-velocity areas of the warmer main-stem. We used a fast-response thermometer (AquaTuff 35232, Cooper Atkins, Middlefield, Connecticut, USA) to verify that temperatures were homogeneous within each thermal treatment, and placed temperature data loggers in each treatment to monitor water temperature. Remaining individuals in the holding tank (*n* = 7) were sacrificed to measure their stomach capacities. At 24 h, 49.5 h, and 72 h after the onset of the experiment, we sacrificed two fish from each trap and immediately brought them to the laboratory for analysis. In the lab, we recorded the wet weight of each fish and then removed the gut (stomach, pyloric caeca, and intestine) and weighed it to the nearest 0.01 g. We made a single incision along the length of the gut, carefully removed all contents from the stomach and intestines, and then weighed the empty gut. We used the difference between the weight of the full and empty gut to calculate the weight of food remaining in the gut. We calculated the remaining ration as the mass of food in the gut divided by the total body mass of the fish (not including gut contents).We aggregated the data into the mean remaining ration per trap and used this value as our replicate for summary statistics.

Results

Spatial patterns of trophic resources and thermal heterogeneity in Bear Creek Groundwater springs located 1360 m and 1670 m upstream augmented stream flows and generated a stair-step pattern of downstream cooling along the stream thalweg (Fig. 1a). Upstream of these springs, the mean temperature during the period when sockeye salmon spawn (21 July to 21 Aug) was 10.8°C in 2008 (not recorded in 2007) (Fig. 1a). In the stream reach between the two groundwater springs, the mean temperatures were 9.7°C and 8.9°C in 2007 and 2008, respectively (Fig. 1a); in the lower 1360 m of stream, the mean temperature ranged from 7.1 to 7.4°C in 2007 and 6.1 to 7.0°C in 2008 (Fig. 1a).

In 2005-2008, sockeye salmon spawning occurred in the cold downstream reaches of Bear Creek (Fig. 1a), most of which was in the lower 600 m of the stream (mean = 85% of fish, range = 82-94%). The upstream extent of the sockeye distribution extended 800-1200 m upstream depending on the sampling event. Numerous presence/absence surveys in 2007 and 2008 confirmed that spawning sockeye salmon were not present in the warm region upstream (region *III*).

Field sampling of juvenile coho salmon

Before and after the peak of the sockeye salmon run, coho salmon occurred in all three regions of Bear Creek (Figure S1). When the sockeye salmon run peaked in early August, the majority of juvenile coho salmon occurred in region *III* (2007: 65%, 2008: 80%), whereas no coho salmon occurred in region *I* (Fig. 1b). Throughout the sockeye salmon run, the highest densities of coho salmon occurred in the 200 m unit just upstream of the major thermal gradient (Fig. 1, Fig. S1). Despite the absence of spawning sockeye salmon, coho salmon captured in region *III* consistently had sockeye salmon eggs in their diet. During the sockeye salmon run, 18-88% of the coho salmon in the upstream warm region (III) had eggs in their stomach contents (mean = 48%, *n* = 7 sampling events).

Juvenile coho salmon movement

28 percent of the juvenile coho salmon detected by PIT tag antennas exhibited diel movement between the cold region with eggs and the warm region upstream (30/109 individuals) (Fig. 2a). This behavior consisted of fish leaving region *III* at dusk (modal time = 22:52 Alaska Daylight Time), moving quickly downstream through region *II* (930-1360m upstream), and arriving in region *I* shortly thereafter (modal time = 23:25 ADT) (Fig. 2b). These individuals remained downstream for variable amounts of time (median = 4.3 h, SD ± 8.2 h, *n* = 83), but 80% of the individuals returned upstream within 7.5 h (Fig. 2c). The modal time of upstream movements from region *I* to *II* was 5:34 ADT, and the modal time of upstream

movements from region *II* to *III* was 6:42 ADT (Fig. 2b). After completing a feeding foray downstream, individuals remained upstream 1-5 d prior to the next feeding foray (median duration = 52.5 h, $n = 88$) (Fig. 2d). The distribution of time spent between feeding forays exhibited multiple modes with 80% of individuals spending 1-3 d upstream (Fig. 2d).

Stomach capacity and rates of gastric evacuation:

After roughly 20 minutes of *ad.lib*. feeding on sockeye salmon eggs, juvenile coho salmon were visibly full and the mass of salmon eggs in their stomach averaged 13.3% of their total body mass ($n = 7$, range = 10.5-17.6%). The gastric evacuation of eggs followed a roughly linear trend (Fig. 3a). In the warm treatment (mean temperature = 10.5°C, SD ± 0.47°C) the remaining ration was 8.8% of body mass after 24 h (SD ± 2.4%, $n = 4$) and 1.8% after 72 h (SD ± 0.95%, $n = 4$). In the cold treatment (mean temperature = 6.6°C, SD ± 0.28°C,) the remaining ration was 12.3% of body mass after 24 h (SD ± 1.9%, $n = 4$) and 7.3% after 72 h (SD ± 1.6%, $n = 4$) (Fig. 3a).

Growth rates of juvenile coho salmon:

The best model for predicting growth of juvenile coho salmon included a single slope describing the effect of body mass on growth with different intercepts for each movement strategy (Fig. 3b, Table. S1).The *diel mover* strategy exhibited the highest growth rates (Fig. 3b). For the average size fish during the resource pulse (~7 g), predicted growth for the *diel mover* strategy was 217% higher than the *upstream non-mover* strategy ($p<0.0001$), 63% higher than the *unassigned mover* strategy ($p=0.0001$), and 22% higher than the *downstream non-mover* strategy (*n.s.*) (Fig. 3b).The *downstream non-mover* strategy occurred in only ten individuals and eight of them were either tagged or recaptured in warm off-channel habitats.

Discussion:

The spatial distribution of water temperature and sockeye salmon in Bear Creek presented juvenile coho salmon with a trade-off between trophic and thermal resources. Sockeye salmon eggs were only available in the downstream reaches of the stream, where cold water temperatures (6-7°C) constrained the assimilative capacity of coho salmon and, thus, their potential to convert food into growth and energy reserves (Fig. 1). Warmer temperatures (9-11°C) providing over 2-fold higher rates of assimilation occurred > 350 m from the upstream extent of the sockeye salmon distribution (Fig. 1a, Fig. 3a). We observed behavior that enabled fish to simultaneously exploit both trophic and thermal resources through diel horizontal movement. Fish exhibiting this behavior moved into the cool downstream region to feed on eggs, and then returned to the warm upstream region to digest —a round trip of at least 860 m, or roughly 10,000 body lengths in less than a day. These feeding movements were interspaced temporally with long digestive pauses that usually lasted 1-3 days (Fig. 2d). Feeding experiments demonstrated that the observed movement behavior would reduce thermal constraints on food processing, and individuals that exhibited this behavior grew at faster rates than individuals exhibiting other behavioral strategies (Fig. 3).

Coho salmon feeding movements occurred during the low light period of the day, with fish moving downstream around dusk and returning around dawn. This crepuscular timing of movement enabled juvenile coho salmon to forage during the darker, colder time of day and process food during the brighter, warmer part of the day. This likely increases not only assimilative capacity, but also the ratio of energy intake to predation risk (Scheuerell and Schindler 2003). Feeding behavior exposes animals to predation (Clark and Levy 1988, Stoks et al. 2003), so it is not surprising that coho salmon fed on eggs during low light periods, when they were less vulnerable to piscivores (e.g. river otters and larger fish) or territorial sockeye salmon.

However, low light levels would also reduce the ability of coho salmon to visually detect sockeye salmon eggs, forcing them to find eggs through olfaction alone (Quinn et al. 2012), and reducing the probability of feeding to full stomach capacity.

We observed substantial variation in the duration of time spent between feeding forays (range = 16-169 h, *n* = 30). Most of this variation occurred within rather than among individuals. For example, of the individuals that we could monitor long enough to record multiple inter-feeding periods (digestive pauses), all but one individual exhibited digestive pauses ranging by a day or more in duration (median range = 48 h, *n* = 20). This likely reflected variation in the meal size (number of sockeye salmon eggs consumed) during feeding forays. Our feeding experiment suggested that rations of 20-100% of stomach capacity would require periods ranging from about the shortest observed digestive pause (16 h) to upwards of 100 h for complete assimilation in region *III*. Combined with the crepuscular timing of movement, this explains the multimodal distribution in the durations of digestive pauses--individuals moved upstream at around dawn, assimilated variable quantities of salmon eggs, and then waited until the next dusk to begin another feeding foray.

The digestive pauses that we observed in coho salmon are some of the longest recorded in fish. For example, larval sculpin exhibiting post-feeding movements to warm water required less than 1 day to process a full meal obtained in colder waters (Wurtsbaugh and Neverman 1988, Neverman and Wurtsbaugh 1994). The shorter digestive pause observed in sculpin was likely due to differences in initial ration size and body weight; the larval sculpin consumed half as much food prior to thermotaxis (7-9% of body weight vs. 11-18% in this study), and were 3-4 orders of magnitude smaller in body weight (2.4 mg vs. ~10 g this study), which would confer a much higher mass-specific metabolic rate and thus a shorter digestive pause. The time required to assimilate salmon eggs may be longer than that required by other food items because eggs are especially rich in lipids, which are retained for long periods in the gut (Windell et al. 1969). Also, coho salmon consume eggs whole, and it is possible that the intact egg shell is resistant to digestion.

Our *in situ* feeding experiment revealed that coho salmon can consume up to 18% of their body mass in less than 20 minutes, a foraging rate 200 to 400-times faster than what their digestive machinery can keep pace with. This excess foraging capacity may be common among predators (Kersten and Visser 1996, Essington et al. 2000, Trumble et al. 2003), yet it is rarely measured or reported. The excess foraging capacity of juvenile coho salmon represents the highest level of excess capacity yet to be formally measured in a serial biological system (Diamond 2002, Piersma and van Gils 2010). For example serial components of the respiratory chain (Wiebel et al. 1991), enzyme reaction chains (Diamond 2002), and the latter portion of the food-processing chain (Piersma and van Gils 2010) exhibit levels of excess capacity 10-100 times smaller than what we documented in coho salmon foraging and assimilation. Stomach capacity provides a buffer that allows animals to ingest food faster than they can assimilate it. Large stomachs have been described as an adaptive response to patchy foraging opportunities, enabling predators to opportunistically capitalize on large prey items or intermittent prey encounters (Essington et al. 2000). Our results suggest that large stomachs are not merely for feeding conditions that are inherently patchy—they are also fundamental to foraging strategies that exploit habitat heterogeneity. With no stomach capacity, an animal would have to acquire and process food in the same location—facing potential trade-offs among ecological resources if they don’t overlap in space. With a large stomach, an individual can exploit spatial heterogeneity by foraging where food is abundant, and then moving to digest food in areas that are safer or provide more favorable temperatures for metabolism. A higher stomach capacity allows longer periods between feeding forays, thus reducing the activity cost and predation risk per unit of gross energetic profit. It appears the “excessive” foraging capacity exhibited by coho salmon is actually an economic feature of their evolutionary design, enabling them to efficiently integrate across the thermal and trophic heterogeneity of their environment.

Researchers are increasingly recognizing the existence and ecological importance of thermal heterogeneity in streams (Torgersen et al. 1999, Armstrong et al. 2010, Ruff et al. 2011), yet understanding of behavioral thermoregulation is limited to cold-seeking thermotaxis during heat stress (Torgersen et al. 1999, Keefer et al. 2009, Breau et al. 2011). Our study is unique because it shows fishes exploiting thermal heterogeneity not just to slow metabolism and minimize losses, but instead to accelerate metabolism and maximize gains. Recent evidence suggests foraging opportunities for fish are highly variable (i.e. right-skewed), with opportunities for growth and energy storage occurring as pulsed events that exceed the assimilative capacity of consumers (Armstrong and Schindler 2011). Behavioral thermoregulation provides an adaptive physiological response to ecological heterogeneity, enabling poikilotherms to rapidly and reversibly adjust their assimilative capacity to match ambient foraging conditions. However, unlike other physiological adaptations to ecological heterogeneity (e.g., phenotype flexibility, excess capacity) the potential for behavioral thermoregulation is inextricably linked to landscape heterogeneity (Huey 1991, Sears et al. 2011). Thus human activities that homogenize or fragment habitat may inhibit the adaptations that allow animals to survive in dynamic environments. While recent technological advances have improved the ability to quantify habitat heterogeneity, our study emphasizes that we must also understand how animals interact with this heterogeneity to fully appreciate the constraints and opportunities that habitat variation poses to stream organisms. Restoration efforts in lotic ecosystems should also consider physical processes that produce and maintain thermal heterogeneity that may be a critical but underappreciated habitat feature in these ecosystems.

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References

Armstrong, J. B. and D. E. Schindler. 2011. Excess digestive capacity in predators reflects a life of feast and famine. Nature **476**:84-87.

Armstrong, J. B., D. E. Schindler, K. L. Omori, C. P. Ruff, and T. P. Quinn. 2010. Thermal heterogeneity mediates the effects of pulsed subsidies across a landscape. Ecology **91**:1445-1454.

Baxter, C. V. and F. R. Hauer. 2000. Geomorphology, hyporheic exchange, and selection of spawning habitat by bull trout (*Salvelinus confluentus*). Canadian Journal of Fisheries and Aquatic Sciences **57**:1470-1481.

Beechie, T. J., D. A. Sear, J. D. Olden, G. R. Pess, J. M. Buffington, H. Moir, P. Roni, and M. M. Pollock. 2010. Process-based Principles for Restoring River Ecosystems. Bioscience **60**:209-222.

Benton, T. G., J. A. Vickery, and J. D. Wilson. 2003. Farmland biodiversity: is habitat heterogeneity the key? Trends in Ecology & Evolution **18**:182-188.

Bond, M. H., C. V. Hanson, R. Baertsch, S. A. Hayes, and R. B. MacFarlane. 2007. A new low-cost instream antenna system for tracking passive integrated transponder (PIT)-tagged fish in small streams. Transactions of the American Fisheries Society **136**:562-566.

Breau, C., R. A. Cunjak, and S. J. Peake. 2011. Behaviour during elevated water temperatures: can physiology explain movement of juvenile Atlantic salmon to cool water? Journal of Animal Ecology **80**:844-853.

Brett, J. R. 1971. Energetic responses of salmon to temperature. A study of some thermal relations in physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). American Zoologist **11**:99-&.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer Verlag.

Campana, S. E., A. Dorey, M. Fowler, W. Joyce, Z. L. Wang, D. Wright, and I. Yashayaev. 2011. Migration Pathways, Behavioural Thermoregulation and Overwintering Grounds of Blue Sharks in the Northwest Atlantic. Plos One **6**.

Clark, C. W. and D. A. Levy. 1988. Diel vertical migrations by juvenile sockeye salmon and the antipredation window. American Naturalist **131**:271-290.

Denton, K. P., H. B. Rich, and T. P. Quinn. 2009. Diet, Movement, and Growth of Dolly Varden in Response to Sockeye Salmon Subsidies. Transactions of the American Fisheries Society **138**:1207-1219.

Diamond, J. 2002. Quantitative evolutionary design. Journal of Physiology-London **542**:337-345.

Elliott, J. M. and L. Persson. 1978. Estimation of daily rates of food-consumption for fish.

Journal of Animal Ecology **47**:977-991.

Essington, T. E., J. R. Hodgson, and J. F. Kitchell. 2000. Role of satiation in the functional response of a piscivore, largemouth bass (*Micropterus salmoides*). Canadian Journal of Fisheries and Aquatic Sciences **57**:548-556.

Genin, A. 2004. Bio-physical coupling in the formation of zooplankton and fish aggregations over abrupt topographies. Journal of Marine Systems **50**:3-20.

Gilbert, J. J. and S. E. Hampton. 2001. Diel vertical migrations of zooplankton in a shallow, fishless pond: a possible avoidance-response cascade induced by notonectids. Freshwater Biology **46**:611-621.

Glodek, G. S. 1978. The importance of catfish burrows in maintaining fish populations of tropical freshwater streams in western Ecuador.

Hall, P., G. S. Watson, and J. Cabrera. 1987. Kernel density-estimation with spherical data. Biometrika **74**:751-762.

Hohausova, E., G. H. Copp, and P. Jankovsky. 2003. Movement of fish between a river and its backwater: diel activity and relation to environmental gradients. Ecology of Freshwater Fish **12**:107-117.

Huey, R. B. 1991. Physiological consequences of habitat selection. American Naturalist **137**:S91-S115.

Junk, W. J. 1985. Temporary fat storage, an adaptation of some fish species to the waterlevel fluctuations and related environmental changes of the amazon river. Amazoniana-Limnologia Et Oecologia Regionalis Systemae Fluminis Amazonas **9**:315-351.

Keefer, M. L., C. A. Peery, and B. High. 2009. Behavioral thermoregulation and associated mortality trade-offs in migrating adult steelhead (*Oncorhynchus mykiss*): variability among sympatric populations. Canadian Journal of Fisheries and Aquatic Sciences **66**:1734-1747.

Kersten, M. and W. Visser. 1996. The rate of food processing in the Oystercatcher: Food intake and energy expenditure constrained by a digestive bottleneck. Functional Ecology **10**:440-448.

Mac, M. J. 1985. Effects of ration size on preferred temperature of lake charr salvelinus-namaycush. Environmental Biology of Fishes **14**:227-231.

Magnuson, J. J., L. B. Crowder, and P. A. Medvick. 1979. Temperature as an ecological resource. American Zoologist **19**:331-343.

McKinney, M. L. 2006. Urbanization as a major cause of biotic homogenization. Biological Conservation **127**:247-260.

Muhlfeld, C. C., S. Glutting, R. Hunt, D. Daniels, and B. Marotz. 2003. Winter diel habitat use and movement by subadult bull trout in the upper Flathead River, Montana. North American Journal of Fisheries Management **23**:163-171.

Neverman, D. and W. A. Wurtsbaugh. 1994. The thermoregulatory function of diel vertical migration for a juvenile fish, *Cottus extensus*. Oecologia **98**:247-256.

Orians, G. H. and N. E. Pearson. 1979. On the theory of central place foraging. Analysis of ecological systems. Ohio State University Press, Columbus:155-177.

Owensmith, N. 1989. Megafaunal extinctions - the conservation message from 11,000 years bp. Conservation Biology **3**:405-412.

Palmer, M. A., H. L. Menninger, and E. Bernhardt. 2010. River restoration, habitat heterogeneity and biodiversity: a failure of theory or practice? Freshwater Biology **55**:205-222.

Piersma, T. and J. A. van Gils. The flexible phenotype: a body-centred integration of ecology, physiology, and behaviour. Oxford University Press Oxford and New York.

Poff, N. L., J. D. Olden, D. M. Merritt, and D. M. Pepin. 2007. Homogenization of regional river dynamics by dams and global biodiversity implications. Proceedings of the National Academy of Sciences of the United States of America **104**:5732-5737.

Rahel, F. J. 2002. Homogenization of freshwater faunas. Annual Review of Ecology and Systematics **33**:291-315.

Ruff, C. P., D. E. Schindler, J. B. Armstrong, K. T. Bentley, G. T. Brooks, G. W. Holtgrieve, M. T. McGlauflin, C. E. Torgersen, and J. E. Seeb. 2011. Temperature-associated population diversity in salmon confers benefits to mobile consumers. Ecology **92**:2073-2084.

Scheuerell, M. D. and D. E. Schindler. 2003. Diel vertical migration by juvenile sockeye salmon: Empirical evidence for the antipredation window. Ecology **84**:1713-1720.

Schindler, D. E., J. F. Kitchell, X. He, S. R. Carpenter, J. R. Hodgson, and K. L. Cottingham. 1993. Food-web structure and phosphorus cycling in lakes. Transactions of the American Fisheries Society **122**:756-772.

Sears, M. W., E. Raskin, and M. J. Angilletta Jr. The world is not flat: defining relevant thermal landscapes in the context of climate change. Integrative and comparative biology **51**:666-675.

Stewart, D. J. and M. Ibarra. 1991. Predation and production by salmonine fishes in lake-michigan, 1978-88. Canadian Journal of Fisheries and Aquatic Sciences **48**:909-922.

Stoks, R., M. A. McPeek, and J. L. Mitchell. 2003. Evolution of prey behavior in response to changes in predation regime: Damselflies in fish and dragonfly lakes. Evolution **57**:574-585.

Team, R. R: A language and environment for statistical computing. R Foundation for Statistical

Computing Vienna Austria.

Thrush, S. F. and P. K. Dayton. 2002. Disturbance to marine benthic habitats by trawling and dredging: Implications for marine biodiversity. Annual Review of Ecology and Systematics **33**:449-473.

Torgersen, C. E., D. M. Price, H. W. Li, and B. A. McIntosh. 1999. Multiscale thermal refugia and stream habitat associations of chinook salmon in northeastern Oregon. Ecological Applications **9**:301-319.

Trumble, S. J., P. S. Barboza, and M. A. Castellini. 2003. Digestive constraints on an aquatic carnivore: effects of feeding frequency and prey composition on harbor seals. Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology **173**:501-509.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. River continuum concept. Canadian Journal of Fisheries and Aquatic Sciences **37**:130-137.

Wang, G. M., N. T. Hobbs, R. B. Boone, A. W. Illius, I. J. Gordon, J. E. Gross, and K. L. Hamlin. 2006. Spatial and temporal variability modify density dependence in populations of large herbivores. Ecology **87**:95-102.

Watters, J. V., S. C. Lema, and G. A. Nevitt. 2003. Phenotype management: a new approach to habitat restoration. Biological Conservation **112**:435-445.

Weibel, E. R., C. R. Taylor, and H. Hoppeler. 1991. The concept of symmorphosis - a testable hypothesis of structure-function relationship. Proceedings of the National Academy of Sciences of the United States of America **88**:10357-10361.

Windell, J. T., D. O. Norris, J. F. Kitchell, and J. S. Norris. 1969. Digestive response of rainbow trout, salmo gairdneri, to pellet diets. Journal of the Fisheries Research Board of Canada

26:1801-1812.

Wurtsbaugh, W. A. and D. Neverman. 1988. Post-feeding thermotaxis and daily vertical migration in a larval fish. Nature **333**:846-848.

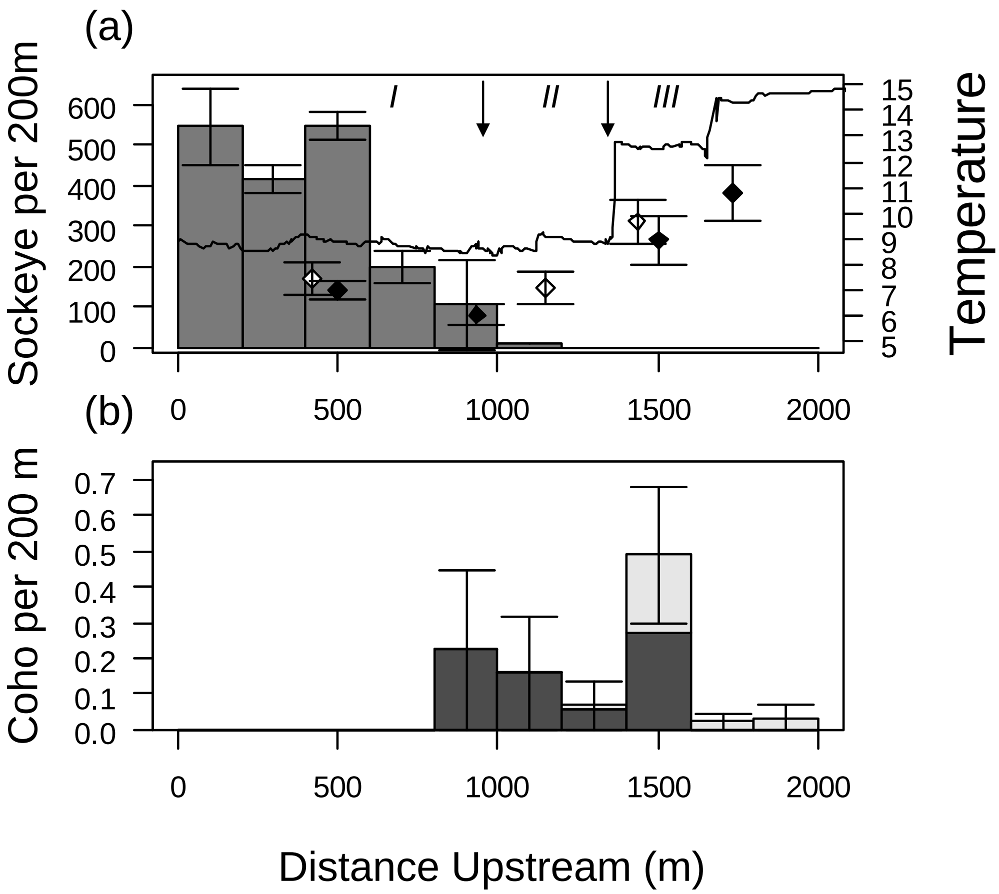
(a)
Sockeye per 200m
600
500
400
300
200
100
0
I
II
III
Temperature
15
14
13
12
11
10
9
8
7
6
5
0
500
1000
1500
2000
(b)
Coho per 200 m
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0
500
1000
1500
2000
Distance Upstream (m)

Figure 3.1 Spatial distribution of water temperature, spawning sockeye salmon, and juvenile coho salmon in Bear Creek. (a) Bars: average annual count of spawning sockeye salmon per 200 m unit of stream (± SD, *n*=4), 2005-2008. Line: longitudinal profile of water temperature recorded at the peak of the diel temperature cycle (17:00). Points: mean daily temperatures (± SD) during the sockeye salmon run in 2007 (open symbols) and 2008 (filled symbols). Arrows indicate location of antenna sites for monitoring movement among 3 regions of the stream. (b) Daytime spatial distribution of juvenile coho salmon during the peak of the sockeye salmon run in 2007-2008. Bar height indicates the proportion of the total catch that occurred in each 200 m unit (± 1SE, *n* = 2). Gray fill shows proportion of individuals in each section with salmon eggs in their stomachs.

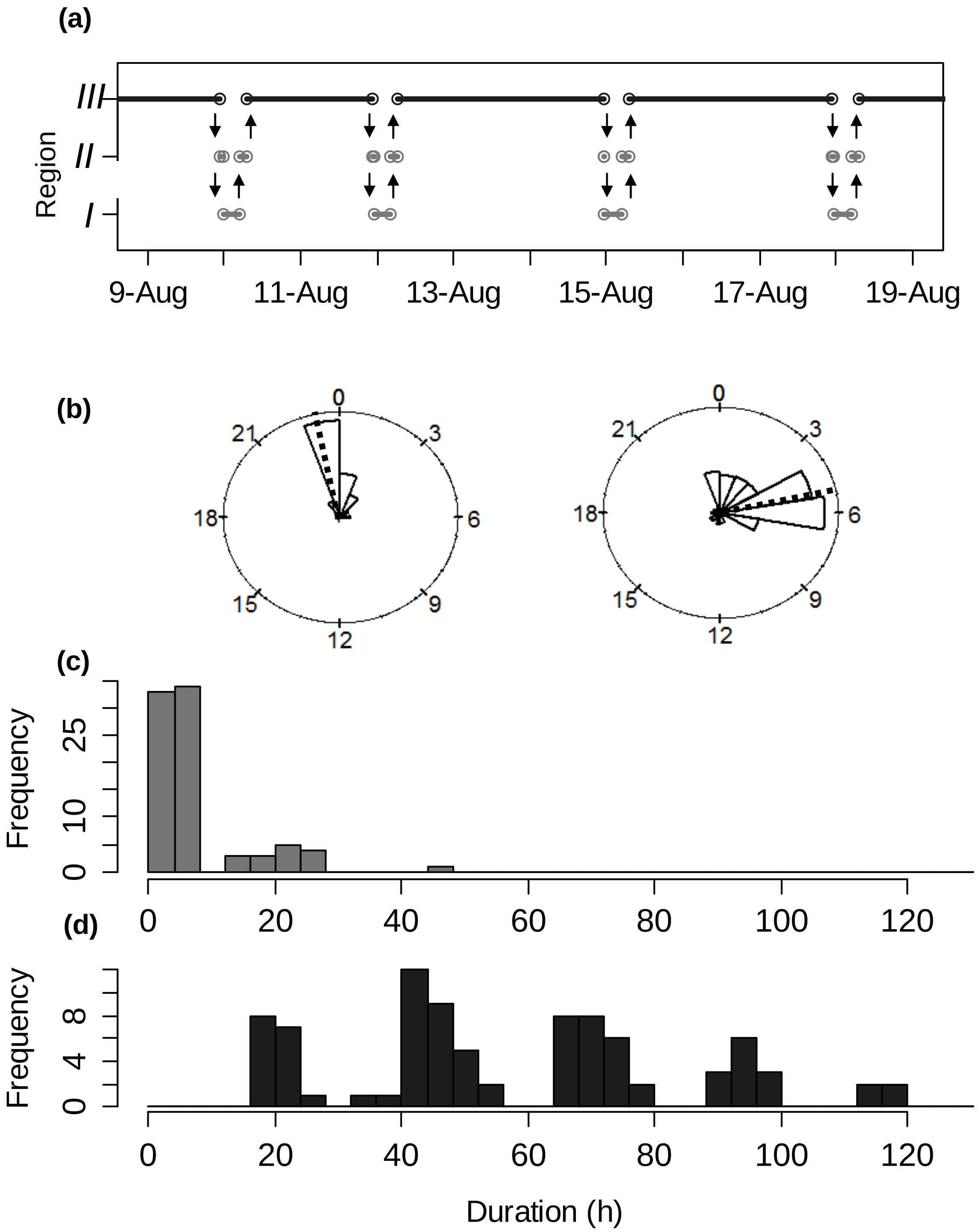
(a)
III
II
I
Region
9-Aug
11-Aug
13-Aug
15-Aug
17-Aug
19-Aug
(b)
0
3
6
9
12
15
18
21
0
3
6
9
12
15
18
21
(c)
Frequency
0
10
25
0
20
40
60
80
100
120
(d)
Frequency
0
4
8
0
20
40
60
80
100
120
Duration (h)

Figure 3.2 Diel movement behavior in juvenile coho salmon: (a) Example of feeding forays in a juvenile coho salmon that grew from 7.1 g to 17.6 g between 24 July and 21 August. Points show antenna detections indicating transitions between the three regions of stream (see Fig. 1a); arrows indicate direction of transition. Segments show the regions of stream occupied through time. (b) Rose diagram showing the daily timing of upstream and downstream movements. Dotted lines indicate modal time based on non-parametric density estimate. (c,d) Histograms showing the durations of feeding forays in region *I* (lt. gray bars), and the durations of inter-feeding periods in region *III* (dk. gray bars, includes transit time through region *II*).

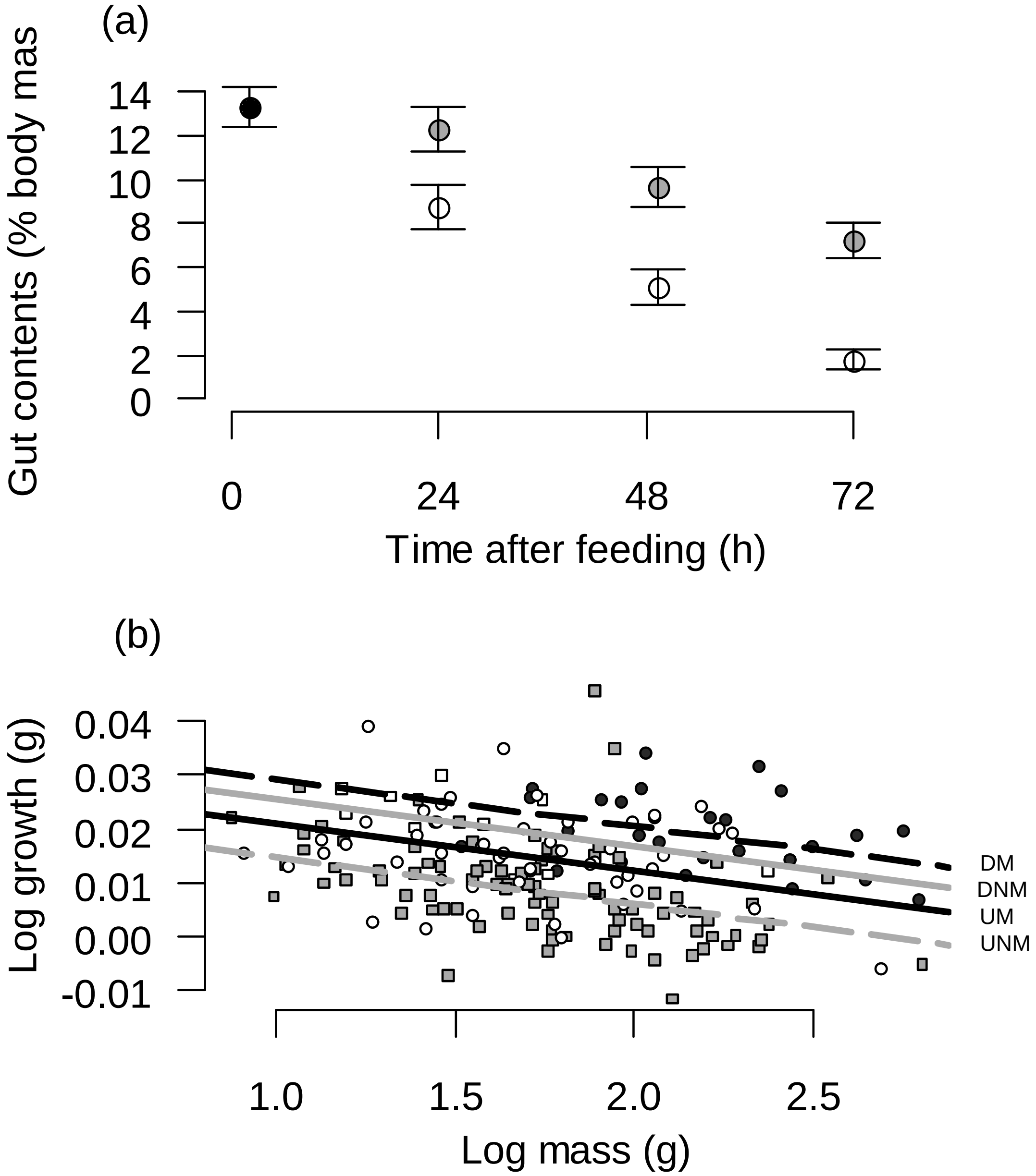
(a)
Gut contents (% body mas
14
12
10
8
6
4
2
0
0
24
48
72
Time after feeding (h)
(b)
Log growth (g)
0.04
0.03
0.02
0.01
0.00
-0.01
1.0
1.5
2.0
2.5
Log mass (g)
DM
DNM
UM
UNM

Figure 3.3 (a) Stomach capacity and thermal effects on gastric evacuation in juvenile coho salmon. Black circle: the average ration of sockeye salmon eggs consumed by juvenile coho salmon after ~20 minutes of *ad libitum* feeding (± SE). The ration remaining in the gut over time is shown for fish held in 6.5°C water (gray circles) and 10.5°C water (open circles) (± SE). (b) Growth as a function of body weight. Symbols represent different behavioral strategies (●: *diel mover (DM)*, ○: *unassigned mover (UM)*, ■: *upstream non-mover (UNM)*, □: *downstream non-mover (DNM*). Lines show fitted relationships from a mixed effects model accounting for the effect of behavioral strategy on the relationship between body size and growth.

Chapter 4: Going with the flow:

spatial distributions of juvenile coho salmon track a shifting mosaic of water temperature

Abstract:

There is much known about the spatial heterogeneity of floodplain habitat and how it shifts through time due to variation in stream flow. However, much less is understood about how organisms interact with this shifting habitat mosaic, especially in terms of how animal behavior responds to flow pulses and floodplain expansion. Here I explore how inter-annual variation in stream flows affects the spatial distribution of water temperature, and the opportunities for juvenile coho salmon to thermoregulate while exploiting an annual resource pulse comprised of sockeye salmon eggs. I found that episodic summer precipitation events lead to inter-annual variation in the spatial distribution of warm water in Bear Creek during the mid-July to mid-August period when sockeye salmon spawn. The spatial distribution of juvenile coho salmon tracked warm water habitats as they shifted from the upstream thalweg to off-channel regions downstream. This shows how an intact portfolio of stream habitats can allow fish to capitalize on resource pulses across a wide range of flow conditions.

Introduction:

Stream ecosystems exhibit some of the most dynamic habitat conditions found in nature and are characterized by flow regimes that typically include large fluctuations in water quantity, expressed at a range of frequencies and magnitudes (Poff et al. 1997). Temporal variation in stream habitat occurs not only in habitat conditions themselves, but also in the spatial configuration of habitat types across the landscape, resulting in a shifting mosaic of habitat patches (Stanford et al. 2005, Whited et al. 2008). At annual to supra-annual time scales, high magnitude flood-pulses trigger erosion and sedimentation that reorganize stream-channels and change the spatial configuration of floodplains (Tockner et al. 2000, Stanford et al. 2005). At finer time-scales, streams exhibit lower magnitude flow pulses that lack the erosive power needed to reorganize stream channels, yet may have large affects on the spatial patterning of habitat as oscillating water levels interact with floodplain topography to generate expansion and contraction of floodplain habitats (Mertes et al. 1995, Malard et al. 2000, Tockner et al. 2000). For example, the aquatic habitat available to stream organisms during low flows is often dominated by main-channel (i.e., thalweg) habitat, whereas additional off-channel habitats become ephemerally flooded and connected to the thalweg during higher flows (Tockner et al. 1997) .Though technological advancements are increasing our ability to quantify spatial and temporal variation in lotic habitat conditions (Whited et al. 2008, Tonolla et al. 2010, Torgersen et al. 2012) there is weaker understanding of the constraints and opportunities that shifting habitat mosaics generate for mobile organisms, and the adaptations that enable animals to survive and thrive in these dynamic environments.

Much of the understanding of biological adaptation to flow regimes concerns the synchronization of life-histories with seasonal flooding events in large rivers (Junk et al. 1988), or refuge-seeking behavior to survive episodic, extreme flow events in smaller rivers (Lytle and Poff 2004). Less is known about how animals respond to the episodic low-magnitude variations in flow that generate expansion and contraction of floodplain habitat in low-order streams. Fluctuating water levels may change the spatial patterning of trophic and thermal resources, which should in turn affect the riverscape of growth potential for fish (Brett 1971, Brandt et al. 1992, Fausch et al 2002). However, fish movements can selectively integrate across spatio-temporal variation in habitat conditions (Wurtsbaugh and Neverman 1988, Ruff et al. 2011, Armstrong et al. *in review*), so the fitness consequences of flow pulses ultimately depend on how fish respond to the shifting habitat mosaic (Rypel et al. 2012). One of the more complex, yet nearly ubiquitous movement behaviors in dynamic environments is that of habitat-cycling, where animals move back-and-forth between alternative habitat patches, typically at hourly-to-weekly timescales. For example, diel vertical migration (DVM) is a dominant feature of lentic and marine ecosystems, occurring in organisms ranging from plankton to sharks (Gilbert and Hampton 2001, Campana et al. 2011). There is accumulating evidence that analogous horizontal movements (DHM) generate habitat cycling in lotic systems. For example, roach exhibited DHM between off-channel and thalweg habitats (Hohausova et al. 2003), bull trout exhibited DHM between deep pools and riffles (Muhlfeld et al. 2003), and juvenile coho salmon exhibited DHM across longitudinal temperature gradients in the thalweg (Armstrong et al. in review). There is little known about how diel movement behavior responds to the expansion and contraction of floodplain habitat during flow pulses. Specifically, how do behaviors that exploit spatial habitat heterogeneity function when the pattern of habitat heterogeneity shifts through time? Here we explore how spatial patterns of water temperature change with floodplain expansion and contraction, and how this affects the capacity for juvenile coho salmon (*Oncorhynchus kisutch*) to behaviorally thermoregulate through DHM behavior.

Coho salmon rear in physically heterogeneous streams, often overlapping with other species of Pacific salmon (*Oncorhynchus* spp.) during their spawning period. In regions of the Pacific Rim where salmon are still abundant, such as Alaska, the eggs of spawning salmon comprise a resource pulse that can provide a critical, high-quality food source for juvenile coho salmon (Armstrong et al. 2010). For example, egg consumption by juvenile coho salmon was associated with a 5x increase in the total energy content of their diet contents (Armstrong et al. 2010), and individuals of coho salmon and other species appeared reach the asymptote of their functional response when gorging on eggs of other salmon (Bentley et al. *in press*, Armstrong et al. *in review*). When food is superabundant, individuals become limited not by how much food they can acquire through foraging, but instead how much they can process through assimilation (i.e., digestion and absorption, Armstrong and Schindler 2012, Armstrong et al. *in review*). For fishes, assimilation rates are mediated by water temperature (Brett 1971, Elliot and Persson 1978), so the ability to capitalize on resource pulses is intrinsically linked to physical habitat conditions. In many instances, salmonids spawn in habitat with upwelling groundwater (Lorenz and Filer 1989, Baxter and Hauer 2000), which exhibits a stable thermal regime that is much colder than alternative habitats during the summer salmon spawning season. These habitats can also be warmer and less likely to freeze during the winter when salmon eggs incubate. Selection for groundwater influenced habitat by spawning salmon generates foraging trade-offs for juvenile coho salmon, in which salmon eggs are most abundant in cold patches of habitat that offer low digestive capacity, whereas warmer patches of habitat provide high digestive capacity but little food (Armstrong et al. in review).

Recent evidence demonstrated that juvenile coho salmon evade trade-offs between trophic and thermal resources by exhibiting DHM between cold habitats with abundant salmon eggs and warm habitats that offer high digestive capacity (Armstrong et al. in review). Individuals exploited longitudinal gradients in water temperature and spawning salmon abundance by moving back and forth along the stream thalweg. Fish moved to cold downstream habitat at night, gorged on eggs, and then returned to warm upstream habitats for periods of ~1-3d , which corresponded to the time required to assimilate large meals of salmon eggs (Armstrong et al. *in review*). These observations occurred during a two-year study in which stream flows were relatively low during sockeye salmon spawning, which occurs from mid-July to mid-August in the study stream.

In coastal Alaska watersheds, populations of salmon spawn asynchronously during the late summer period (July-October, Schindler et al. 2010), which is characterized by episodic rainfall events that comprise the majority of annual precipitation. Rain storms trigger flow pulses and floodplain habitat expansion that may last for days to weeks. Because single populations of salmon typically spawn for roughly 1 month or less (Schindler et al. 2010), episodic rainfall events may change the spatial patterning of habitat and associated thermal conditions available to consumers during the salmon resource pulse, and lead to strong inter-annual variation in the habitat options available to fish during this critical foraging opportunity. We explored how inter-annual variation in stream flows affects the spatial distribution of water temperature, and the opportunities for juvenile coho salmon to thermoregulate while feeding on sockeye salmon eggs. Our specific objectives were to (1) monitor how the spatial patterning of water temperature changed in the thalweg and off-channel areas of a stream across a 5-y period with inter-annual variation in magnitude and timing of flow pulses, and (2) explore how the daytime spatial distribution of coho salmon, an indication of their post-feeding habitat selection, changed in response to the changing landscape of thermal conditions.

Methods:

Study system

This research occurred in the Wood River watershed, which consists of five interconnected lakes that drain into Bristol Bay in southwest Alaska, USA. Our study system is Bear Creek, a 4 km long tributary of Lake Aleknagik. The thalweg of Bear Ck. exhibits thermal heterogeneity driven by two groundwater springs located 1360 and 1670 m upstream from the outflow. Each spring generates a distinct drop in the thalweg temperature as cold groundwater (3-5°C) augments the stream flow (Armstrong et al. *in review*). The stream width is 1-3 m upstream of these springs, and 4-12 m downstream. Bear Ck. exhibits both perennial and ephemeral off-channel habitat. The perennial off-channel habitats are primarily parafluvial spring brooks (*sensu* Stanford et al. 2005) that are colder than the thalweg during the summer. Ephemeral off-channel habitat occurs through two mechanisms: (1) elevated stream flows fill parafluvial flood channels and generate backwater habitats that persist until the stream returns to base flows and (2) high lake levels flood parafluvial and orthofluvial channels in the lower sections of the stream.

Focal species

Coho salmon are a small portion of the Wood River adult salmon returns, but their juveniles can be numerically dominant in small streams (Armstrong *unpublished* *data*) because juveniles of more numerous species, particularly sockeye salmon, emigrate from streams and in to downstream lakes soon after emerging from the gravel. Coho salmon rear in streams for 1, 2, or 3 years and cannot consume salmon eggs until they grow to ~70 mm fork length (distance from nose to fork of tail), which in Bear Ck. occurs in their second year of life in Bear Ck. (Armstrong et al. 2010). Sockeye salmon spawn in Bear Creek from late-July to late-August, primarily in the downstream 600 m of the stream thalweg and adjacent groundwater springs, which occur as shallow ponds (<50 cm depth), ranging in size from ~20-800 m^2.

Monitoring inter-annual variation in precipitation, flow, and temperature

Precipitation was measured by a rain gauge at the Alaska Salmon Program's Lake Nerka field camp (30 km NNW of Bear Ck.) and recorded daily from June through September during the years 2003-2012. Stream flow was monitored using standard methods (Buchanan and Somers 1969). Briefly, we installed a stage gage (XX brand) 300 m upstream of the mouth of Bear Ck. and recorded water height at 1 h intervals throughout the summer from 2008-2011. In 2007 we were only able to record stage during the latter portion of the summer, so we estimated the missing data based on the correlation in stream heights between Bear Ck. and a nearby stream (XX Ck.) during the remaining portion of the summer (r=0.XX). Cross-sectional flow profiles were recorded approximately bi-weekly during the summers of 2008-2012 and used to generate a rating curve between stage and flow.

To monitor thalweg stream temperature we placed calibrated i-button temperature loggers (Dallas Semiconductor, Dallas, Texas, USA) at point locations representing the different patches of thermal heterogeneity existing in the thalweg and recorded time-series of temperature at 90-minute intervals (± 1°C). During summers from 2008-2011 we also recorded a spatially continuous longitudinal profile of water temperature along the length of Bear Ck. (methods outlined in Ruff et al. 2011, Torgersen et al. 2012), to confirm that the i-button sites adequately summarized thermal heterogeneity in the thalweg. We measured thermal heterogeneity in off-channel habitat by recording point measurements of temperature in the off-channel habitat units we sampled while surveying juvenile coho salmon. In 2009, we also mapped the temperatures of all off-channel habitats in the lower 2500 km of stream using an AquaTuff 35200-J fast-response thermometer (Cooper Atkins, Middlefield, Connecticut, USA). We walked down the stream from 1700-1821 h on Aug-9 and recorded the temperature and GPS coordinates of all off-channel habitats. We estimated the areas of off-channel habitats by tracing the outline of habitat units over a high resolution image of Bear Ck. using the polygon tool in Google Earth Pro. We estimated the area of thalweg habitats by recording stream width at 100m intervals along the thalweg and considering the stream as a rectangle.

Field monitoring of coho salmon foraging behavior

We monitored the spatial distribution and diet of age-1 and age-2 coho salmon during the sockeye salmon subsidy in the years 2007-2011. Pilot surveys revealed that coho salmon were not present in riffle habitat, but instead only in pools and off-channel habitat (Armstrong *unpublished data*). Coho salmon are known to avoid high-velocity habitat (Bisson et al. 1988) and the riffles in our focal system have gravel substrate that is too small to create an adequate boundary layer to provide velocity refuge. We conducted surveys of pool and off-channel during the midday period (1100-1800 h), surveying all habitat in the lower 1800 m of stream on each survey. A researcher in a dry suit visually surveyed each habitat unit for the presence of juvenile coho salmon, through a combination of snorkeling and aerial survey with polarized glasses. If fish were present, the researcher herded the fish into a school and forced them into a ~2.5 x 4 m seine net until no fish remained visible in the unit. Fish were anesthetized in a 50 ppm solution of MS-222 (tricane methane sulfonate), measured to the nearest 1 mm fork length, and released. A random subset of these fish was sampled for diet by gastric lavage. We conducted 2 sampling events during the resource pulse in 2007, 2008, and 2011, 3 events in 2009, and 5 events in 2010.

Quantifying the spatial distribution of spawning sockeye salmon

As part of a long term monitoring effort, the abundance of spawning sockeye salmon was visually enumerated 3 times per year and recorded as the total count of live and dead fish per 200 m section of stream. We supplemented these surveys by recording spatially continuous distributions of live sockeye salmon in the summers from 2008-2011. These surveys allowed us to discriminate counts between thalweg and off-channel habitats.

Data analysis

We defined the period of the salmon resource pulse as July-21 to Aug-21, as these are the approximate dates (± <1 week) that sockeye salmon spawn in Bear Ck. We computed daily summaries during the resource pulse as 24-h averages for temperature, flow, and stage, and 24-h totals for precipitation. We calculated summary stats across the entire period based on these daily summaries (i.e. days as replicates). To compare the habitat use by juvenile coho salmon among years, we classified each sampled habitat unit according to distance upstream (in 200 m sections), habitat type (thalweg vs. off-channel), temperature at the time of sampling, number of coho salmon present, and the proportion of sub-sampled individuals that exhibited sockeye salmon eggs in their diet contents. We then aggregated the habitat-unit-level data, binning it by distance upstream and habitat type, and calculating for each bin the sum of juvenile coho salmon, the average temperature (weighted by number of coho salmon captured per unit), and the average proportion of fish with eggs in their diet (weighted by the diet sample size per unit). To compute summary stats for coarse comparisons of habitat selection among years, we classified temperatures relative to the cool downstream thalweg habitats where the majority of the sockeye salmon spawn as cold, neutral, and warm, based on a threshold difference of ±1°C at the time of sampling. We converted count data into relative abundance (% of total fish captured per sampling event), and aggregated the data by year and the combination of habitat type and temperature category.

Results (need to reference the figures here)

Inter-annual variation in precipitation and water level

Total summer precipitation (June-13 to September-8) ranged from 166-562 mm during the years 2003-2012 (min: 2004, max: 2010), exhibiting a CV of 0.32. During the portion of the summer when sockeye salmon spawn in Bear Ck. (June-21 to August-21), total precipitation ranged from 50-352 mm (minimum: 2008, maximum: 2010) with a CV of 0.62 (Fig. 1a). Water level in Bear Ck. during the sockeye salmon resource pulse was highly variable among years due to the episodic nature of summer precipitation (Fig. 1b-f). In 2007, 2008, and 2009, the mean stage (± standard deviation) was 300 ± 59 mm, 225 ± 36 mm, and 250 ± 34 mm, respectively. During 2009 and 2010, high magnitude precipitation events occurred during the salmon run resulting in much higher stage levels of 462 ± 96mm and 470 ± 177 mm, respectively (Fig.1). Hereafter I refer to 2007, 2008, and 2011 as dry years, and 2009 and 2010 as wet years.

Spatial and temporal variation in water temperature: The spatial patterning of water temperature in Bear Ck. was substantially different in the dry and wet years (Fig. 2). During the dry years, there was a strong longitudinal gradient in thalweg water temperature where groundwater springs 1360 m and 1670 m upstream generated discrete drops in temperature from 9-11°C water flowing out of beaver-meadow complex habitat was augmented with cold 3-5° C groundwater to produce a lower thalweg temperature of 6-7°C. The off-channel habitat available at low water levels was comprised almost entirely of spring networks that exhibited cold temperatures (3-7° C) (Fig. 2).

In wet years, floodplain habitat expanded as rising lake and stream levels submerged areas that were previously dry, or restored connectivity to backwater areas that were isolated from the main channel at lower flows. Flooded backwaters throughout the lower 1 km of the stream exhibited warmer temperatures than the adjacent thalweg, with daytime temperatures up to 6°C warmer than the adjacent main channel. While higher water levels increased the lateral thermal heterogeneity across the floodplain, they eliminated longitudinal heterogeneity along the thalweg (Fig. 2). The upstream-downstream gradient in water temperature along the 2 km of thalweg averaged 3.3 ± 1.3° in the dry years, and 0.1 ± 0.4°C in the wet years.

Spatial distribution of juvenile coho salmon during the resource pulse: In the dry years, coho salmon exhibited strong selection for the warm waters of the upstream thalweg; the relative abundance of juvenile coho salmon in the upstream thalweg was 76 ± 14%, whereas these habitats comprised a small fraction of the total thalweg habitat available

(13% by stream area and 32% by stream length) (Fig.3-4). In the wet years, the daytime coho salmon distribution shifted downstream and to new warm off-channel habitat (Fig. 2-4). Approximately 80 ± 6% of individuals occurred in these habitats despite their only accounting for 1% of total habitat by area (Fig. 3). The distribution of spawning sockeye salmon was similar among years, except that the upstream tail of the distribution extended further up the thalweg in 2010, coincident with the cooler water temperatures observed there during high flows (Fig. 2).

In all years, spawning sockeye salmon were never observed in warm habitats (Fig. 2), but juvenile coho salmon captured in warm habitats during the daytime consistently exhibited sockeye salmon eggs in their diets. Of coho salmon sampled in warm upstream thalweg habitat, 51 ± 22 % (*n* = 3 years) of individuals had sockeye salmon eggs in their diet contents. Of coho salmon sampled in warm off-channel habitat, 89 ± 7% (*n* = 2 years) had sockeye salmon eggs in their diets. This indicates that the post-feeding movements of juvenile coho salmon were able to track the shifting mosaic of water temperature as it changed among years in response to changes in the extent of inundation.

Discussion:

Due to variation among years in the timing and magnitude of summer precipitation, hydrology in Bear Ck. exhibited strong inter-annual variation during the mid-July to mid-August period when sockeye salmon spawn (Fig. 1). The spatial patterning of water temperature across the floodplain differed substantially among years with high and low flows, but the range of temperatures available to fish across the riverscape remained relatively constant among years, with daily mean temperatures ranging ~4-12°C across space (Fig. 2,4). The warmest temperatures (9-12°C) occurred in upstream thalweg habitat during low flows, but shifted to downstream off-channel habitat during high flows (Fig. 2). The daytime spatial distribution of juvenile coho salmon also shifted among years to track the changing distribution of warm-water habitat (Fig. 2-4). Although sockeye salmon never occurred in warm habitats (Fig. 2), the stomach contents of juvenile coho salmon residing in warm habitats were comprised nearly exclusively of sockeye salmon eggs, reflecting their cyclic horizontal movements between cold habitats with high foraging potential and warm habitats that enable substantially higher rates of assimilation (Armstrong et al. in review). Thus, coho salmon appear to enhance their energy intake rates across a range of flow conditions, exhibiting thermoregulatory movements that track a shifting mosaic of thermal conditions.

Several studies have shown that fish can improve their energy budgets by exploiting thermal heterogeneity in the environment, whether seeking cooler refuge habitat to avoid thermal stress (Glodek 1978, Torgersen et al. 1999, Keefer et al. 2009) or as in this study, moving to warmer habitat to accelerate metabolism and increase physiological performance (Wurtsbaugh and Neverman 1988, Armstrong et al. *in review*). The ability of fish to exploit a diversity of thermal "options" appears critical to their persistence and productivity in many systems; a key challenge is to identify and conserve not only the features of stream ecosystems that *generate* a heterogeneous landscape of thermal habitat, but also those that *maintain* this thermal diversity and enable it to persist throughout the range of hydrologic conditions that characterize the flow regime of rivers and streams.

In Bear Ck. the scope of summer water temperatures available to fish results from spatial variation in extent of upwelling groundwater, which sets the minimum temperature of ~3°C, and the warming effects of heat exchange with the atmosphere and insolation, which set the maximum temperature as a function of the residence time of water and, therefore, the amount of heating it can accrue before leaving the system (Caissie 2006). Because groundwater temperatures are relatively stable through time and groundwater-influenced habitats are extensive in Bear Ck (Fig. 2-3), cold thermal options are always available to fish. In contrast, the existence of warm habitat patches depends on the ability of the riverscape to retain water in habitat patches with long residence times and little groundwater influence. Although the source of water in Bear Ck. becomes warmer in wet years, comprised increasingly of precipitation rather than groundwater, high velocities in the stream thalweg reduce the residence time of water and, therefore, the extent of heat exchange in headwater reaches. This would reduce the maximum water temperature available to fish, except that rising water levels lead to floodplain expansion that generates warm habitat in stagnant backwaters ~3-60 m from the main-channel. It appears the persistence of thermal diversity in Bear Ck. is dependent on connectivity between the thalweg and floodplain, which enables the expansion of habitats during high flows and results in a compensatory gain of warm water habitat that is lost from the thalweg during high flow events.

It is widely recognized that lotic habitats turnover at coarse timescales due to disturbance events that simultaneously destroy and generate physical features of the riverscape (Reeves et al. 1995). The Shifting Habitat Mosaic theory (SHM: Stanford et al. 2005) describes how high-magnitude flood-pulses generate and destroy habitats, such that the patterning of the floodplain mosaic changes through time, yet the assemblage of habitat types remains diverse and relatively stable (Whited et al. 2008). Our results demonstrate that analogous processes play out at seasonal-to-annual timescales as well, thereby stabilizing the extent of high quality habitat options available for fish. Summer flow pulses in Bear Ck. generally lack the erosive power to reorganize stream channels, yet they clearly reorganize the spatial patterns of water temperature available to fish. Although the proportions of different thermal habitats in Bear Ck. change somewhat as the floodplain expands and water residence time decreases in the thalweg, the scope of water temperatures available to fish persisted across flow levels ranging from base flows (0.1 m^3s^{-1}) to flood conditions (> 2 m^3s^{-1}). Thus, the foundation of the SHM, derived from flood pulses in mid-sized rivers, appear to underlie the stability of thermal habitat in low order streams subject to episodic flow pulses.

This study adds to others that demonstrate the complex ways by which animal behavior integrates across spatio-temporal variation in habitat conditions (Huey 1991, Fryxell et al. 2005, Ruff et al. 2011). Juvenile coho salmon in Bear Ck. exhibit cyclic habitat use between cold and warm habitats at daily timescales (Armstrong et al. *in review*), and showed annual variation in the location and type of warm post-feeding habitat that they selected (Fig. 2). The complex interactions between coho salmon and their environment emphasize the challenges that conservation efforts face in defining which habitats are critical for the persistence and productivity of species. Despite the ubiquity of diel habitat cycling in birds (Orians and Pearson 1979), reptiles (Huey 1991), and aquatic organisms in lentic and marine systems (Narver 1970, Campana et al. 2011), habitat cycling has received extremely little study in streams. If sampling efforts are biased toward one portion of the habitat cycle, for example daytime sampling of fish that exhibit nighttime feeding forays (Muhfeld et al. 2003, Armstrong et al. *in review*), then essential components of a fish’s habitat assemblage may be excluded from critical habitat definitions. Further, while it is recognized that critical habitat varies seasonally (Junk et al. 1988, Nickelson et al. 1992, Wigington et al. 2006), much less is known about annual variation in critical habitat. Our results showed that the critical thermal resources for juvenile coho salmon occurred in different habitats depending on flow conditions, which exhibited high levels of inter-annual variation (CV=0.6). The dry years (2007, 2008, 2011) of our study demonstrated the importance of headwater beaver-meadow complex habitat, whereas the wet years (2009, 2010) demonstrated the importance of ephemeral off-channel habitat. Detecting annual or supra-annual variation in critical habitat may require long time-scales due to the temporal autocorrelation of many climate patterns (Mantua 2002). For example, the critical river basins for production of Bristol Bay sockeye salmon appear to change in concert with the Pacific Decadal Oscillation (Hilborn et al. 2003), but detecting this results required nearly half a century of highly accurate monitoring. In reality, many conservation efforts lack the resources to understand how animal behavior interacts with spatio-temporal variation in habitat conditions, and how habitat conditions change across years and decades. However, there remains a tangible approach for conserving species in the face of these uncertainties. Maintaining the processes that generate and maintain habitat heterogeneity ensures that animals continue to have the portfolio of habitat options that their behaviors and life-histories have evolved to take advantage of (Poff et al. 1997, Beechie et al. 2010, Schindler et al. 2010). In stream ecosystems, maintaining variation in flow regimes and connectivity between thalweg and off-channel habitats should minimize the risks associated with current and projected variation in climate.

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References

Armstrong, J. B. and D. E. Schindler. 2011. Excess digestive capacity in predators reflects a life of feast and famine. Nature **476**:84-88.

Armstrong, J. B., D. E. Schindler, K. T. Bentley, G. T. Brooks, C. P. Ruff, and C. E. Torgersen. *in review*. Juvenile fish exploit heterogeneity in thermal and trophic resources through diel horizontal migrations in streams. Ecology.

Armstrong, J. B., D. E. Schindler, K. L. Omori, C. P. Ruff, and T. P. Quinn. 2010. Thermal heterogeneity mediates the effects of pulsed subsidies across a landscape. Ecology **91**:1445-1454.

Baxter, C. V. and F. R. Hauer. 2000. Geomorphology, hyporheic exchange, and selection of spawning habitat by bull trout (Salvelinus confluentus). Canadian Journal of Fisheries and Aquatic Sciences **57**:1470-1481.

Beechie, T. J., D. A. Sear, J. D. Olden, G. R. Pess, J. M. Buffington, H. Moir, P. Roni, and M. M. Pollock. 2010. Process-based Principles for Restoring River Ecosystems. Bioscience **60**:209-222.

Bentley, K. T., D. E. Schindler, J. B. Armstrong, C. P. Ruff, and P. J. Lisi. *in review*. Inter-annual variation in a pulsed resource subsidy mediates the foraging and growth response of stream-dwelling salmonids. Ecosphere.

Brandt, S. B., D. M. Mason, and E. V. Patrick. 1992. Spatially-explicit models of fish growth-rate. Fisheries **17**:23-34.

Breau, C., R. A. Cunjak, and S. J. Peake. 2011. Behaviour during elevated water temperatures: can physiology explain movement of juvenile Atlantic salmon to cool water? Journal of Animal Ecology **80**:844-853.

Brett, J. R. 1971. Energetic responses of salmon to temperature - study of some thermal relations in physiology and freshwater ecology of sockeye salmon (Oncorhynchus-nerka). American Zoologist **11**:99-111.

Caissie, D. 2006. The thermal regime of rivers: a review. Freshwater Biology **51**:1389-1406.

Campana, S. E., A. Dorey, M. Fowler, W. Joyce, Z. L. Wang, D. Wright, and I. Yashayaev. 2011. Migration Pathways, Behavioural Thermoregulation and Overwintering Grounds of Blue Sharks in the Northwest Atlantic. Plos One **6**.

Elliott, J. M. and L. Persson. 1978. Estimation of daily rates of food-consumption for fish. Journal of Animal Ecology **47**:977-991.

Fausch, K. D., C. E. Torgersen, C. V. Baxter, and H. W. Li. 2002. Landscapes to riverscapes: Bridging the gap between research and conservation of stream fishes. Bioscience **52**:483-498.

Fryxell, J. M., J. F. Wilmshurst, A. R. E. Sinclair, D. T. Haydon, R. D. Holt, and P. A. Abrams. 2005. Landscape scale, heterogeneity, and the viability of Serengeti grazers. Ecology Letters **8**:328-335.

Gilbert, J. J. and S. E. Hampton. 2001. Diel vertical migrations of zooplankton in a shallow, fishless pond: a possible avoidance-response cascade induced by notonectids. Freshwater Biology **46**:611-621.

Glodek, G. S. 1978. The importance of catfish burrows in maintaining fish populations of tropical freshwater streams in western Ecuador.

Hohausova, E., G. H. Copp, and P. Jankovsky. 2003. Movement of fish between a river and its backwater: diel activity and relation to environmental gradients. Ecology of Freshwater Fish **12**:107-117.

Huey, R. B. 1991. Physiological consequences of habitat selection. American Naturalist **137**:S91-S115.

Junk, W. J., P. B. Bayley, and R. E. Sparks. 1989. The flood pulse concept in river-floodplain systems. Canadian Special Publication of Fisheries and Aquatic Sciences **106**:110-127.

Keefer, M. L., C. A. Peery, and B. High. 2009. Behavioral thermoregulation and associated mortality trade-offs in migrating adult steelhead (Oncorhynchus mykiss): variability among sympatric populations. Canadian Journal of Fisheries and Aquatic Sciences **66**:1734-1747.

Kushlan, J. A. 1979. Temperature and oxygen in an everglades alligator pond. Hydrobiologia **67**:267-271.

Lorenz, J. M. and J. H. Eiler. 1989. Spawning habitat and redd characteristics of sockeye-salmon in the glacial taku river, british-columbia and alaska. Transactions of the American Fisheries Society **118**:495-502.

Lytle, D. A. and N. L. Poff. 2004. Adaptation to natural flow regimes. Trends in Ecology & Evolution **19**:94-100.

Malard, F., K. Tockner, and J. V. Ward. 2000. Physico-chemical heterogeneity in a glacial riverscape. Landscape Ecology **15**:679-695.

Mantua, N. J. and S. R. Hare. 2002. The Pacific decadal oscillation. Journal of Oceanography **58**:35-44.

Mertes, L. A. K., D. L. Daniel, J. M. Melack, B. Nelson, L. A. Martinelli, and B. R. Forsberg. 1995. Spatial patterns of hydrology, geomorphology, and vegetation on the floodplain of the amazon river in brazil from a remote-sensing perspective. Geomorphology **13**:215-232.

Muhlfeld, C. C., S. Glutting, R. Hunt, D. Daniels, and B. Marotz. 2003. Winter diel habitat use and movement by subadult bull trout in the upper Flathead River, Montana. North American Journal of Fisheries Management **23**:163-171.

Narver, D. W. 1970. Diel vertical movements and feeding of underyearling sockeye salmon and limnetic zooplankton in babine-lake, british-columbia. Journal of the Fisheries Research Board of Canada **27**:281-293.

Nickelson, T. E., J. D. Rodgers, S. L. Johnson, and M. F. Solazzi. 1992. Seasonal-changes in habitat use by juvenile coho salmon (oncorhynchus-kisutch) in oregon coastal streams. Canadian Journal of Fisheries and Aquatic Sciences **49**:783-789.

Orians, G. H. and N. E. Pearson. 1979. On the theory of central place foraging. Analysis of ecological systems. Ohio State University Press, Columbus:155-177.

Poff, N. L., J. D. Olden, D. M. Merritt, and D. M. Pepin. 2007. Homogenization of regional river dynamics by dams and global biodiversity implications. Proceedings of the National Academy of Sciences of the United States of America **104**:5732-5737.

Reeves, G. H. B., L.E.; Burnett, K.M.; Bisson, P.A.; Sedell, J.R. . 1995. A disturbance-based ecosystem approach to maintaining and restoring freshwater habitats of evolutionarily significant units of anadromous salmonids in the Pacific Northwest American Fisheries Society Symposium 334-349.

Ruff, C. P., D. E. Schindler, J. B. Armstrong, K. T. Bentley, G. T. Brooks, G. W. Holtgrieve, M. T. McGlauflin, C. E. Torgersen, and J. E. Seeb. 2011. Temperature-associated population diversity in salmon confers benefits to mobile consumers. Ecology **92**:2073-2084.

Rypel, A. L., K. M. Pounds, and R. H. Findlay. Spatial and Temporal Trade-Offs by Bluegills in Floodplain River Ecosystems. Ecosystems **15**:555-563.

Schindler, D. E., R. Hilborn, B. Chasco, C. P. Boatright, T. P. Quinn, L. A. Rogers, and M. S. Webster. 2010. Population diversity and the portfolio effect in an exploited species. Nature **465**:609-612.

Stanford, J. A., Lorang, M.S., and Hauer F.R. 2005. The shifting habitat mosaic of river ecosystems. Verh. Internat. Verein. Limnol.:123-136.

Tockner, K., F. Malard, P. Burgherr, C. T. Robinson, U. Uehlinger, R. Zah, and J. V. Ward. 1997. Physico-chemical characterization of channel types in a glacial floodplain ecosystem (Val Roseg, Switzerland). Archiv Fur Hydrobiologie **140**:433-463.

Tockner, K., F. Malard, and J. V. Ward. 2000. An extension of the flood pulse concept. Hydrological Processes **14**:2861-2883.

Tonolla, D., V. Acuna, U. Uehlinger, T. Frank, and K. Tockner. Thermal Heterogeneity in River Floodplains. Ecosystems **13**:727-740.

Torgersen, C. E., D. M. Price, H. W. Li, and B. A. McIntosh. 1999. Multiscale thermal refugia and stream habitat associations of chinook salmon in northeastern Oregon. Ecological Applications **9**:301-319.

Whited, D. C., M. S. Lorang, M. J. Harner, F. R. Hauer, J. S. Kimball, and J. A. Stanford. 2007. Climate, hydrologic disturbance, and succession: Drivers of floodplain pattern. Ecology **88**:940-953.

Wigington, P. J., Jr., J. L. Ebersole, M. E. Colvin, S. G. Leibowitz, B. Miller, B. Hansen, H. R. Lavigne, D. White, J. P. Baker, M. R. Church, J. R. Brooks, M. A. Cairns, and J. E. Compton. 2006. Coho salmon dependence on intermittent streams. Frontiers in Ecology and the Environment **4**:513-518.

Wipfli, M. S., J. P. Hudson, J. P. Caouette, and D. T. Chaloner. 2003. Marine subsidies in freshwater ecosystems: Salmon carcasses increase the growth rates of stream-resident salmonids. Transactions of the American Fisheries Society **132**:371-381.

Wurtsbaugh, W. A. and D. Neverman. 1988. Post-feeding thermotaxis and daily vertical migration in a larval fish. Nature **333**:846-848.

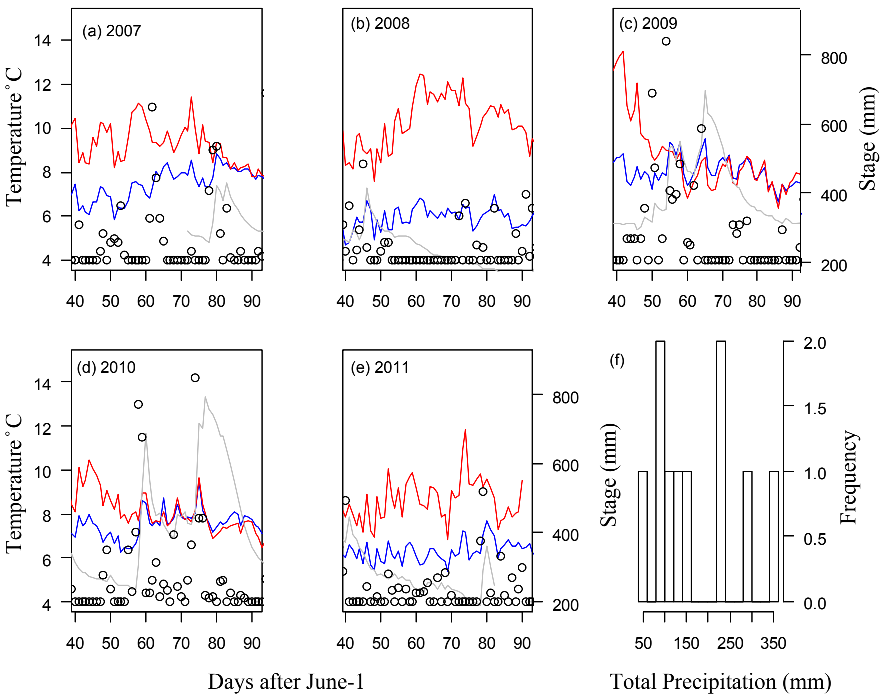

Figure 4.1 Annual variation in flow conditions and thalweg thermal heterogeneity during the summer in Bear Ck. (a-e) Time series of precipitation (dots), thalweg water temperature (red = 1800 m upstream, blue = ~500 m downstream), and stage (gray line) for the summers from 2007-2011. (f) Annual variation (2002-2012) in the total amount of precipitation during the one month period when sockeye salmon spawn and generate resource pulses for juvenile coho salmon (July-21 to Aug-21, day 51-81 on panels b-f).

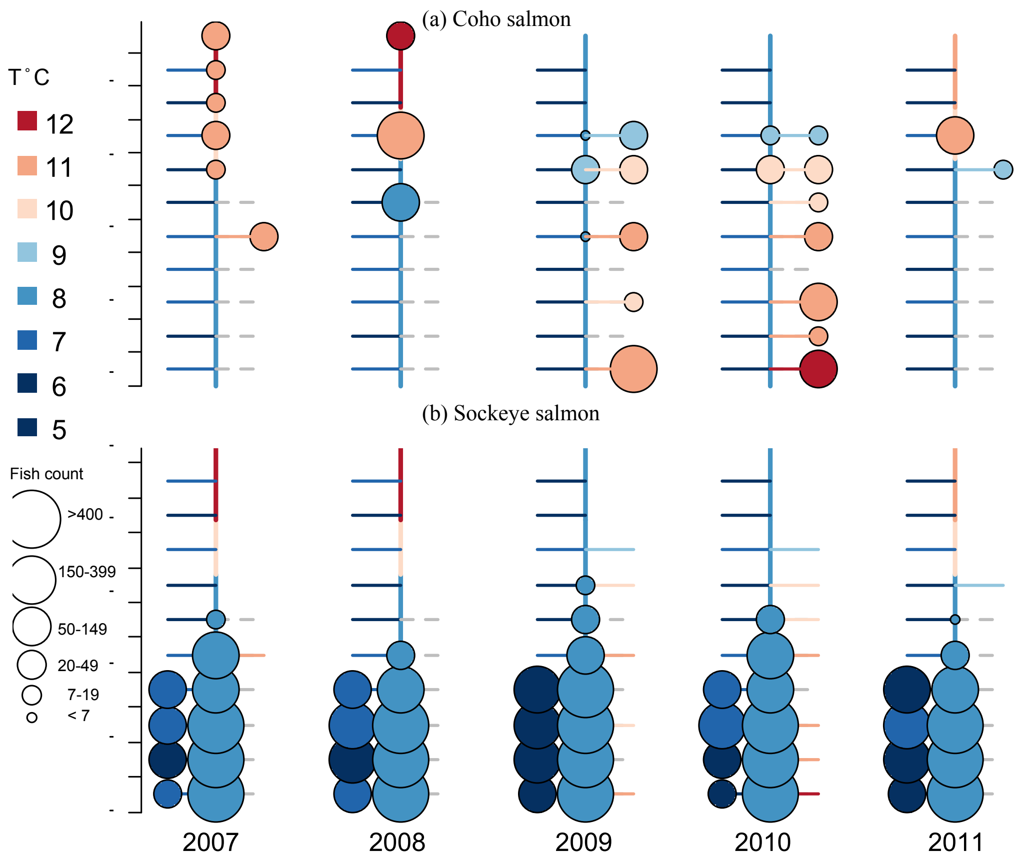

Figure 4.2. The daytime spatial distribution of juvenile coho salmon and spawning sockeye salmon in Bear Ck. during the sockeye salmon run. Each vertical line represents the stream thalweg for a given year, colored according to the average daytime temperature (900h-1800h) during the sockeye salmon run. Horizontal lines are drawn at 200 m intervals starting at 100 m upstream and increasing upwards to 2100 m. Dots on line sized (log-scale) according to the average sum of fish observed in each 200 m section of stream thalweg. Dots on the right and left represent the average sum of fish observed in warm and cold off-channel habitats (resp.) adjacent to each section of thalweg. The color of dots represents the average daytime recorded at the time of sampling, weighted by the sum of fish recorded (see methods). Dotted grey lines represent off-channel habitat that was not available due to low flows.

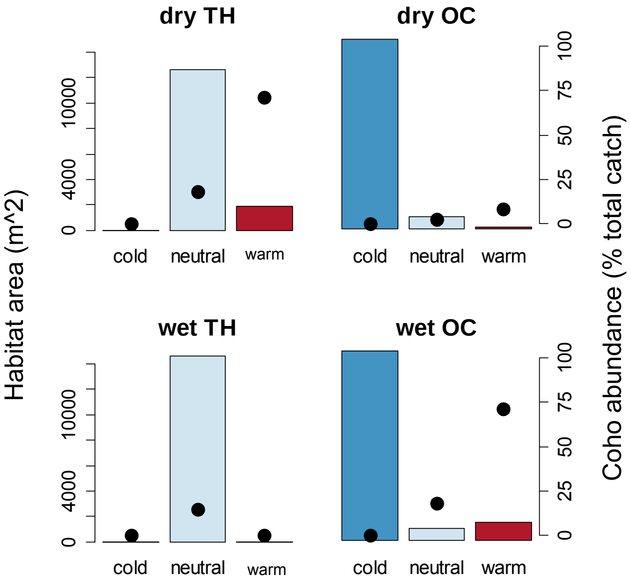

Figure 4.3. Changes in habitat selection by juvenile coho salmon in wet vs. dry years during the period sockeye salmon run. Top: dry summers (2007, 2008, 2011), bottom: wet summers (2008, 2009), right: off-channel habitats (OC), left: thalweg habitats (TH). Bars show the total area of different habitat types, classified by their temperature relative to the cool downstream thalweg area where the majority of sockeye salmon spawn (mean daily temperature = 6-7°C). Habitats > ± 1° C different than the downstream thalweg at the time of sampling were classified as warm (8-12°C) and cold (3-5°C). Points show relative abundance of juvenile in each habitat type, calculated as the percent of the total number of fish observed.

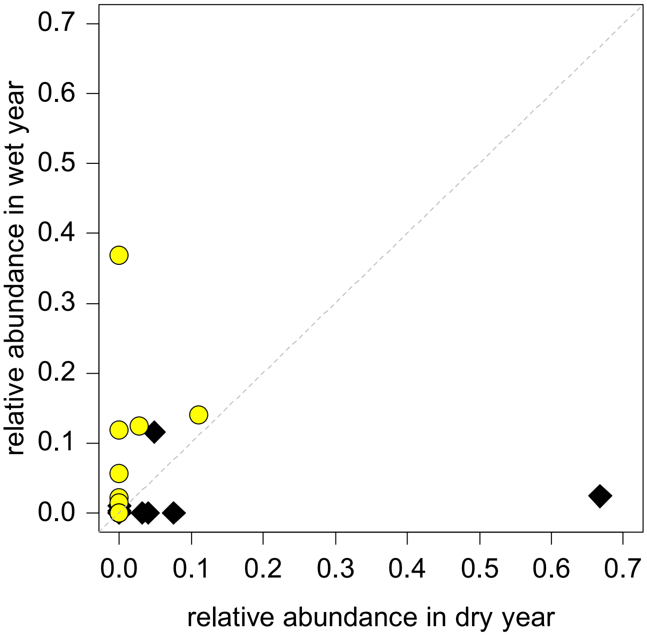

Figure 4.4. Changes in habitat use by juvenile coho salmon among dry and wet summers. For each bin of stream in fig. 2 (i.e. each 200m longitudinal section of thalweg and each corresponding off-channel section), the mean relative abundance of fish in dry years is plotted verses the mean relative abundance of fish in wet years. Black diamonds represent thalweg habitat, whereas yellow circles indicate off-channel habitat.