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Research in Thermal Biology: Burning Questions for Coldwater Stream Fishes

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With the increasing appreciation of global warming impacts on ecological systems, in addition to the myriad of land management effects on water quality, the number of literature citations dealing with the effects of water temperature on freshwater fish has escalated in the past decade. Given the many biological scales at which water temperature effects have been studied, and the growing need to integrate knowledge from multiple disciplines of thermal biology to fully protect beneficial uses, we held that a survey of the most promising recent developments and an expression of some of the remaining unanswered questions with significant management implications would best be approached collectively by a diverse research community. We have identified five specific topic areas of renewed research where new techniques and critical thought could benefit coldwater stream fishes (particularly salmonids): molecular, organism, population/species, community and ecosystem, and policy issues in water quality. Our hope is that information gained through examination of recent research fronts linking knowledge at various scales will prove useful in managing water quality at a basin level to protect fish populations and whole ecosystems. Standards of the past were based largely on incipient lethal and optimum growth rate temperatures for fish species, while future standards should consider all integrated thermal impacts to the organism and ecosystem.

Keywords water temperature, global warming, genetics, physiology, ecosystem, salmonids

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INTRODUCTION

Most scientists agree that the earth's climate is undergoing rapid change (Oreskes 2004; IPPC 2007). One of the main

changes predicted is an increase in temperature. In the U.S., air temperatures have increased by 0.6°C over the past century and are predicted to rise as much as 6°C by 2100 (Houghton et al., 2001). Water temperature is expected to increase over the next 50 years, especially in higher latitudes. If so, the geographic distribution of salmonids is likely to shift in response. Recent changes in climate have already caused habitat shifts for some salmonids and caused temperature-related shifts in dominance. In Switzerland, several brown trout populations shifted to higher elevations in response to warmer water temperatures and increased disease at lower elevations (Hari et al., 2006). Rhône River grayling (*Thymallus thymallus*) have been extirpated from a 30-km reach (Daufresne et al., 2003) due to disruption of vital life history functions, especially reproduction, by elevated temperatures. In France's Nivelle River, higher temperatures have reduced successful Atlantic salmon (*Salmo salar*) reproduction during the last 20 years (Beall et al., 2003) by denying females sufficient time (8–10 days) with suitable temperatures after they complete ovarian maturation (de Gaudemar and Beall, 1998).

How much do salmonid metapopulations have the capacity to adapt to climate change? Depending on the temporal rate of climate change and the spatial details, we might expect adaptive responses to occur at various levels. We hypothesize that plastic behavioral traits that rely on temperature cues are likely to respond first. For example, movements to avoid stressful temperatures or timing of reproduction are important behavioral adaptations to changing spatial and temporal patterns of temperature. Physiological adaptations to higher temperatures and metapopulation responses, which include regional shifts in geographic range mediated by extirpation, are likely to be slower. Can we predict which populations will shift their ranges geographically and which will be extirpated? Keleher and Rahel (1996) made an attempt to address this question by predicting how climate warming will reduce and fragment trout habitat in the Rocky Mountains of the U.S. Genetic adaptation through natural selection on relevant traits is another response, expected to occur over longer periods of time.

We anticipate that salmonid population responses will be more complex than those predicted based solely on the thermal requirements of a single species. Understanding interactions between temperature and other resources and species that define the realized niche will also be important (Magnuson et al., 1979). For example, one model predicted that climate change in western U.S. streams would influence the abundances of rainbow and brown trout through an interaction of higher temperature and a shift in peak flows toward winter months (Jager et al., 1999). Complex non-additive interactions between mortality factors during incubation (e.g., redd scouring, dewatering, extreme high temperature) and accelerated development by juveniles suggested that both flow and temperature must be taken into account to predict responses to climate change. The rate of climate change is also expected to influence salmonid responses. Understanding both the transient and long-term responses to climate change is an important applied area of climate change science. Interactions with other factors that influence water temperature may also be important. Attempts have been made to differentiate water temperature changes due to effects of global warming from those due to the background of land-use impacts, such as riparian harvest, hydroelectric projects, water diversion, etc.) (e.g., Holtby, 1988). The joint effect of land use changes and climatic effects on long-term stream temperature trends highlights the need to merge these areas of study in salmon and trout protection, restoration, and management.

Interest in global warming effects is likely responsible for a recent resurgence in research related to temperature effects on fishes. We queried the Fish and Fisheries Worldwide electronic database for the proportion of freshwater fish entries that had water temperature as a key word between 1970 and 2005 (Figure 1). This pattern of scientific publication on thermal effects reflects periods of high activity, lulls, and revitalization. Initial interest
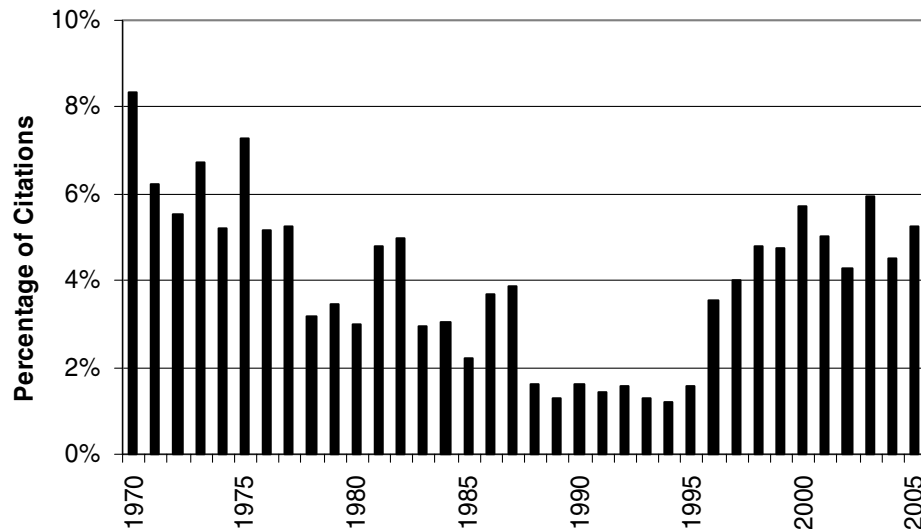
Figure 1 Search results from Fish and Fisheries Worldwide (2006), tabulating the annual proportion of freshwater fish citations that were key worded with "water temperature."

in water temperature effects arose from fish culture challenges sparked by the many hatcheries constructed as mitigation for the 1960s peak in dam building (Graf, 1999) in combination with passage of the Water Quality Act of 1965. Hatchery interest was followed in the early and mid 1970s by relatively well-funded research efforts to understand the mechanics and effects of thermal discharges (Federal Water Pollution Control Administration, 1968), particularly cooling water from power plants (Geyer and Jensen, 1976). Interest in water temperature effects waned in the early 1990s, but this calm was followed by a new storm of information fueled by critical questions that span endangered species recovery and continued efforts to understand the nuances of the physical processes of heating water bodies. These motivating management concerns have now been joined by concerns about global warming effects on fishes.

Anthropogenic impacts (e.g., watershed development and global warming) create thermal challenges that threaten to further shrink the range of coldwater fishes. Although some of the negative thermal consequences of human actions can be mitigated, the costs of such mitigation strategies are often high and can only be justified if anticipated outcomes are supported by a strong scientific foundation. Predicting benefits from actions taken to reduce high water temperatures will depend on increasing our understanding of how temperature drives fish performance at the individual and population levels over a range of spatial extents.

We believe it would be beneficial to advance some provocative questions that, if answered, would advance the science and stimulate a new round of research targeting pressing issues in thermal biology. We raise questions that address over-arching problems in ecology, fine-scaled inquiries concerning fish physiology and genetics, and explorations of physical phenomena. It is our hope that some of the questions we raise will stimulate both the imagination and productivity of scientists at all levels who have an interest in these topics. We need to view these questions with fresh eyes and, perhaps, approach problems using new analytical tools. In addition, though, we do not stress the implications of needed research on thermal standards development until well into this article, we hope that we will also attract the attention of those involved with water quality policy and funding agencies will recognize the many critical questions that are worth supporting and pursuing.

DEVELOPING THE QUESTIONS

We selected ideas from a wide spectrum of the aquatic science community concerned with thermal biology and categorized our ideas to collectively identify the breadth of thermal issues that might tend to be overlooked in more narrowly focused studies. Many of these issues highlight scientific uncertainties and areas of contention, and all are linked to interpreting the potential of fish populations to sustain themselves and maintain their ranges in aquatic communities stressed by the combination of anthropogenic and climatic warming (Table 1).

We chose questions that we believe are testable or solvable and also would likely contribute to understanding the response of coldwater fishes to global warming. Our goal here is to express why we think each question is important without specifically addressing how these questions might be studied. We hope that researchers will devise clever research designs to resolve some of the uncertainties that we present.

Specific Topics

Key gaps exist in our understanding of whether fish can adapt to global warming (Roessig et al., 2004; Ficke et al.,

Table 1 Topics we considered important to understanding the freshwater thermal biology of stream fishes and to predicting their responses to global warming

Topic area	Specific topics
Molecular level	Genetic adaptation in temperature tolerance
	Physiological indicators of thermal adaptation
	Application of biomarkers
Organism level	Lethal effects: Thermal tolerance
	Sublethal effects: growth
	Sublethal effects: reproduction and intergenerational effects
	Behavior: movement and migration
Population/species level	Adaptation in thermal tolerance
	Adaptations in seasonality
	Effects of fitness on the population.
Community and ecosystem levels	Interactions among fish species
	Food web dynamics
	Disease and parasites
Policy implications	Development of thermal standards
	Effects of habitat alterations on temperature
	Thermal heterogeneity
	Interactions of water quality and flow with temperature
	Application of new technology to study of thermal pattern and fish use

2007). Temperature controls almost all rate reactions (chemical and biological) and is thus a strong influence on biological systems at all levels. Responses might occur at various levels: molecular, organism, population, and community. We begin at the molecular level by reviewing genetic studies of adaptation in thermal tolerance. Next, we address the organism-level, including lethal, sublethal, and behavioral, responses to temperature. At the population level, we explore promising trends and questions concerning adaptations to the thermal environment within stream systems and across the landscape. After this, we consider community-level responses to temperature via interactions among fish species, impacts of diseases and parasites, and linkages in the food web. Tackling the complex interactions among stressors, including temperature, is addressed next. Finally, we focus on how science might be used to reduce uncertainty in the management of river ecosystems that support salmonids. The most promising trends linking biological response to temperature indices and other water quality or habitat indices, with application to management are summarized in Table 2.

Molecular Level

Can salmonid species adapt to global warming through evolution in ways that can be studied via molecular changes? To address this question, we review genetic studies that sought to identify genes that control thermal tolerance.

Genetic Adaptation in Thermal Tolerance

Research on evolutionary adaptation has advanced considerably, with study designs that today can address questions that previously were only speculative (Feder et al., 2000). A key question is whether understanding the physiology and genetic underpinnings of temperature tolerance can improve prediction of the ability of fishes to adapt to higher temperatures. At high temperatures, survival depends on a fish's capacity for anaerobic metabolism, the protection of molecular functions by heat shock proteins, and antioxidative defense (Portner, 2002). The genetic architecture that underlies temperature tolerance is better understood for rainbow trout than for other fishes. Genetic variation explains roughly half of the phenotypic variability in the upper temperature tolerance (UTT) of individual rainbow trout (Danzmann et al., 1999). Specific chromosomal regions influencing this tolerance have also been identified (Jackson et al., 1998; Danzmann et al., 1999; Perry et al., 2001). Future study of the expression of heat shock proteins may reveal other genes that influence UTT (Coleman et al., 1995).

It appears from molecular studies that adaptations in thermal tolerance are either limited by physiological constraints or come at the cost of tradeoffs. Enhanced performance at high temperatures might evolve through adaptations that redirect energy from growth to increase either the concentrations of enzymes that perform well at high temperature or intracellular stabilizers that prevent protein denaturation at high temperatures (an energy-allocation trade-off). Alternatively, improved performance at a higher temperature might evolve at the cost of poorer performance at lower temperatures (a specialist-generalist trade-off) by increasing the production of enzymes that function better at high temperatures and reducing production of enzymes that perform well at lower temperatures (Angilletta et al., 2003). Another important limit to thermal adaptation in proteins is caused by a trade-off between lability (a change in function with a change in form) and thermal stability (Somero, 1995). Do negative genetic correlations among traits and the resulting selective trade-offs explain the resistance to change in thermal tolerance? Such trade-offs occur when the same genes have opposite effects on the fitness of two traits (antagonistic pleiotropy). Angilletta et al. (2003) reviewed different types of trade-offs that have been shown to shape the evolution of thermal reaction norms for growth in fishes.

Clearly, additional research is needed to understand the scope for genetic adaptation to higher temperatures. Integrated expressions of the limits to genetic adaptations can be seen in terms of variation among populations or species in spatial distribution of thermal tolerance characteristics. Finally, we need more research into the underlying molecular and physiological processes that result in different degrees of thermal tolerance. Most readily available research looks at whole-organism responses. Thermal responses at lower levels of biological organization might lead to better understanding thermal damage and repair and, ultimately, to improved models of thermal tolerance.

PHYSIOLOGICAL INDICATORS OF THERMAL ADAPTATION

Past studies on physiological adaptation to temperature have tended to emphasize the relatively integrative responses such as growth rates and swimming speed that reflect the whole organism. More recent studies have expanded the use of physiological indicators to include finer biochemical responses to temperature focused on the organism or individual tissues. These studies reveal, in addition, the variation in response by sex, size, season, and water chemistry (e.g., dissolved oxygen, ammonia concentration, etc.). Explanation of the ability of salmonids to survive in environments with elevated temperature benefits from greater understanding of tissue biochemistry as controlled jointly by temperature and dissolved oxygen.

Recent studies of cardiac metabolism in rainbow trout show complex biochemical responses to temperature and dissolved oxygen that vary by sex. Female rainbow trout ventricle tissue has a lower aerobic capacity than males, evidenced by lower citrate synthase activity and a reduced level of fatty acid oxidation. This may explain their greater tolerance to hypoxia. Male trout have a greater capacity for aerobic and lipid metabolism (Battiprolu et al., 2006). Sexual differences in circulating sex steroids (e.g., androgens) appear to promote

Table 2 Summary of the foundation and application of current promising trends in thermal biology

Level of organization of knowledge	Research/surveys		Biological issues	Management application
	Focal water quality issue	Auxiliary WQ/habitat issues		
Molecular	Maximum, mean, minimum daily T;	Fish density	Heat shock	Early warning of stress in aquaculture and in the field;
	Duration of exposure to max. T or T above critical thresholds.	DO	Stress responses	Determination of smolt readiness for migration; residualism
	Rate of T change	Season	Enzyme system function; physiological tradeoffs	Adaptation in UTT
		Photoperiod	Muscle physiology Na-K-ATPase Genetic structure	
Organism	Maximum, mean, minimum daily T;	Presence of cover;	IULT laboratory tests	Point source thermal discharge
	Duration of exposure to max. T or T above critical thresholds;	Current velocity	Swimming speed for predator avoidance and upriver migration/dam passage	Hatchery practices
	Cumulative exposure to T > critical thresholds over multiple days;	Abundance of food	Behavioral thermoregulation	Survival under critical T exposure levels, duration, multiple stresses
	Degree days	Turbidity	Resistance to crowding effects in hatcheries and barging of fish past dams	Cumulative effects of temperature stress combined with other WQ and habitat stressors
	Diel T fluctuation	Fish ladders, turbines	Disease resistance	Mainstem reservoir and dam operations
	Rate of T change	Fish density, condition factor, photoperiod, nutrition level	Bioenergetics and feeding	Use of thermal refuges
	Cumulative exposure to T prior to spawning		Pre-spawning mortality; gamete viability; fitness	Fish health during migration and holding
	T heterogeneity		Intergenerational effects	Growth rates in the lab and field; egg quality; energy available for spawning; survival for multiple year spawning
Population	Maximum, mean, minimum T;	Intragravel DO, water column DO	Production, abundance, genetic or phenotypic diversity, spatial structure	ESA—threatened, endangered species protection
	Duration of exposure to max. T or T above critical thresholds.	DO stratification in mainstem reservoirs	Variation in IULT and CTM	CWA—protection of beneficial uses; non-point source discharges;
	Rate of T change	% fine sediment in spawning gravel;	Competition, predation	Cumulative watershed impacts
	Shift in timing of peak T	Latitude	Potential geographic range	Keystone species; indicator species
	T stratification	Refuge frequency	Evolution of thermal tolerance	Geographic distribution of species/subspecies
	Cross-channel T distribution	Channel gradient	Life history, phenotypic, behavioral variation	Forest practices; agricultural practices
		Riparian vegetation density, canopy height	Fitness	Thinning, salvage of forests, riparian vegetation
Ecosystem/ Community	Long-term T trend	DO, sediment, LWD, substrate composition	Fish, macroinvertebrate, algal biodiversity, production, species composition, integrity	Advanced warning of climatic warming impacts
	Increasing monthly maximum, mean, minimum T	Refuge frequency	Parasites, pathogens	Shifts in cold/cool/warm zonation
	Maximum T; duration of exposure to max. T or T above critical thresholds.	Elevation, latitude	Metabolism	Perturbation to energy pathways to fish production

(Continued on next page)

Table 2 Summary of the foundation and application of current promising trends in thermal biology *(Continued)*

| Level of organization of knowledge | Research/surveys | | Biological issues | Management application |
	Focal water quality issue	Auxiliary WQ/habitat issues		
	Spatial frequency distribution of T (daily maximum and mean) in stream network for current condition and historic potential	Sea surface temperature	Food webs	Expansion of range of predators, competitors
	El Nino/La Nina; PDO	Nutrients, light; Population density. Pool distribution Current velocity distribution Floodplain connection with stream channel Watershed road density	Multiple fish populations. Competition, predation. Exotic species. Index of biotic integrity Community composition, dominance Shift in geographic location of community transition zones;	Loss of rare species CWA—bioassessment Cumulative watershed impacts Shifts in ecosystem processes

ventricle enlargement in rainbow trout males that is linked to their greater activity on spawning grounds than females (Battiprolu et al., 2006). Male rainbow trout heart tissue inotropism is stimulated by additive effects of testosterone and cortisol (a primary stress hormone in both sexes). In females, 17β-estradiol and cortisol non-additively stimulate heart muscle inotropism (Farrar and Rodnick, 2004). Studies will be needed to ascertain the relevance of these *in vitro* sex differences in tissue metabolism to whole organisms in the field.

Some indications of field-based adaptation to temperature and dissolved oxygen come from recent studies on redband trout (*Oncorhynchus mykiss*) metabolism. In redband trout adapted to the relatively cold conditions in the Little Blitzen River, Oregon (annual temperature variation of 0 to 18°C), relative ventricle mass was 27% greater than in redband trout from Bridge Creek (annual temperature variation of 6 to 24°C). The greater total mass of ventricular mitochondria permitted increased aerobic capacity (evidenced by greater citrate synthase activity) at 12°C. The enlarged ventricle size and greater heart rate promoted enhanced oxygen transfer in the Little Blitzen River redband (Gamperl et al., 2002). The more warm-adapted Bridge Creek redband had 40–60% higher lactate dehydrogenase activity in white muscle, promoting ATP generation via anaerobic pathways at 24°C, as well as faster swimming rates.

Fish metabolism studies help us understand the interaction of elevated water temperature and the added stress of water pollution (e.g., ammonia). Rainbow trout exposed to a simulated global warming temperature increment of 2°C over a 14-month period had enhanced winter and spring weight gain. This growth advantage was lost during the summer as temperatures exceeded optimum (Linton et al., 1998a). However, the 2°C increment to the annual temperature regime plus ammonia pollution 70 μmol l^{-1}) resulted in greater annual growth than under the base regime or the base plus ammonia pollution, despite a growth rate reduction under the highest summer temperatures. This effect was linked to N quotient or extent of aerobic protein catabolism (i.e., ratio of moles of N produced to moles of O_2 consumed). Lipid and protein metabolism and nitrogen absorption efficiency vary with temperature, ammonia concentration, food availability, sex, reproductive condition, and factors controlling appetite and food intake (Newsome and LeDuc, 1975; Cunjak et al., 1987; Cunjak, 1996; Linton et al., 1998a, b). Such complex controls on seasonal versus long-term energy balance via oxygen consumption and N metabolism emphasize the need to take a life-cycle view to metabolism.

APPLICATION OF BIOMARKERS

One issue that continues to impede the transfer of new knowledge to management is the degree to which laboratory results can be reliably applied in the field. In the river environment, fishes have the capability to avoid or otherwise mitigate for adverse thermal conditions. One way of helping to bridge this gap is to develop techniques that can be used in the field. Biomarkers may provide this diagnostic capability in the future.

A biomarker is broadly defined as a molecular indicator of exposure or sensitivity of organisms or tissues to environmental perturbations. For example, the activity of an enzyme, gill Na-K-ATPase, in fresh water has been used to predict adaptation to salt water in juvenile Chinook salmon. This enzyme appears to provide reasonable relative estimates of seasonal changes in saltwater tolerance for groups of fish but seems less useful at the individual level (Beckman et al., 1999). Further, at least some biomarkers produce ambiguous results when used to infer physiological status in fish that have been thermally stressed (Zaugg et al., 1972; McCormick et al., 1999). Biomarkers to gauge thermal stress have been used in the laboratory, although there are questions of interpretation and validity (Iwama et al.,

2004). We need more information on responses of individual species, time courses, and multiple stress effects. In addition, we need to be able to discriminate between biomarkers that signal heat stress and those that signal thermal acclimation in the absence of stress (Huey and Bennett, 1990). Then, if transferable methods of measuring biomarkers were available, we might be able to more readily compare field and lab results using a common yardstick other than mortality or growth, both of which are difficult and costly to measure, and difficult to interpret unambiguously. Any ability to confirm lab results in the field will considerably aid both science and management.

Organism Level

At the organism level, responses to increased temperature depend on thermal tolerance (survival) and sub-lethal effects (e.g., growth, reproduction, and intergenerational effects). In addition, fish exposed to temperature changes are able to behaviorally accommodate elevated temperatures to some extent by moving to seek preferable temperatures in thermally heterogeneous environments. We review each of these phenomena below and highlight main research questions related to them.

Lethal Effects: Thermal Tolerance

Like many of the issues we are addressing, this one raises several candidate questions. First, we ask whether a single metric, such as average or maximum daily water temperature, is adequate to predict fish production. Hokanson et al. (1977) revealed the influence of fluctuating temperatures relative to constant temperatures in controlling the balance between growth of a group of organisms vs. mortality. Hokanson et al. (1977) computed the total yield of juvenile rainbow trout raised in environments with either a fixed mean or a $\pm3.8°C$ diel fluctuation. They found peak yields in fluctuating temperature regimes occurred at mean temperatures $1.5°C$ colder compared to fish held in constant temperatures and concluded that, although trout growth cannot be predicted strictly from the mean in a fluctuating regime, it is similar to growth at a constant temperature between the mean and the maximum. They also found that a laboratory population of trout in a fluctuating regime would achieve a zero net biomass gain (i.e., balancing growth vs. mortality) at a maximum temperature $1.5°C$ lower than a population in a constant temperature.

There have also been studies of the influence of cumulative exposure to adverse high temperatures in a fluctuating regime in which mortality results from successive thermal cycles (DeHart, 1975; Golden, 1976). These studies demonstrated that, although a single thermal cycle was not sufficient to produce mortality, accumulated stress from consecutive thermal cycles resulted in mortality. Additional research is needed to understand how different thermal fluctuations influence fish. For example, there are unknowns concerning the influence of amplitude and rate of rise, the number of cycles that can produce cumulative effects

at various mean and maximum temperatures, and the effective acclimation temperature for any fixed cycle. The influence of nonconsecutive days of stressful thermal cycles would add greater complexity to the experiment but might also yield greater understanding.

We believe it would also be prudent to more closely examine the effects that minimum daily temperatures have on an organism's ability to survive or thrive. Schrank et al. (2003) and Johnstone and Rahel (2003) suggested that daily minima provide a respite from elevated daily maximum temperatures if there is sufficient time to repair protein damage. If true, the exact functional relationships (duration, magnitude trade-offs) remain largely unexplored. In addition to simple daily cyclic effects, exactly how does a variable time series of daily minimum and maximum water temperatures affect acclimation, performance, and stress? Exploring this question may be especially relevant since global warming may be more likely to raise daily minimum temperatures than daily maximum temperatures, with a corresponding decrease in the diurnal temperature range and an increase in mean daily temperature (Easterling et al., 1997).

Sublethal Effects: Growth

Significantly more research is needed to understand sublethal performance. Heath (1990) created a taxonomy for performance indices (e.g., egg production, swimming stamina, growth rate, disease resistance, learning ability, and survival), any of which singly or in combination may be compromised by thermal distress. Have we cataloged all of the important sublethal effects that arise from thermal exposure? Although recent research has focused on particular sublethal effects (e.g., Barton, 2002; Iwama et al., 2004; Marine and Cech, 2004), more comprehensive research is needed to link indicators of cumulative stress to individual and population level responses.

We focus here on one important sub-lethal effect of elevated temperatures: sub-optimal growth. Understanding feeding, metabolism, and activity is a key to predicting growth. Hokanson et al.'s (1977) work on fish growth in fluctuating thermal regimes showed that, as temperatures approach lethal limits, fluctuating regimes result in higher mortality and lower growth than constant regimes equal to the mean of the cyclic regime. Subsequent research by Spigarelli et al. (1982), Threader and Houston (1983), and others continued this research, but obtained seemingly contradictory results. Jobling (1997) suggested that the nature and extent of thermal effects are related to the cycle's mean and amplitude: growth is enhanced when temperatures fluctuate (±2–$3°C$) below the constant-temperature growth optimum, is neutral when the mean in the fluctuating regime is close to that optimum temperature, and is depressed when fluctuations cycle above the optimum. Jobling further suggested that the magnitude of growth inhibition that occurs under a cyclic regime, when the mean of the cycle is at or above the growth optimum, increases with increasing cycle amplitude. Since growth

optima have a direct bearing on setting protective thermal standards under field conditions (McCullough, 1999), it is important that Jobling's hypothesis be experimentally verified or rejected.

Bioenergetic modeling has been used to understand the relative importance of the various components of energy consumption and expenditure in overall energy allocation and to provide insight into fish behavior (Wurster et al., 2005). A popular entrée to these investigations has been the Wisconsin Model (Hanson et al., 1997), which has greatly facilitated the application of bioenergetics by non-specialists in the field to a variety of environmental questions. Refinements called for in model parameterization include consideration of variation in activity level as a function of water temperature and prey size and abundance, variation in prey selection and energy density with predator size or age, routine metabolism related to extent of food deprivation, whether specific dynamic action (SDA) is a constant proportion of consumption or assimilation, whether egestion and excretion are functions of temperature and consumption or body size, and individual variation in consumption, routine metabolism, and maximum ration (Boisclair and Sirois, 1993; Ney, 1993; Bajer et al., 2003). Fish activity is a major uncertainty in bioenergetic models (Boisclair and Sirois, 1993). Trade-offs between energy devoted to activity and digestion (SDA) are an important area of future research (McCue, 2006).

Brett and colleagues' bioenergetic studies on sockeye (e.g., Brett et al., 1969) and those of Elliott (1994) on brown trout are landmark achievements not duplicated on other fish species. We believe that it would be valuable to conduct additional bioenergetic experiments to tease apart the factors that lead to the characteristic shape of Brett et al.'s (1982) growth curves (i.e., the breadth of the optimum range, the steepness of decline in growth beyond the optimum temperatures, and the effect of food availability on the shift in optimum), and allow for development of bioenergetic models that consider the physiological constraints placed on the fish simultaneously by temperature and food supply. Food supply under field conditions is directly linked to potential ingestion rates. Given the potential influence of gross growth efficiency (growth/ingestion) on modeling the growth curve, it is vital to be able to accurately measure ingestion at each level of food availability. Further, clarity in modeling can be achieved by expressing ingestion as a proportion of satiation or maximum energy intake (Elliott and Hurley, 1999), given the variation that can occur by expressing ration as a proportion of body size and also the variation in weight-specific energy content of laboratory vs. field foods. In summary, the physiological processes interacting with temperature and food to control growth rates should be better understood by renewed application of bioenergetic modeling with input from both laboratory and field studies.

Bioenergetic understanding of temperature and ration interactions may be useful in explaining salmonid growth and distribution in the field. In rivers where available ration is high, salmonids may be able to exploit a higher temperature thermal niche.[1] Brett et al. (1982) and Elliott (1994) showed that the optimal temperature for growth shifts downward as ration declines. We hypothesize that juvenile salmonids in highly productive rivers might exploit realized thermal niches at higher temperatures than individuals of the same species and lifestage found in less productive rivers. The ability of coldwater fishes to compete for both food and space with species that are more warm-adapted in a warmed, productive stream may depend upon food being non-limiting as well as for critical thresholds for ingestion and competitive dominance not being exceeded. The work of Reeves et al. (1987) revealed that temperature thresholds can control a species' competitive dominance and ability to feed and grow. Given that enriched rivers might not simply increase ration relative to nutrient-poor rivers for a given fish species, but might also stimulate an increase in population density as well as diversity of competitors, the implications for survival are likely not as simple as portrayed in this simple model. Bioenergetic approaches, paired with field studies of realized thermal niches (e.g., Wurtsbaugh and Davis, 1977; Huff et al., 2005) could help clarify such interactions. Theoretically, bioenergetics should also be capable of explaining differences in thermal preference between the sexes. We are aware of very little literature on this subject, but Spigarelli et al. (1983) reported that, although wild female brown trout (*Salmo trutta*) selected temperatures 3°C above those selected by males in late summer, they selected cooler temperatures in the fall. Do the existing bioenergetic or fitness models adequately explain these differences, and have we carefully examined thermal tolerance limits by sex?

Sublethal Effects: Reproduction and Intergenerational Effect

An important area of research that we believe will improve our understanding of the effects of temperature on salmonid reproduction is in the area of pre-spawning gamete mortality. Quite a few studies have reported reduced embryo and fry fitness associated with high temperatures during adult migration and holding (Billard, 1985; Berman and Quinn, 1991; Van der Kraak and Pankhurst, 1997; King et al., 2003; Patterson, 2004; Mann and Peery, 2005). Work by Jensen et al. (2004) revealed that thermal exposure even 21 days prior to spawning can significantly affect adult mortality, maturation rate, and gamete viability of pink salmon. It appears, at least for salmonids, that the period from ovulation through egg deposition and incubation includes critical stages during which temperature can reduce egg viability and survival through hatching (Van der Kraak and Pankhurst, 1997). Despite convincing evidence of thermal effects on gametes, a host of other problems such as small sample sizes, intervening diseases, low-dissolved oxygen, and toxics

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[1]Thermal niche is defined as the range of water temperature occupied or chosen by one species in concert with a variety of biotic and abiotic niche dimensions, such as food supply, habitat characteristics, or predator abundance (Magnuson et al., 1979).

have prevented definitive cause-effect attribution under field conditions.

Intergenerational effects are defined as any change in the fitness of individuals that resulted from their parents' phenotypic response to environmental conditions (Patterson, 2004). Identifying how parental stresses, including thermal stresses, affect a fish's offspring would be a significant contribution. Can we isolate intergenerational effects from fertilization effects? Do intergenerational thermal effects explain a portion of the annual variability in egg-to-fry or fry survival not accounted for by annual temperature-regime effects imposed in the egg-to-fry stages? To what extent can intergeneration effects be traced to parental exposure during early gametogenesis vs. later thermal exposure prior to or during spawning?

Behavior: Movement and Migration

Do salmonids use behavioral thermoregulation to decrease the variation in temperatures that they experience? Though we often ascribe a variety of fish movements to water temperature (e.g., Kahler and Quinn, 1998), few articles seem particularly clear and compelling. Bjornn (1971) found some evidence, but no consistent role, for water temperature in stimulating longitudinal movements of trout and salmon. Torgersen et al. (1999) found that Chinook salmon were most abundant in river reaches cooled by inflowing ground water. Jonsson and Ruud-Hansen (1985) found that water temperatures occurring between two dates were only one of a set of environmental variables (flow, cloudiness, lunar cycle) that were significantly correlated with outmigration of Atlantic salmon (*S. salar*), but the regressions they constructed were not particularly sensitive to the time windows examined, nor was there any evidence for a specific thermal trigger. Instead, they hypothesized that outmigration was related to the *combination* of increasing temperatures and the time-averaged temperature level. This is consistent with the idea that anadromous juvenile salmonids require a threshold number of degree days to reach the smolt stage, after which other environmental cues act as triggers. Brown and Mackay (1995) observed that cutthroat trout (*O. clarki*) tended to migrate for spawning at certain temperatures, but the response was not universal in all tagged fish. McBride (2002) compiled radiotelemetry data showing the movement of over a hundred large rainbow and brown trout in Delaware River tailwaters. Although water temperature seemed to be associated with the movement of some trout, there was a wide range of movement behavior through time, both of individual trout and the group as a whole. Goniea et al. (2006) observed migration rates and use of thermal refuge by radio-tagged adult fall Chinook salmon (*O. tshawytscha*) in the Columbia River. Although many individuals ceased migrating and entered cooler tributaries at high (>20°C) mainstem water temperatures, others continued migrating through presumably stressful conditions. The authors surmised that fall Chinook have a limited ability to alter migration timing in response to high water temperatures.

The only literature we are familiar with that seems to unequivocally relate specific water temperature to longitudinal movement is Pettit and Wallace (1975) for mountain whitefish (*Prosopium williamsoni*) in Idaho, Jakober et al. (1998) for bull trout (*Salvelinus confluentus*) and cutthroat trout (*O. clarki lewisi*), Swanberg (1997) and Salow and Hostettler (2004) for bull trout, and Zydlewski et al. (2005) for Atlantic salmon. Water temperature alone may not trigger movements, but some combination of temperature, temperature change, weight or condition factor (Cunjak et al., 1990), streamflow, turbidity, fish density, availability of cover, photoperiod, presence of thermal refuges, fishing pressure, other (potentially independent) movement stimuli such as day length, presumed continuous searching for more energetically profitable territories, or seemingly random exploratory behavior may collectively stimulate or reduce movement. Identifying how such factors act singly and in combination will likely be a daunting, but highly useful, statistical task.

In warmed river systems where thermal refuges might provide critical oversummer habitat, juvenile salmonids have been observed moving out of presumed refuge areas into the mainstem during the cooler periods of the day and returning to refuge during the warmest periods of the day (Belchik and Turo, 2003; Sutton et al., 2007). This diel movement appears to be temperature dependent, with a threshold mainstem temperature around 22–23°C. How do fish find refuges in the first place? Do juveniles moving through warm mainstem rivers do so opportunistically (e.g., move when cold air temperature fronts pass through)? Given that fish do not always position themselves in the coolest water but rather appear to make choices between water temperature and other habitat features determining ability to hide or feed (velocity, cover), what can we learn about composite habitat preferences within a refuge? Do refuge habitat conditions affect the trigger temperature? Isolating the mechanisms necessary or sufficient to trigger movement at various spatial scales would be a worthwhile area of investigation.

Population/Species Level

Experiments at the organism level, as described above, can be extremely revealing, but population-level studies are important in terms of exploring the capability of a species to grow and reproduce throughout its range. Evidence for the extent of thermal adaptation within a species can be found in variations among populations of the species at a location or across space. Spatial variation in adaptation for a species can be examined in variation among populations on gradients of latitude, among ecoregions, with elevation, or with position in a river continuum.

Adaptation in Thermal Tolerance

We are puzzled as to why the thermal tolerances of stream fishes do not show more evidence of rapid genetic adaptation to

elevated temperature regimes and why adaptation often involves variation in growth rates or life-cycle timing. For example, Myrick and Cech (2004) found little variation in upper temperature tolerances among native California strains of rainbow trout, which also did not differ from tolerances of non-native introduced species. Myrick and Cech (2000) found no differences in food consumption, gross conversion efficiency, resting routine oxygen consumption rate, upper CTM, or critical swimming velocity in two subspecies of California rainbow trout, but did find significant differences in growth rates at temperatures of 22–25°C.

Similarly, McCullough (1999) found that variation in ultimate upper incipient lethal limits among species within genera was relatively small and further decreased to that among subspecies within species.

In contrast, there are studies that indicate some intraspecific variation in thermal tolerance. One non-salmonid example of the limits to intraspecies variation is provided by a comparison in thermal tolerance of subspecies of largemouth bass from the northern U.S. relative to Florida (Fields et al., 1987). The critical thermal maximum (CTM) for the Florida subspecies was greater than that for the northern subspecies by less than 1°C. Other literature supports the existence of some latitudinal differences coupled with strict limitations. For example, Beacham and Withler (1991) carefully interbred several generations of individuals from northern and southern British Columbia Chinook salmon (*O. tshawytscha*) stocks. Juveniles from the southern stock proved better adapted to survive high temperatures than the northern stock but seemed to reach a limit beyond which they could no longer achieve additional tolerance. Redding and Schreck (1979) observed that inland steelhead (anadromous rainbow trout, *O. mykiss*) populations, which experience higher average temperatures, tended to have a higher temperature tolerance but slower growth than coastal steelhead populations.

This apparent discrepancy may resolve itself by studies that pay careful attention to two important features. First, studies of latitudinal differences should take care to investigate the thermal niche of a species, not just thermal limits (e.g., Huff et al., 2005). Second, differences in temperatures may not strictly follow latitudinal gradient. Yamahira and Conover (2002) pioneered exploration of the first approach. Comparing two species of silverside (*Menidia spp.*), Yamahira and Conover showed that growth reaction norms (Figure 2) in the northern species (*M. menidia*) peak at approximately 4°C lower temperature than those of the southern species (*M. peninsulae*). This revealed an interspecies adaptation to temperature. Among populations within each species, maximum growth rates increased with latitude. This effect counteracted the decline in length of growing season such that there was no effective decline in body size with increasing latitude. Yamahira and Conover asked, if northern populations can evolve an ability to accelerate growth at lower temperatures, why did they not evolve an even lower optimal temperature (or broaden the peak in growth rates), effectively extending their growing season even more? The intraspecies
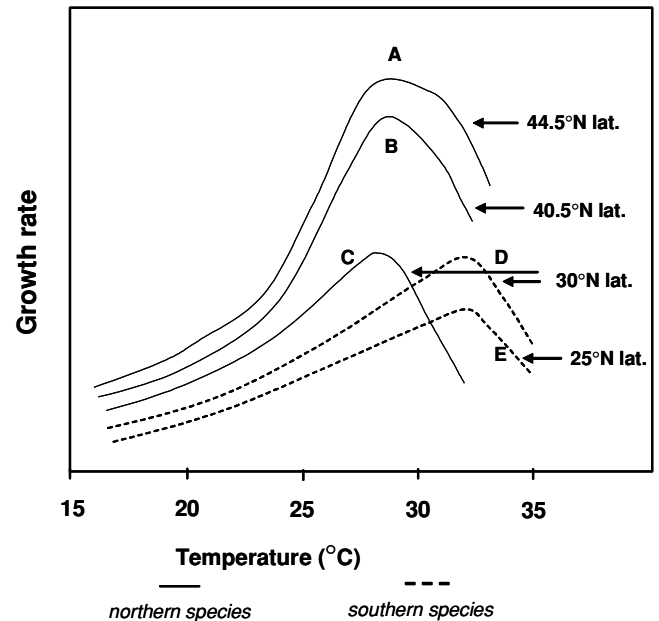
Figure 2 Representative reaction norms illustrating growth rates for coastal marine fishes *Menidia menidia* and *M. peninsulae* relative to water temperature and latitude. *M. menidia* has a northern range on the eastern coast of North America from ∼46°N to 30°N, while *M. peninsulae* populations are distributed to the south from ∼30°N to 22°N. *M. menidia* is represented by populations A, B, and C at various latitudes from 30°N to 44.5°N; *M. peninsulae* is represented by populations D and E from 25°N to 30°N. Abstracted from Yamahira and Conover (2002).

increase in growth rate with latitude exemplifies a countergradient adaptation to seasonality, whereby the growth peak occurs at the same temperature among populations. They speculated that the evolved patterns cause reproduction to occur at similar temperatures for both species, resulting in almost identical thermal exposures for their larvae and small juveniles across latitudes. Thus, past evolutionary responses have avoided solutions that would require a shift in thermal tolerances of early life stages. The remaining question is whether traits expressed during early life stages are canalized (i.e., although genetic variation is present, this variation is not expressed as different phenotypes (Flatt, 2005)). If so, might evolutionary responses that involve early life history traits be less likely than those that involve other traits?

The second approach questions whether temperature is the only environmental gradient that controls observed latitudinal differences. Huff et al. (2005) reported that thermal niches for rainbow trout (*O. mykiss*) and other species seemed to vary considerably among ecoregions at roughly the same latitude. They suggested that latitudinal differences in thermal tolerance reflect indirect effects of temperature that operate by controlling the species composition of the ecological community. For example, laboratory studies of growth rates of salmonids from contrasting latitudes indicate that the presence of competitors with different thermal tolerance alters success in utilizing nonthermal resources (Reeves et al., 1987; Reese and Harvey, 2002).

Differences in microclimate or elevation may be other factors that can confound determination of any latitude-thermal

tolerance relationship. For example, some species distributions may be protected by moderating maritime climate. Many streams in the U.S. coast range, particularly smaller ones, are dominated by the influence of the Pacific Ocean, but the marine influence can vary with distance from the ocean (Lewis et al., 2000). Streams that originate close to higher inland mountain ranges may initially have relatively cool thermal regimes as snowmelt waters are delivered via surface water flow or springs. As these high mountain streams coalesce into lowland rivers on their way to the coast, however, they often experience large increases in summertime temperatures (Beschta et al., 1987). Microclimate and elevation effects must be factored out when exploring whether there is or is not a variation in thermal tolerance by latitude. In addition, because many streams are degraded to various degrees, it may be useful to look for streams where most habitat components are of high quality to eliminate the possibility that non-thermal habitat factor variation among streams adds to the existing variation in adaptation to temperature occurring in high-quality habitats. If such streams can be found, a more rigorous test of thermal adaptation to latitude may be possible.

Adaptations in Seasonality

Bradshaw and Holzapfel (2006) reported that many species (not just fish) have shown rapid adaptation (genetic, behavioral, and phenotypic) to seasonal events (e.g., timing of prey emergence) or season length that accompany global warming, but none have evolved higher thermal optima or heat tolerance in response to higher temperatures alone. An example of such a shift in timing is the earlier spawning migrations made by sockeye salmon in the Columbia River in response to earlier spring warming of the river, which has lagged the environmental change in temperature (Quinn and Adams, 1996).

Is it true that timing is typically an easier target of selection than thermal tolerance? If so, why? Evolution in UTT is not the only way that fish populations might adapt to elevated temperatures. Traits that allow fish to control their thermal exposures during critical life stages provide an alternative evolutionary strategy—a different kind of trade-off. For example, salmonids can influence the thermal environment experienced by early life stages, which are often more sensitive to high temperatures, by seeking cooler or warmer water in which to spawn, by adjusting cues for spawning or maturation (e.g., thermal, photoperiod), or by adjusting development rate. Some of these traits may be canalized. For example, studies have shown that in some cases, variation in the number of degree-days from fertilization to hatch is low (Beacham and Murray, 1986); in others, variation in the timing of emergence is low (Tallman and Healey, 1991). Phenotypic response by adjusting time budgeting among microenvironments of varied temperature in a heterogeneous thermal environment can mean that a cold-adapted species must occupy a minor habitat in a generally warm environment. This imposes unique predator prey, dominance, and feeding behaviors

on species occupying marginal habitats. Can research predict circumstances when one strategy has an evolutionary advantage over the other?

Another phenotypic response to alterations to temperature regimes in rivers is a shift in life history. In the mainstem Columbia and Snake Rivers, the majority of fall Chinook salmon historically followed an ocean-type life history. In the Snake River, many juvenile fall Chinook salmon can avoid warm summertime temperatures by emigrating downstream in late spring to early summer and enter the ocean as subyearlings. In contrast, many juveniles spawned in the Clearwater River (tributary to lower Granite Reservoir on the Snake River) adopt a reservoir-type life history (Connor et al., 2005) and emigrate seaward after rearing a full year in freshwater. Hypotheses for this shift include decreased survival of juveniles that migrate the first spring after emergence and increased survival of yearling emigrants. Delayed fry emergence timing due to cooler incubation temperatures in the Clearwater River exposes later migrating subyearlings to higher summer temperatures rather than cooler, late-spring temperatures. Flow augmentation from the very cold Dworshak Reservoir on the Clearwater River is now used to improve subyearling passage temperatures in the Snake River (Connor et al., 2005); however, this augmentation may also lead to the unintended consequence of delaying juvenile fall Chinook salmon growth in the Clearwater River. This delay may explain why many juveniles produced in the Clearwater River adopt a reservoir-type life history, rear in downstream reservoirs, and emigrate the following spring at a larger size that confers higher survival.

Assuming substantial global warming, declining fish populations face lower chances of adaptation than healthier populations for several reasons. First, small populations lose alleles as a result of random genetic drift. Second, the likelihood of acquiring a radical genetic mutation that confers a thermal advantage is proportional to population size—a simple fact of more genes available for alteration. Third, the frequency of new alleles is more likely to increase in growing than in declining populations. Fourth, supplementation with native broodstock (if poor hatchery practices are used), and especially broodstock from neighboring populations, have the potential to slow local adaptation to higher temperatures. Is it the case that fish populations such as anadromous salmonids that are in decline (Nehlsen et al., 1991; USFWS and NMFS, 1999) are faced with demographic factors preventing genetic adaptation to such a degree that they are in the ultimate depensatory extinction vortex, as suggested by Soule (1980)?

Effects of Fitness on the Population

The subject matter for further research on fish thermal effects at the organismal level will provide needed components for thermal effects studies at the population level. Temperature provides the physical linkage governing metabolic rate across the biological hierarchy from organism to community/ecosystem

(Brown et al., 2004). Metabolic rate, in turn, governs the rate of allocation of resources to essential processes that define fitness: survival, growth, and reproduction (Calow, 1985; Brown et al., 2004). The ability of individuals to maximize their fitness is related to their fecundity, age at first reproduction, and ability to reproduce multiple times. These characteristics are influenced by metabolic rates and overall productivity of the ecosystem. Calow (1985) took growth efficiency (percentage of energy consumed that is directed to growth) to be a good index of fitness. At the organismal level, lethal temperature studies have provided guidance for the maximum thermal bounds for a species, but optimum temperatures that produce high growth and reproduction rates are key to identifying conditions that can increase individual fitness. Improvements in juvenile growth rates have been associated with maximizing fitness (Yamahira and Conover, 2002).

At the population level, the same kinds of factors under control of the thermal regime influence population viability. Population viability has been described as being a function of population abundance, productivity, genetic diversity, and spatial distribution (McElhany et al., 2000). Productivity in freshwater can be indexed by survival from egg to emergence, juvenile, or adult stages. Spatial distribution throughout historical habitat range and genetic/phenotypic adaptation to the thermal conditions found improve the survival and growth potential and the ability to produce a population size near carrying capacity. Deviations from normal water temperature ranges due to global warming can be anticipated to have ramifications in all elements of population viability. Studies of thermal effects that bridge the gap between organismal and population levels would assist in predicting trends in population or species viability.

New insights to local thermal adaptation among fish populations have come from detailed metabolic studies of rainbow and redband trout populations (both *O. mykiss* subspecies). Conventional estimates of critical thermal maximum, preferred temperatures, and growth optimum indicate no differences between rainbow and redband trout populations (Rodnick et al., 2004). However, redband populations had higher maximum metabolic rate and metabolic power (difference between maximum metabolic rate and routine metabolic rate) than rainbow trout (Rodnick et al., 2004). But, for redband trout, there were intrapopulational metabolic adaptations. The Little Blitzen River redband adapted to a colder annual thermal regime (0–18°C), had a significantly greater maximum metabolic rate and metabolic power at 12°C than did the Bridge Creek redband population, and adapted to a higher thermal regime (6–24°C). The Bridge Creek population had a significantly greater maximum metabolic rate, metabolic power, and critical swimming speed at 24°C than at 12°C. Swimming efficiency (cal/kg/km) was greater for Bridge Creek fish at both 12 and 24°C (Gamperl et al., 2002). More studies such as these may help reveal how fitness may exceed the expectations based upon conventional incipient lethal and optimum growth indices.

One approach to predicting population-level response uses individual-based models that link individual habitat use (e.g.,

Railsback and Harvey, 2002; Jager and Tyler, 2001) and fitness (e.g., Van Winkle et al., 1998; Railsback and Harvey, 2002) to environmental factors such as water temperature. Sensitivity analysis of such models has consistently shown parameters related to temperature to be important, in part because temperature often appears as an exponent in biological relationships. Simulations by Van Winkle et al. (1998) and Railsback and Harvey (2002) allowed trout to select habitats that would maximize growth rate, probability of survival, or the probability of reaching reproductive maturity—all fitness factors. Such physiological models have also been combined with models based on the ideal-free distribution theory, whereby competition for resources on the basis of temperature results in size segregation due to swimming ability change with body size (Hughes and Grand, 2000). These more complex models can generate novel hypotheses to be tested that may involve the influence of food availability and energetic cost of movement among resource patches. Individual-based simulations have also been done incorporating GIS in predictions of the viability factors listed above for trout species in sympatry and allopatry (Clark et al., 2001). Such studies reveal the importance of factors other than temperature, such as flows and episodic floods, in directing trends in abundance.

More difficult questions revolve around how we scale up the conceptually simple thermal biology of an individual fish in a laboratory setting to the level of entire populations within landscapes. We know that small thermal alterations in a stream system can have effects throughout a watershed or a life cycle (e.g., Tschaplinski et al., 1998), but our ability to accurately predict such effects is extremely limited. Simply stated, we know little about how individuals and populations respond in natural environments where temperature regimes vary through time and space. Even though we have an abundance of strong evidence that temperature-induced stress is a function of the frequency, magnitude, duration, and rate of change in water temperature that an individual fish experiences, we have not yet succeeded in adequately integrating this information to understand and predict physiological, behavioral, and abundance or productivity responses of populations at a watershed scale.

Extrapolation of individual-based studies to entire populations is challenging. There is much additional need to incorporate new tools in this work, such as GIS. Predicting the effects of temperature for a population is more complicated than simply determining when temperatures exceed a regulatory standard, such as 20°C (as noted by van Winkle et al., 1998). Temperature experienced by the population cannot be effectively defined by an average or maximum applied to a geographic range as might be appropriate for an organismal-level study at a specific point in a stream in order to infer survival or growth potential. Within each reach of the river continuum, the temperature regime would need to be defined statistically, potentially in three dimensions. Temperature modeling would be an ideal technique for estimating historical temperatures under restored stream conditions. McHugh et al. (2004) estimated productivity of spring Chinook salmon populations in selected streams in the Pacific Northwest

by applying daily mean temperatures and a few other key limiting factors in a life-stage model. More similar studies are needed, but with more refined spatially distributed environmental data for current and restored condition.

Community and Ecosystem Level

Distribution of fish species is partially a function of the distribution of water temperature, the lower and upper thermal limits of the species, their optimum and zero net growth thresholds, and other physiological functions. But this pattern is also controlled by the interactions among competing species and prey-prey relationships. These effects and various adaptations (as discussed) can cause distribution to be altered from what might be predicted purely on the basis of organism physiology. Temperature also is a controlling factor in the productivity and species composition of the trophic levels, supporting the fish species. In addition to the food web-temperature relationships, the influence of disease and parasites on fish distribution, abundance, and productivity has received little attention in the realm of water quality regulation. These added community components create a complex, interacting system where the general community patterns can be described by indices such as the IBI (index of biotic integrity), but prediction of community transitions from environmental causes remains challenging (Torgersen et al., 2006).

Interactions among Fish Species

Temperature changes can influence the competitive abilities of salmonids. De Staso and Rahel (1994) showed, for example, that brook trout (*Salvelinus fontinalis*) were competitively dominant over Colorado River cutthroat trout at 20°C, but not at 10°C. McHugh and Budy (2005) showed that the presence of brown trout negatively affected cutthroat trout performance under relatively warm temperatures, but they found no evidence of the converse effect under cooler temperatures. This finding led McHugh and Budy (2005) to suggest that abiotic factors other than temperature were responsible for mediating competition between the two trout species. In Coweeta Creek, North Carolina, rainbow trout and rosyside dace (*Clinostomus funduloides*) of similar size utilized similar velocities, yet exerted minimal influence on each other's microhabitat selection. Each species optimized its own energy intake relative to size and temperature by selecting higher velocities as temperatures increased (Hill and Grossman, 1993). This study did not, however, examine crossover temperatures beyond which the competitive relationships might change with joint changes in velocities (see Torgersen et al., 2006).

Predator-prey interactions can make understanding the salmonid community's response to temperature even more complex. Seemingly simple predator-prey interactions can rapidly become complex when we consider predator and prey densities, the ratio of predator and prey sizes, how prey vulnerability changes with size, the interaction of habitat complexity with prey capture efficiency, and how temperature may influence relative growth rates (Baltz et al., 1982; Reeves et al., 1987; Leibold, 1996).

Figure 3 illustrates some of these relationships for rainbow trout (RBT) preying on juvenile humpback chub (*Gila cypha*, HBC). Temperature and food availability obviously influence growth rates of both species, usually in a nonlinear and complex manner, though greater food availability may not necessarily result in fast predator or prey growth if temperatures are either too high or too low (Example 1). In some cases, omnivorous predators or juvenile-sized predators may consume food similar to other young fishes that are themselves prey. In this scenario, if population density is high enough and species overlap spatially, there may be competition for resources by selected age classes of species sharing a food base that happen to be classified as predators, omnivores, or prey as adults (Example 2). Finally (Example 3), because specific growth rates are generally higher for younger fish than older fish (prey and predators, respectively, in this example), prey often grow to a size where they are invulnerable to some or all of the predator population. The faster prey grow, the shorter the temporal window of vulnerability to predation.

Information needed to understand and predict these relationships is rarely available for predator-prey interactions. Growth rates for different size fish in a range of temperature and food availability have been measured in the laboratory, but food availability is difficult to quantify in the field (though it should be possible to estimate field food availability by monitoring fish growth in a laboratory that carefully mimics field temperatures and controls food availability—see Jensen, 1990). Bioenergetic models (e.g., Rice and Cochran, 1984; Petersen and Paukert, 2005) can be used to predict growth from temperature and some measure of food availability. Knowledge of the vulnerability of prey at different sizes to predator attack would also be necessary. Sufficient experimentation, literature review, and modeling might provide insights that could be used by fish managers to specify general conditions where prey vulnerability could be minimized by modifying the temperature in a riverine system, as an example.

Food Web Dynamics

The effects of water temperature on stream food webs and communities can be varied and nonlinear. Although we may understand the effects of temperature on physiology of single species of algae, invertebrates, or salmonids quite well in laboratory conditions, we have a poor understanding of how the multitudes of organisms within stream communities interact in response to changes in temperature regimes. Like the balance between food consumption and respiration that largely regulates fish growth, food production in aquatic systems is balanced by photosynthesis, which fuels the bottom of the food web, plant material consumption by invertebrates and fish, and metabolic
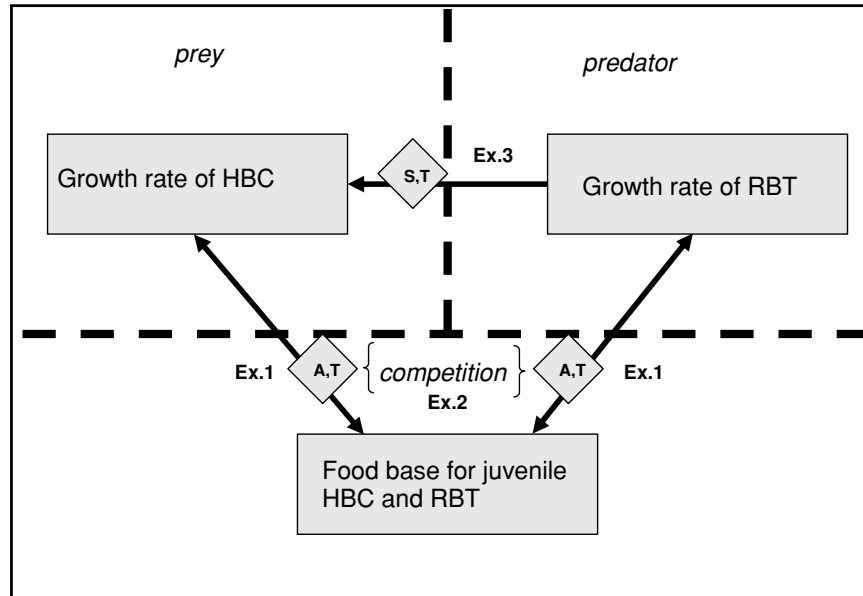
Figure 3 Examples of the complex ways temperature and food availability can mediate predator-prey relations. HBC refers to humpback chub; RBT refers to rainbow trout. Arrows represent direction of interactions. Diamonds represent rate controls exerted by food availability (A), temperature (T), size vulnerability (S). See text for a description of the three examples highlighted. Adapted from Petersen and Paukert (2005).

costs to all of these trophic levels. In principle, we might expect temperature impacts on stream ecosystems to be somewhat predictable because recent analyses suggest that temperature exerts a roughly comparable effect on the rate dynamics of metabolism and growth of a surprisingly broad range of organisms, from bacteria to large fish (Brown et al., 2004). That is, as temperature rises, we would expect considerable increases in the production of primary producers, invertebrates, and the fish that feed on them, yet we also know that an individual's metabolic rate is a function of temperature, body mass, and species-specific thermal adaptations, such that different trophic levels are not likely to be uniformly affected by temperature changes (Gillooly et al., 2001).

The inconsistent relationship between temperature and production may occur because the production of coldwater algal communities in streams is frequently not limited by temperature, but rather by light or nutrients (DeNicola, 1996). Light frequently limits algal growth in canopied streams (Gregory, 1980; Hill, 1996), and nutrients can be limiting in headwater streams (Gregory, 1980; Borchardt, 1996). In these situations, increased temperatures such as imposed by global warming may simply impart a higher metabolic cost on the algae, the invertebrate grazers, and the fish in the system, without increasing primary production at the bottom of the food web. In this case, fish production should decline with increasing temperature except in cases where most of their food is derived from terrestrial sources. Energy budgets of drift-feeding salmonids can be heavily supported by allochthonous inputs from the stream-adjacent terrestrial system (Baxter et al., 2005). Climate change-driven impacts to the magnitude of the energy flux from the riparian zone could affect fish production.

In contrast, in larger, lower-elevation streams with higher light and nutrient levels, moderate increases in temperature might allow increased primary and secondary production, thus leading to higher overall fish production. However, shifts in the relative abundance of fish species in the community may also be expected as well as change in spatial distribution of fish community types with broad-based warming along the entire river continuum, given known associations of fish communities with temperature zonation (Taniguchi et al., 1998).

Unfortunately, there are very few experiments or analyses available to help us test such hypotheses on the effects of temperature on stream food webs, or how such effects are propagated across entire stream networks. Phinney and McIntire (1965) found that, at limiting light levels, temperature had no influence on periphyton productivity, but when light was high, temperature stimulated growth. Marcarelli and Wurtsbaugh (2006) found that algal biomass in an oligotrophic mountain stream was decreased by higher temperatures, supporting the hypothesis that increased metabolic demands of the algae from temperature decreased net growth rates when nutrients limited growth. Their study did not, however, address how grazing could have influenced this relationship, nor the ultimate effect on fishes. In contrast, Lamberti and Resh (1983) found that elevating temperatures 7.5°C increased benthic algal biomass 40 times in a relatively nutrient-rich and open-canopied stream, with a concomitant increase in grazing caddisflies, but they did not study how fish were influenced by these changes. The most complete study of temperature on salmonid stream communities (albeit, in artificial streams) that we are aware of showed that a moderate temperature increase (approximately 3°C) increased algal, invertebrate, and Chinook salmon production, but the increased

algal production eventually led to complex changes in the habitat (e.g., sedimentation) and detrimental effects on the salmon (Bisson and Davis, 1976). A similar study also found that the production and biomass of steelhead and coho salmon (*O. kisutch*) was reduced by temperature increases of 4°C in a heated stream (Hughes and Davis, 1986).

The effects of temperature on complex changes in algal species composition (DeNicola, 1996), timing of distinctive algal successional events (Gerten and Adrian, 2000), and invertebrate species composition (e.g., Vinson, 2001) further complicate our ability to predict impacts on fish. For example, higher temperatures have been shown to lead to faster growth of macroinvertebrates but ultimately smaller body size of the same species at emergence (Vannote and Sweeney, 1980). Does this effect result in negative feedbacks for fish production where, with increasing temperature, the macroinvertebrate prey are smaller, while the metabolic demands of the predator fish species are greater, including the activity cost of capturing more prey items for a fixed caloric intake? Are these smaller insects emerging earlier in the season, resulting in a sharp reduction of prey availability at critical life stages for predators, or does a broadening of the warm season result in multivoltinism (more than one generation per year) that could result in more stable food availability over the growth period?

Understanding the dynamics involved in thermal regulation or mediation of an entire food web will be difficult. Will changes at lower levels in the stream food web associated with temperature tend to be compensated at higher trophic levels of the food chain, or might there be complex interactions that propagate through food webs that confound simple interpretations? Is it possible to develop "rules of thumb" about how complex food webs function as governed by water temperature (Herendeen, 1991)?

Disease and Parasites

The relationship between adverse environmental conditions and disease outbreaks in fish is well illustrated by Snieszko (1974) as the intersection of a susceptible host, environmental conditions, and a virulent pathogen. Elevated water temperature has been shown to increase virulence of many fish pathogens by its positive effect on bacterial or parasitic replication rate, and is a factor in epizootic models (Holt et al., 1975; Udey et al., 1975; Reno, 1988). Elevated water temperature can also act as a stressor and increase susceptibility to disease. Field observations linking stressful environmental condition with disease outbreaks in fish have been supported by experimental data showing that chronically elevated plasma cortisol significantly reduced both the number and function of circulating T and B lymphocytes (Bonga, 1997). The relationship between stress and the innate immune system is more complex as certain elements are activated while others are suppressed, and these changes occur over different temporal spans following the initial stress response (Dalmo et al., 1997). A further complication in measuring cause

and effect of elevated temperature and impaired immune function is the variability related to season, developmental state, and reproductive cycle (Houston et al., 1996; Alcorn et al., 2002).

An experimental approach to evaluate effects of elevated water temperature on disease in wild fish populations needs to quantify the effects of both temperature and exposure duration on immunosuppresion. Although temperature challenges such as incipient upper lethal temperature (IULT) or critical thermal maximum (CTM) provide insight into a fish's maximal thermal capacity, they do not address the significant sublethal effects of elevated temperature on pathophysiology and disease. In addition, these challenges typically do not follow the 3–5°C diurnal fluctuating temperature pattern that occurs in most streams (Vannote and Sweeney, 1980). The extent and cumulative duration of the daily maximum temperature may have a greater relationship to disease response than mean daily temperature. Other considerations in designing meaningful water temperature experiments that examine immune function and disease should include the use of (1) endemic fish that have evolved under the local environmental conditions of concern (i.e., data from northern populations may not represent stocks in the southern range), (2) adequate acclimation prior to the experimental exposures as well as proper water quality (e.g., ammonia, dissolved oxygen) and controlled ration levels similar to those experienced by wild fish, (3) endemic pathogens in waterborne challenges that reflect environmentally relevant infectious load (concentration and exposure duration), and (4) a suite of immune function measurements of both the specific and innate systems to complement disease challenges.

Policy Implications

The science of thermal effects on fishes at levels ranging from molecular to community will continue to be vital to our ability to protect water quality and the accrued beneficial uses. This understanding has been applied in setting standards that fully protect sensitive fish communities (McCullough et al., 2001; USEPA, 2003) and advances in the study of thermal effects on fish and the influence of land management and global warming on stream heating will undoubtedly improve our ability to provide protection via appropriate criteria.

Variations on thermal standards often arise from different interpretations of policy goals under the Clean Water Act (e.g., definition of full protection). There are also differing concepts of how to set standards that are protective not only of a species at a point in space but the population distribution throughout its historic range under a continuum of temperature regime change from headwaters downstream with thermal heterogeneity operating at stream segments along the way. The major land management changes to the temperature regime are well known. However, current research has revealed a need to further explore more subtle and spatially distributed land management effects in relation to other key habitat elements (e.g., large woody debris, channel morphology, vegetative condition adjacent to stream

zones, roads, floodplain, and alluvial interactions, etc.). Interactions of these habitat elements yield thermal heterogeneity at various scales that shapes species distribution and community composition. Interactions of water temperature with other water quality factors create challenges to research concerning the effect of temperature on fish response. These interactions also challenge water quality regulators. Fortunately, there appear to be many new technological tools that can aid in clarifying many previously unapproachable uncertainties in thermal biology.

Development of Thermal Standards

The development of thermal standards has enormous implications for society's water bodies. We need thermal standards that adequately protect aquatic resources and are rigorously supportable, easily measurable, and exceptionally clear.

Sullivan et al. (2000) framed standard setting as an exercise in risk analysis in which reductions in growth rates and survival were considered relative to temperature thresholds. Although their suggestion of a 10% reduction in growth rate may or may not be considered to meet a policy of "full protection" of the beneficial use, their approach is a rational exercise in considering multiple biological impacts. Sullivan et al. (2000) stated that, in the last several decades, in which thermal standards have been applied, there has been more debate over the numeric criteria chosen than debate about the experiments necessary to advance the science. We believe that there actually has been considerable research (implied by Figure 1) and a tremendous amount of effort expended, especially in the U.S. Pacific Northwest, to develop standards that are biologically protective as well as linked to physical potential of stream systems and seasonality of use by fish (USEPA, 2003). We concur with Sullivan et al. (2000), however, that it is remarkable that some truly basic issues have not been satisfactorily resolved. Despite the wealth of laboratory and field experiments that can be assembled on a wide range of thermal effects on salmonids, there is yet a risk that biological effects have not been considered in a sufficiently holistic manner. These biological risks can be addressed by considering a full range of known effects, such as addressed here from the molecular to ecosystem, assessing the knowledge gaps, and applying an appropriate precautionary margin of safety.

The process of weighing a full range of known thermal effects in setting standards, identifying those temperatures that define optimum levels of performance, and surveying thermal guilds to reveal the most thermally sensitive species and life stages can be seen in McCullough (1999) as a biologically based and precautionary approach. The USEPA (2003) has recommended a combination of biological thresholds that apply to core and marginal habitats—essentially a merging of biologically based criteria with physical potential to produce a thermal regime. Other scientists proposed "regime-based water quality standards" (Poole et al., 2004) that describe desirable conditions through space and time in a stream network to facilitate restoration and maintenance of aquatic ecosystems. We would like to see more critical, scientifically based dialogue on the merits and shortcomings of the various approaches from both policy and scientific perspectives. Are all significant biological effects effectively considered? Are there long-term effects not well described by IULT tests, growth studies, or field distribution that must be incorporated into criteria? Will beneficial uses be maintained in the long term by application of thresholds or other criteria? Given a coldwater beneficial use to protect, can biological criteria and physical potential of a drainage both be used to ensure that cumulative effects do not cause long-term shifts in species distribution and community composition? The success of temperature standards will best benefit from research that can help clarify, characterize, and reduce the uncertainty associated with predicting the effects of thermal changes on coldwater fish populations.

Effects of Habitat Alterations on Temperature

We have identified five issues that remain unresolved in assessing the linkages between habitat use changes and stream temperature. These areas needing further research include the shading effect of patchy or thinned riparian vegetation, the extent of thermal recovery as a stream passes downstream into a shaded reach, the influence of alterations to channel geomorphology on thermal patterns, processes involved in loss of thermal refugia, and the behavior of thermal minima with respect to land use alterations.

Effect of Riparian Density. The role of streamside shading has been studied over a long period (Beschta et al., 1987; Johnson, 2004) and is generally well understood. Most scientists agree that incoming solar radiation is the dominant heat flux mechanism (IMST, 2000). In arid lands, however, the effect of shading on heat flux dynamics and maximum summer temperatures continues to be debated (e.g., Larson and Larson, 1996; Beschta, 1997; Larson et al., 2002). Rutherford et al. (2004) concluded that locally dense shade with intermittent openings unquestionably can result in stream cooling under the right circumstances, but left unanswered the question of whether sparse shade could have a similar, but reduced, effect. Is the degree of cooling or warming a linear function of percentage of shade? Does the thickness of the cool canopy atmosphere affect cooling in addition to the shading effect created? Studies to examine stream temperature and associated microclimatic responses to a range of shading, such as those conducted by Johnson (2003), would be valuable to land managers responsible for arid lands and forests. Reestablishment of riparian vegetation, however, can be a simple and effective method for reducing instream temperatures for smaller streams (Johnson and Jones, 2000), although much remains to be learned about the scale of influences attributable to flow and shading. Tangentially, we also believe it is fair to say that there is no consensus on a best method to measure and incorporate shade into mathematical models. Various methods have been put forward (e.g., Cook et al., 1995; Teti,

2001), but no comprehensive testing has been done as far as we know.

Thermal Recovery. We typically assume that maximum temperatures from an exposed stream reach can decrease in the downstream direction as the stream reenters a shaded riparian zone. However, the magnitude and mechanisms for such decreases have been little studied across a range of study sites. Some research has suggested that any temperature increase in small headwater streams dissipates within a short distance upon re-entering a shaded reach and is effectively diluted by the receiving stream (Caldwell et al., 1991). However, others (Society for Ecological Restoration and Western Division of the American Fisheries Society, 2000, unpublished report) have responded that temperature and flow in both cut-over and unimpacted streams are factors in determining recovery length and cite potential cumulative effects on drainage-wide meteorological conditions that could, in turn, affect air and water temperatures throughout the drainage (Bartholow, 2000). It seems important to be able to systematically address this issue considering the variety of circumstances that may be faced in regulatory settings.

Questions include the following: What is the interaction of stream size and shaded buffer length on the stream's ability for thermal recovery in a shaded reach? Would thermal recovery occur to an extent matching pre-development conditions (i.e., to a level defined by pre-development input temperatures to the head of the buffered reach) or simply to a new equilibrium (i.e., defined by elevated input temperatures, microclimatic effects from other clearcuts, and shallow, lateral groundwater heating)? How does the timing of diurnal maximum temperatures of upstream tributaries relate to timing of high temperatures downstream? What are the most effective points of temperature compliance in a stream network in which any cumulative increases of multiple upstream actions are integrated given varying flows and channel complexity?

Channel Morphology. Channel morphology may have a complex influence on stream temperature. If land use changes have resulted in an incised channel (Booth, 1990), what is the thermal trade-off between increased bank shading and potential reductions in evaporative cooling due to wind sheltering (Benner and Beschta, 2000)? How well can we quantify the effects of wider and shallower channels caused by bank erosion or sediment deposition on daily maximum and minimum temperatures? Thermal effects anecdotally attributed to substrate color, emergent boulders, and the like, still need to be carefully studied. In another vein, instream dredging for mineral extraction in many western U.S. streams and rivers has certainly influenced gravel sorting and may have altered subsurface flows through the hyporheic zone. Flows through hyporheic zones can reduce stream temperature maxima and dampen diurnal fluctuations (Johnson, 2004). It would be interesting to compare temperature dynamics in mined and unmined streams to see whether these activities are influencing stream temperatures. Addressing these questions would involve detailed modeling along with micrometeorologic and hydrologic instrumentation.

Processes in Thermal Refuge Loss or Maintenance. Several different processes appear to be involved in loss of thermal refuge abundance: elimination of large woody debris (LWD) or other pool-forming structures (see Welty et al. (2002) for a novel predictive model of LWD and shading); levees that sever the floodplain from the channel (Poole and Berman, 2001); road networks or other infrastructure that divert shallow groundwater flow, warming it and routing it to the floodplain (Gucinski et al., 2001); and groundwater pumping adjacent to the river onto agricultural land. Can these mechanisms be confirmed? A wide variety of human activities (e.g., water resources development, land use modification, channelization) can lead to increased summer temperatures or homogenization of aquatic habitats, resulting in fewer microthermal habitats (Poole and Berman, 2001). Other activities such as hypolimnetic releases downstream from reservoirs result in cooler summer temperatures downstream and shifts in the thermal regime during other seasons (Poff et al., 1997), and storage reservoirs with surface or near-surface water releases can cause a prolongation of high temperatures in the fall. Are there other mechanisms? How can effective refuges be protected, maintained, created, restored, or, in other cases, made irrelevant via reductions in main-channel water temperatures?

Concern about Daily Thermal Minima. Even though thermal minima are not currently considered under regulatory guidelines, which aim primarily at maxima and/or means, they may well be biologically important. Understanding how minima are controlled in the landscape is important to land management. Riparian cover and near-stream land use influence minimum temperatures (e.g., Chen et al., 1993), but the extent of these influences needs clarification. Under what conditions do minimum temperatures at one point on a stream course influence downstream maxima? Initial studies have shown that bedrock reaches can have colder minima than gravel-bed streams, and reaches with hyporheic flows have warmer minima (Johnson, 2004). Does the composition and porosity of stream substrates have a predictable influence on minimum stream temperatures? A combination of monitoring and modeling could be brought to bear on this question with potentially useful results.

Thermal Heterogeneity

Thermal heterogeneity or patchiness is a well-recognized aspect of habitat pattern in temperate streams that affects spatial distribution and population viability. In addition, understanding the role of thermal heterogeneity in the context of salmonid metapopulation structure could lead to important insights regarding the potential for adaptation to global warming and population sustainability in the face of changes in thermal habitat distribution pattern.

Differential rates of water heating, cooling, and mixing; exchange of surface and intergravel flows; and inputs from groundwater or tributaries interact to produce a temporally and spatially dynamic gradient of temperatures within streams (Poole and

Berman, 2001). River margins, off-channel habitats, sections with groundwater inflows, deep pools, and reservoir tailwaters potentially have modified temperatures that could serve either as a thermal refuge or an avoidance zone. Thermal heterogeneity at various scales of investigation creates a template for spatial distribution of species, life-history variation within populations and fish communities, and aquatic ecosystem processes (Schneider, 2001). For example, Torgersen et al. (1999) demonstrated thermal heterogeneity over broad spatial scales in a desert coldwater river. The distribution of lakes in a watershed can influence stream temperatures (Adams et al., 2001; Mellina et al., 2002) and interactions of native and introduced salmonids (Adams et al., 2001). The use of coldwater patches as thermal refuges during thermally stressful periods has been repeatedly demonstrated for coldwater fishes in a variety of stream environments (e.g., Gibson, 1966; Kaya et al., 1977; Berman and Quinn, 1991; Sutton et al., 2007).

Thermal refuges often exist along stream margins in shallow, slowly moving waters, but use of these locations might increase the risk of predation from terrestrial predators or reduce opportunities for foraging on invertebrate drift. River margins can provide zones of coldwater seeps, but can also be zones of warmed water not fully mixed in the main flow (Ebersole et al., 2003a). As the cost-benefit ratio of refuge use increases, do refuges become *de facto* "ecological dead ends," in terms of reduced fitness, as suggested by Coutant (1987)? Use of refuges may represent the only means available for individuals to persist in a generally hostile environment. A stream system where cold refuges exist within a warmed matrix creates trade-offs in biological functions as the organism tries to satisfy multiple biological needs, such as the need to capture food in the matrix temperature, but to reduce R and increase G via use of the refuge. Such trade-offs, and subsequent costs to fitness, are poorly understood and are worthy of future research. In addition, we advance the hypothesis that the salmonid population in the river with more refuges will thrive relative to the population in the river with fewer refuges. Such a study would need a working definition of refuge that relates the magnitude of deviation from average matrix conditions so that significant biologic advantage can be measured.

Management of streamflow and riparian zones would benefit from a better understanding of what makes an effective thermal refuge for coldwater fishes. Key questions include the following: What constitutes a thermal refuge? Under what circumstances do individuals seek out thermal refuges? What characteristics (e.g., temperatures, physical structure and extent, water chemistry, food availability) of thermal refuges are associated with higher rates of survival and persistence of coldwater fishes in warm river reaches? Do bioenergetic savings afforded by thermal refuges increase reproductive success (e.g., reaching spawning areas, finding a mate, and constructing and guarding redds)? Is gamete viability higher for adults holding in thermal refuges? Do thermal refuges serve as corridors or stepping-stones for migrating adults or juveniles that swim from one refuge to another as they move upstream or down, as envisioned

by some in the mainstem Columbia and Snake Rivers (USEPA, 2003) and the Klamath River? For anadromous salmonids, is the abundance of mainstem refugia sufficient to provide summer rearing opportunity for juveniles after leaving natal tributaries?

INTERACTIONS OF WATER QUALITY AND FLOW WITH TEMPERATURE

It has long been clear that temperature is but one of an array of water-quality constituents that, singly or collectively, limit fish populations (Coutant, 1976), yet we rarely have biologically meaningful and comprehensive ways to quantify interactive effects. Broadly speaking, how can we put temperature in perspective with other variables that influence fish populations?

Let's focus briefly on dissolved oxygen (DO), which is influenced by water temperature and has synergistic effects with temperature on the health of individual fish. The science of DO is well developed, but policy is hindered by similar technical uncertainties as with temperature. What metric most effectively and efficiently captures how DO may limit one or more life stages of a fish species? Is it mean water column or intragravel dissolved oxygen, 7- or 30-day averages, average of daily minima, or lowest instantaneous values? Even though we have good basic information on effects of DO and temperature (Warren et al., 1973; Cech et al., 1990), the more specific implementation questions being asked today make this a fertile topic for exploration. Regulators would rather not set standards for single water-quality factors to compensate for extremes in other factors; however, predicting the joint probability of high water temperature and low DO is important in order to find ways to minimize their synergistic effects. This issue is further complicated because elevated water temperatures are often associated with episodic low flow or drought conditions. To what extent are regulatory exemptions due to extreme climatic variation warranted when anthropogenic effects tend to influence temperature, DO, and flow jointly under all climatic conditions?

Do we need more specific or different water-quality standards to better protect streams with cumulative stressors like high temperature and low DO (Karr, 1990; Rossi and Hari, 2004)? Cumulative stress from temperature and other water quality constituents has increasingly been monitored using bioindicators (Karr, 1990) that serve as a reflection of the combined influences of all water-quality factors on aquatic biota.

Quantifying synergistic effects, or teasing single effects from cumulative ones, will clearly be elusive and nontrivial. There are some relatively new statistical techniques, such as quantile regression (Cade and Noon, 2003), that characterize the upper (or lower) limits that one variable imparts on another when multiple factors are involved.

APPLICATION OF NEW TECHNOLOGY TO STUDY THERMAL PATTERN AND FISH USE

The rapid advance of technology is providing new tools and approaches that can ratchet ecology's typical scale of investigation from site-specific to broad geographic coverage, while even enhancing the resolution of data collected. Possibilities include innovative applications integrating forward-looking infrared (FLIR) imagery (Torgersen et al., 1999; Faux et al., 2001; Boyd and Kasper, 2002) to derive an aerially extensive, high-resolution (<1 m^2), point-in-time mapping of surface water temperatures for an entire stream system; a dense array of thermographs to monitor instantaneous temperatures throughout a watershed (Popa et al., 2004; Porter et al., 2005); light detection and ranging (LIDAR) to accurately assess canopy density and cover as a means to model effective shade (Nilsson, 1996); application of GIS (geographic information system) software to map and develop spatial statistics on distribution of temperature and fish (Torgersen et al., 1999) and to calculate riparian and topographic shading; and three-dimensional numerical models to predict spatially explicit temperature changes through time over broad areas (Cook et al., 2006), including temperature in river margins that may provide preferentially used habitats (Dauble, 2000).

A specific issue to address is how to predict the abundance and distribution of thermal refuges not associated with obvious tributaries. It has been shown that refuges are formed at the interface between the channel and groundwater, the distribution of which depends on the basin's underlying geological and geomorphic setting (Baxter and Hauer, 2000). Hydraulic conditions (e.g., LWD and sediment storage) conducive to alluvial head gradients that force subsurface flows might also create thermal refuges (Poole and Berman, 2001). Such correlations might be explored with data gathered using FLIR sensors, but to our knowledge, few have evaluated the linkage of thermal distribution patterns to basin geomorphology with an eye toward predicting the relative occurrence or attributes of thermal refuges (Faux et al., 2001; Ebersole et al., 2003b; Wright et al., 2005). To do so would yield a valuable interdisciplinary study.

Expanding the scale of observation of fish response to temperature from the stream reach to the entire stream system, and from single point-in-time to annual or generational time scales could more meaningfully reveal effects on a population relative to its competitors. At these scales, it is feasible to use temperature-sensing radio transmitters to measure *in situ* behavioral responses of fish in a complex thermal environment (Brandt, 1993; Tiffan et al., 2003). Thermal selection could be determined for a population in a thermally diverse reach using archival temperature tags, provided we can also effectively monitor the three-dimensional thermal environment available at a sufficiently refined temporal and spatial scale. The influence of population density, density of competitors with different thermal sensitivity, and habitat heterogeneity (e.g., velocity distribution) could be evaluated in defining thermal selection and

time budgeting (i.e., allocation of time spent in various habitats during the day, resulting in a specific thermal exposure history) under field conditions. A time budget of swimming speed (see Brown and Geist (2002) for new field monitoring of swimming speed) relative to water velocity, food availability, and temperature distribution would also be instructive. Studies on seasonality of response are also needed. For example, growth rates during the peak summer season vs. cooler seasons relative to these variables would provide a fuller bioenergetic explanation of thermal response such as called for by Berman and Quinn (1991).

Techniques for tracking fish locations simultaneously with their exposure to water temperatures hold promise for advancing our understanding of temperature selection and thermal histories of free-living fishes. Implanted temperature loggers have been used to record internal body temperatures of adult salmonids and smolts, but they are currently too large to use in the smallest juveniles. Individual tags (e.g., PIT tags) combined with sensor arrays would allow detection of movements of fish within streams in relation to thermal gradients (e.g., Raskauskas, 2005), and advancements in tag size and detection range may eventually make remote applications over large spatial extents feasible. Research spurring advancements of these technologies is needed. Field feeding rates inferred from growth rates and thermal history, otolith microchemistry (Radtke et al., 1996; Wurster et al., 2005), or heat shock proteins are other valuable tools that can help elucidate fish thermal habitat selection and influences on fitness.

CONCLUSION

Great questions often engender good science (Siegfried, 2005). We have provided starting points for future research that we believe can lead in the direction of better understanding how riverine salmonids will respond to changes in temperature via either natural short-term patterns, land management effects, or global climate change. We make no value judgment on the importance of our questions relative to other pressing research questions. We merely believe that there is a benefit in asking ourselves what we don't know, recognizing that mysteries and puzzles are opportunities to be explored.

Some problems we are experiencing globally offer fertile opportunities for monitoring and learning that we cannot afford to pass up. Integrated monitoring of fish communities within their abiotic contexts, especially in thermal zones that are transitional for specific species or thermal guilds, provides a window to behavioral and physiological processes important in understanding dynamic population responses to temperature fluctuations. Revolutionary changes in and coupling of technology and modeling (Torgersen et al., 2001; Cooke et al., 2004) offer exciting possibilities for confirming relationships between physical variables and observed population consequences.

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