Hydrobiologia (2008) 603:183–196
DOI 10.1007/s10750-007-9271-2

PRIMARY RESEARCH PAPER

Summer temperature variation and implications for juvenile Atlantic salmon

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Received: 14 February 2007 / Revised: 17 December 2007 / Accepted: 27 December 2007 / Published online: 26 January 2008

Abstract Temperature is important to fish in determining their geographic distribution. For cool- and cold-water fish, thermal regimes are especially critical at the southern end of a species' range. Although temperature is an easy variable to measure, biological interpretation is difficult. Thus, how to determine what temperatures are meaningful to fish in the field is a challenge. Herein, we used the Connecticut River as a model system and Atlantic salmon (*Salmo salar*) as a model species with which to assess the effects of summer temperatures on the density of age 0 parr. Specifically, we asked: (1) What are the spatial and temporal temperature patterns in the Connecticut River during summer? (2) What metrics might detect effects of high temperatures? and (3) How is temperature variability related to density of Atlantic salmon during their first summer? Although the most southern site was the warmest, some northern sites were also warm, and some southern sites were moderately cool. This suggests localized, within basin variation in temperature. Daily and hourly means showed extreme values not apparent in the seasonal means. We observed significant relationships between age 0 parr density and days at potentially stressful, warm temperatures (≥23°C). Based on these results, we propose that useful field reference points need to incorporate the synergistic effect of other stressors that fish encounter in the field as well as the complexity associated with cycling temperatures and thermal refuges. Understanding the effects of temperature may aid conservation efforts for Atlantic salmon in the Connecticut River and other North Atlantic systems.

Keywords Global climate change · *Salmo salar* · Thermal regime

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Handling editor: T. P. Crowe

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Introduction

Temperature is a major force in determining the abundance and distribution of fish (Perry et al., 2005; Kangur et al., 2007; Pörtner & Knust, 2007). As ectotherms, fish species are greatly affected by water temperature (Schmidt-Nielsen, 1990). Temperature in streams fluctuates naturally according to daily and seasonal variation usually associated with the surrounding air temperature (Caissie, 2006). In addition, humans directly and indirectly alter temperatures of stream ecosystems both at global and local scales; e.g., through urbanization, changing land use, flow modifications, and dam construction (Dynesius & Nilsson, 1994; Wang et al., 2003; Kishi et al., 2004; Wheeler et al., 2005; Habit et al., 2007). Hence, many natural and anthropogenic stressors directly affect the thermal regime that fish experience. The conundrum with temperature is how to characterize this easily measured variable in a manner that is meaningful to fish.

Temperature in streams is important for cool- and cold-water fish (Meisner, 1990; Stoneman & Jones, 2000; Isaak & Hubert, 2004; Franco & Budy, 2005; Lobón-Cerviá & Mortensen, 2005). Distribution (Dunham et al., 2003), survival (Schrank et al., 2003), growth (Meeuwig et al., 2004), and general health of stream dwelling salmonids (Cairns et al., 2005) can be adversely affected by high temperatures. For example, fish distribution can be limited by high summer water temperatures (Keleher & Rahel, 1996). Reduction in the riparian canopy can increase temperatures (Johnson, 2004; Poole & Berman, 2004). As a result of deforestation, agriculture, and urbanization within a watershed, temperatures can increase even in less-developed areas (Poff et al., 1997). Thus, in areas that marginally support cool-water species, direct alterations within the watershed or indirect alterations through global climate change could reduce fish distribution (Eaton & Scheller, 1996; Flebbe et al., 2006; Crozier et al., 2006; Preston, 2006).

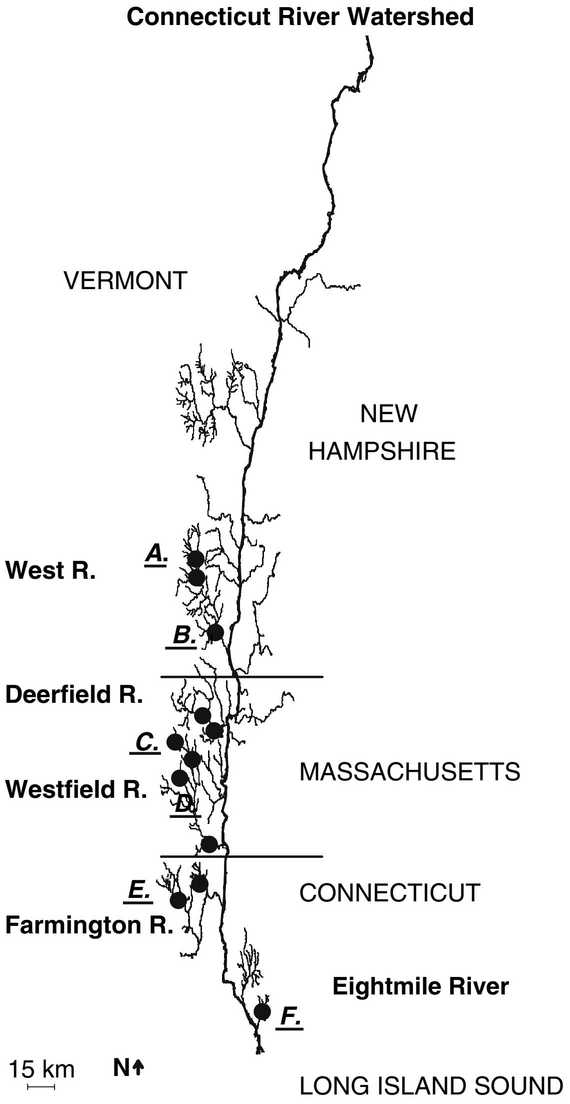

Fig. 1 Map of the Connecticut River watershed including the five basins in this study. The 12 filled circles indicate sites at which temperature and fish data were collected. The West River is in Vermont ($n = 3$ sites), Deerfield ($n = 2$) and Westfield rivers ($n = 4$) are in Massachusetts, and the Farmington ($n = 2$) and Eightmile ($n = 1$) rivers are in Connecticut. Sites A through F are those used to illustrate a range of specific temperature patterns

The Connecticut River, the largest river in New England, is a model watershed in which to study the effects of temperature on cool-water fish. The Connecticut River extends more than 660 km from near the Canadian border to Long Island Sound. This river passes through four states (Vermont, New Hampshire, Massachusetts, and Connecticut; Fig. 1) and drains an area of over 29,100 km^2. Based on its north to south orientation, latitudinal trends may exist. Due to morphometry, land use, elevation, and human settlements, within-basin differences in temperature also may exist. Thus, the Connecticut drainage has a range of temperatures that may have detrimental effects on stream fish as well as temperatures that may not. By using a natural temperature record in this system, we seek to provide guidance on how to distinguish these two categories of temperature effects.

Within the Connecticut River, Atlantic salmon (*Salmo salar*) is an ideal species for studying the effects of temperature. The river lies near the southern end of the natural range for Atlantic salmon (Parrish et al., 1998), and we might expect temperatures, especially high temperatures, to cross thresholds for Atlantic salmon. Atlantic salmon were extirpated from the system in the early 1800s (Moffitt et al., 1982), but a restoration program is currently underway that seeks to restore salmon to the watershed (Meyers, 1994; Connecticut River Atlantic Salmon Commission, 1998). Since 1994, up to 10 million Atlantic salmon fry were stocked annually in suitable habitat throughout the watershed. Since there is negligible reproduction of adult salmon in the river, stocking fry at similar densities in all sites using standard methods provides a framework to test the effects of temperature on juvenile salmon distribution.

In order to interpret temperature in a biological meaningful way, field temperature data need to be linked to conditions relevant to stream fish. For Atlantic salmon parr, ultimate lethal temperatures at which 50% of the test animals survive for only 10 min, are 30–33°C (Huntsman, 1942; Elliott, 1991). Incipient lethal temperatures at which 50% of the test animals survive 7 days are lower, 24.8–27.8°C (Garside, 1973; Elliott, 1991). Lethal temperatures, as measured in the laboratory, may overestimate the ability of juvenile salmon to withstand extreme temperatures in the field. For example, for Atlantic salmon from the Miramichi River, Hsp 70 mRNA and related proteins were not induced in heat stress tests in the laboratory, but were elevated in the field at 23°C (Lund et al., 2002). Although temperatures for growth do not directly affect mortality, reference points related to growth provide measures of sublethal temperature effects. For English salmon, the optimum temperature for growth is about 16°C (15.9°C) and 21.6–22.5°C is the upper threshold for normal feeding (Elliott, 1991; Elliott & Hurley, 1997). In recent models, the optimal temperatures for growth of Atlantic salmon from Norwegian rivers were higher than those reported above (18–19°C; Forseth et al., 2001, 16–20°C; Jonsson et al., 2001).

Herein, we examine the impact of summer temperature on abundance of Atlantic salmon parr in the Connecticut River. Specifically, we asked: (1) What are the spatial and temporal temperature patterns in the Connecticut River during summer? (2) What metrics might detect effects of high temperatures? and (3) How is temperature variability related to density of age 0 Atlantic salmon during their first summer? Since fish in the Connecticut River are exposed to a number of stresses, we assess if 23°C is a useful sublethal, upper-temperature, reference point. In addition, we examine if moderate temperature variation related to temperatures documented for optimal growth (≥18.5°C), is related to juvenile salmon abundance. We are not suggesting that fish die at temperatures ≥23°C or that temperatures for growth directly affect mortality. We only test if these are sensitive, conservative, and biologically based reference points with which to explore temperature differences across sites. Thus, a naturally complex temperature dataset was summarized to illustrate seasonal, daily, and hourly variability along the longitudinal gradient of the Connecticut River. We related this variability to thresholds based on literature values relevant to Atlantic salmon. Finally, we determined which summer temperature patterns were related to density of age 0 Atlantic salmon.

Methods

Field data

In 1998, temperature was recorded hourly at 12 juvenile Atlantic salmon sample sites from May to December with HOBO Temperature Loggers (Onset Computer Corporation®). These temperature sites were located within five tributary basins of the Connecticut River watershed including the West ($n = 3$), Deerfield ($n = 2$), Westfield ($n = 4$), Farmington ($n = 2$), and Eightmile rivers ($n = 1$). These basins span about half the geographic range of the watershed. Sample sites with temperature loggers are indicated with a solid circle; sites that are discussed in detail are lettered (Fig. 1). Summer temperatures were recorded from June through August.

Each spring, 6–10 million fry were scatter stocked at similar densities throughout the watershed. Fry were all from the Connecticut River restoration stock and so had a similar genetic background. In addition, the location where fry were stocked was not related to the tributary origin of the parent. Our sample sites were stocked at an average density of 55 Atlantic salmon fry per 100 m^2 (SE = 3.6, $n = 12$). In the sites discussed here, stocking occurred from 13 April to 20 May, 1998 (range = 37 days, mean date = 29 April). Our sample sites were an average of 96 m long (SE = 10.4 m).

At the end of the first summer, age 0 parr were 4–6 months old and 60–140 mm in total length (TL) (Campbell, 1999). In fall, 1998, concurrent with temperature monitoring, juvenile Atlantic salmon were electrofished at 12 sample sites using methods similar to those of McMenemy (1995). In the sites we discuss here, juvenile sampling occurred from 4 August to 23 September, 1998 (mean date = 4 September, SE = 4.2 days). Atlantic salmon populations were sampled using DC electroshocking. Wherever possible, sites were isolated by block nets or natural barriers. Population estimates for each station were made using the removal method. Two or three sampling runs were made at each site. After electrofishing, juvenile salmon were tallied by run. Density was calculated as the number of fish caught divided by the area of the sample site (length times width) and these counts were standardized to 100 m^2 for comparison across sites. Population estimates were calculated by age class using a maximum weighted likelihood modification of the Zippin removal method (Carle & Strub, 1978). Since across site patterns in survival and density were similar, we present results only for density of age 0 Atlantic salmon at the end of their first summer.

We chose sites that were qualitatively representative of the habitat in adjacent stream reaches for sites that spanned the lower half of the Connecticut River watershed. Our sampling sites were relatively small (width: X = 7.3 m, SE = 0.99 m, $n = 12$), shallow (depth, X = 18.9 cm, SE = 1.27), had a moderate gradient (% gradient change per meter, X = 1.9, SE 0.35, Campbell, 1999), mean bottom velocities of 0.2 cm/s (SE = 0.04; $n = 12$), and a range of large substrates (% boulder = 26.9, SE = 5.05, % cobble, X = 44.6, SE = 4.87, M.E. Mather, unpublished data). In general, our sample sites had relatively simple fish communities. Trout (*Salvelinus fontinalis*, *Salmo trutta*, *Oncorhynchus mykiss*) were sampled but typically their numbers were low compared to salmon parr (Raffenberg & Parrish, 2003). Several other species of fish were observed across sites, e.g., cyprinids, cottids, catastomids. The density of age 1+ Atlantic salmon varied across sites (X = 6.14, SE = 1.16). On average, age 0 parr were about half of the total juvenile salmon (X = 53%, SE = 8%).

Quantifying field temperatures in a biologically relevant way

In order to relate temperature to counts of age 0 Atlantic salmon standardized to 100 m^2, we used Poisson regression analysis. This is a general linear model with a Poisson error term and a log link function (Quinn & Keough, 2002). Poisson regression is especially appropriate when count data are the dependent variable (Myers, 1990). Here, we examined the relationship between temperature and numbers of salmon at each of 12 sample sites using PROC GENMOD (SAS, 2003). In the regressions, site-specific measures of temperature were made in several ways. We calculated the seasonal mean and standard deviation based on mean daily temperatures. We also calculated the average daily variation and total seasonal degree-days based on hourly temperatures. Daily variation was the maximum variation within a day; degree-day was the sum of hourly temperatures across the three month summer season. In addition, we looked at the number of days and number of hours that the maximum hourly temperatures exceeded potential biological thresholds: 18.5, 20, 23, 25, and 27°C. Finally, to examine importance of time at high temperatures, we determined the number of intervals that each site was continuously $\geq$23°C, a potentially stressful, non-lethal, conservative high temperature benchmark. For this consecutive hour analysis, we considered intervals of 1–12 h. We examined the relationship among 14 overall summer temperature metrics and numbers of under yearling salmon (age 0). For these, we used an overall α(of 0.1 with a Bonferroni correction for 14 regressions for general temperature metrics (0.1/14 = 0.007) and an α of 0.1 with a Bonferroni correction for 12 regressions that analyzed consecutive hours (0.1/12 = 0.008 (Quinn & Keough, 2002)). For the Poisson regression, we used Wald 95% confidence intervals and an R^2 goodness of fit measure for count data calculated as 1—(Intercept deviance/full model deviance) (Cameron & Windmeijer, 1996). All trends discussed are significant at these adjusted α values unless otherwise noted.

Results

Scope of temperature variation

None of the12 sample sites in the Connecticut River basin had a summer mean that was ≥23°C (Fig. 2). Most central sites had means close to 16°C (South 2 to Belden). Although the warmest site was in southern Connecticut (Eightmile), we did not see a north-south temperature gradient because warm sites also occurred in Vermont (West 2a, West 4a) and cooler, more moderate sites were observed in Connecticut (Belden, Fig. 2).

Additional temperature variability, not seen in seasonal means, emerged when temperatures were examined by day. In summer (June–August), daily temperature means at each site varied by 8–15°C (Fig. 3). Most sites maintained mean daily temperatures below 23°C. Time spent within the 16–20°C range varied by site. Predictable latitudinal variation still occurred in that a Connecticut stream was the warmest (Fig. 3F, Eightmile). However, site-specific variation was detected in warm, northern (Fig. 3A) and cool, southern (Fig. 3E) sites. Each state, along the latitudinal gradient, had warmer (Fig. 3A, C, F) and cooler (Fig. 3B, D, E) sites. In all sites, the rapid increase from spring to summer and consequent early season fluctuations only emerged by examining daily means (Figs. 3 vs. 2). Daily means also produced new information about extreme values, especially in northern and southern sites. For example, in the two warmest sites (Fig. 3A, F, West 4a, Eightmile), temperatures ≥23°C were seen in the daily but not the seasonal means.

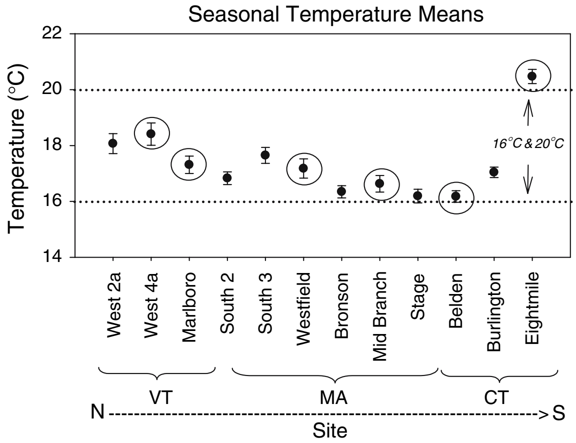

Fig. 2 Summer temperatures across 12 sites in three states within the Connecticut River watershed at which juvenile Atlantic salmon (age 0) data were collected in 1998. Sites are shown from north to south (left to right). Seasonal means and standard errors (SE) were calculated by taking the average of daily temperatures within a season based on 64–92 days. (*Note:* temperature data at some sites on some days were lost, i.e., those less than 92 d, due to mechanical failure). The dotted lines, 16–20°C, represent moderate, reference points related to growth optima that allow visual comparisons across sites. Circles indicate sites corresponding to A through F in Figs. 1, 3, 4

Not surprisingly, extreme variations were even more exaggerated when we calculated hourly variation (Fig. 4). In warm and moderate temperature sites, hourly data frequently (Fig. 4A, F) or occasionally (Fig. 4B, C, D) exceeded 23°C. The number of consecutive hours that a site exceeded a high temperature threshold like 23°C varied across sites (Fig. 5A). In the warm sites (Fig. 5B, G), there were over 35 intervals where hourly temperature exceeded 23°C, including a number where high temperatures were experienced for more than 12 h. In the Westfield, over 25 intervals ≥23°C were experienced in the 3-month summer period but the most common interval of consecutive temperatures was 2 h (Fig. 5 D). In the more moderate sites (Fig. 5C, E), less than 25 intervals of temperatures ≥23°C were observed with most ≤5 h. In the coolest site (Fig. 5F), summer temperatures never exceeded 23°C.

Temperature effects on age 0 Atlantic salmon

Across all 12 sites, density of age 0 Atlantic salmon ranged from 0.18 (Westfield) to 21.34 (Marlboro) with an average of 9.24 (SE = 2.18, Fig. 6). When the Bonferroni corrections were made (critical $\alpha = 0.007$ in A and 0.008 in B; Table 1), a number of high summer temperature metrics were significantly and negatively related to age 0 Atlantic salmon density. Mean summer temperature, standard deviation and daily variation were not significantly related to age 0 parr density (Table 1; Models A1–A3). Degree days, days where the maximum temperature ≥18.5, 23, and 25°C (Table 1; Models A4, A5, A7,

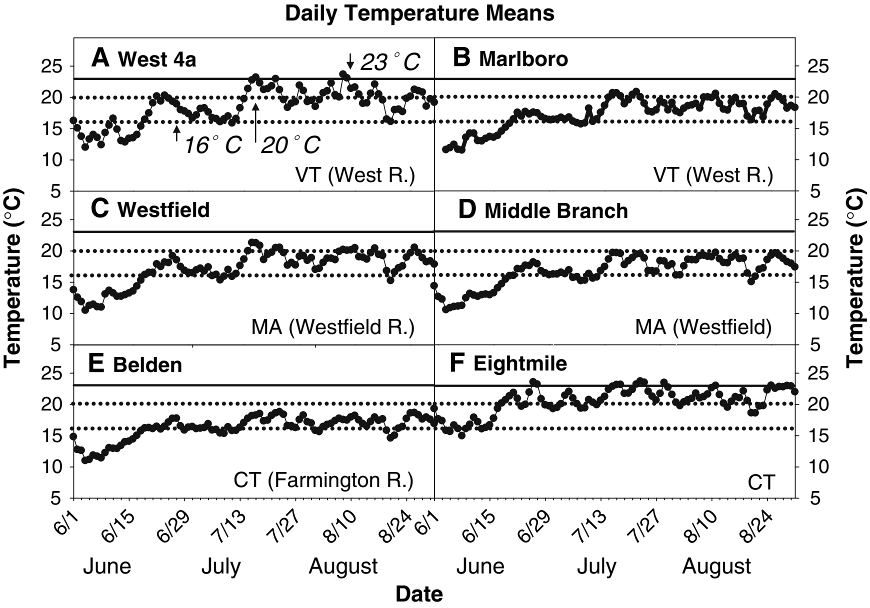

Fig. 3 Daily temperature means for June–August, 1998, at six sites within the Connecticut River watershed (A–F in Fig. 1). Sites are listed from north to south. In each row are pairs of contrasting patterns within a state including examples of sites in Vermont (**A**, **B**), Massachusetts (**C**, **D**), and Connecticut (**E**, **F**). Within each plot frame, listed are the site name (upper left), state, and basin (lower right). All temperature plots include three reference lines. The upper solid line (≥23°C) indicates extreme values that could be related to Atlantic salmon distribution in the field. The lower pair of dotted lines, 16–20°C, represent moderate reference points, related to growth, that allow visual comparisons across sites

and A8) were all significant ($P = 0.001$–0.0001) and inversely ($\beta_1 = -0.002, -0.011$) related to age 0 salmon density (Fig. 7). Thus, there is a relationship between high summer temperatures and numbers of age 0 salmon. However, because these significant models only explained between 10 and 26% of the variation in age 0 salmon density, other factors were also important. The confidence intervals for β_1 overlap suggesting that any of the significant overall temperature metrics (Table 1; Models A4, A5, A7, and A8) could be useful in understanding how temperature affects the distribution of age 0 salmon. Days where the maximum exceeded the extremely high temperature of 27°C (Table 1; Model A9) and number of hours at high temperatures (Table 1; Models A10–A14), with the exception of hours >18.5°C, were not good predictors of age 0 salmon distribution.

In order to determine if how long a fish experienced a high temperature was related to density of age 0 salmon, we examined the numbers of consecutive hours ≥23°C. In our study, number of intervals where the temperature was ≥23°C for 1–6 h (Table 1, models B1–B6) were significantly ($P = 0.0001$–0.008) and inversely related to age 0 parr density ($\beta_1 = -0.124$ and -0.368). These metrics explained an average of 20% of the variation in age 0 density (McFadden's R^2 range: 10–60%; Table 1). Numbers of intervals ≥23°C for 7–12 h (Table 1; Models B7–B12) were not useful in understanding the relationship between age 0 salmon density and high summer temperature. As with the overall temperature metrics, based on overlapping 95% CI around β_1, any of the significant metrics for consecutive hours at temperatures ≥23°C (i.e., 1–6 h, Models B1–B6) could be useful in explaining variation in numbers of age 0 salmon parr.

Discussion

Here, we examined multiple summary metrics for temperature. Our results indicated that degree days and days where the maximum temperature was ≥18.5, 20, 23, and 25°C were related to age 0 salmon density. These metrics were simple, biologically based ways to illustrate variation across sites, had the potential to separate sites of different quality

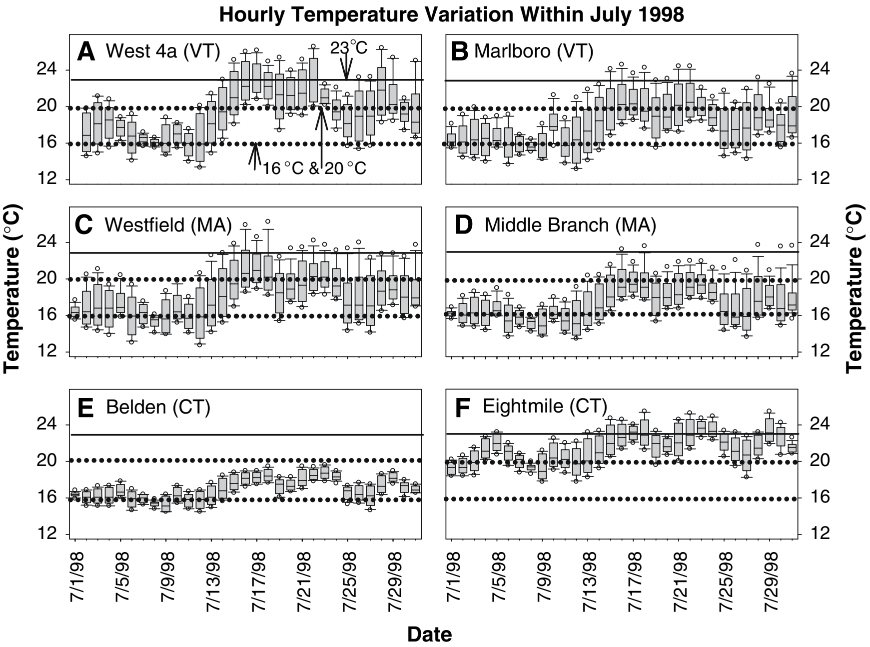

Fig. 4 Box and whisker plot showing hourly variation in temperature at six sites (A–F in Fig. 1) for July, 1998. In each row are pairs of contrasting patterns within a state including examples of sites in Vermont (**A**, **B**), Massachusetts (**C**, **D**), and Connecticut (**E**, **F**). Within each plot frame, listed are the site name (upper left), and state. The box represents the 25–75th quantiles and the horizontal line is the median. The whiskers encompass 95% of the data and the open circles represent the lower and upper ranges. Daily means were calculated based on 24 hourly temperatures within each day. All temperature plots include three reference lines. The upper solid line (≥23°C) indicates extreme values that could be related to Atlantic salmon distribution in the field. The lower pair of dotted lines, 16–20°C, represent moderate, reference points, related to growth, that allow visual comparisons across sites

for stream fish, and provided insights into patterns of Connecticut River Atlantic salmon. On the other hand, seasonal mean and hours above 18.5, 20, 23, and 25°C, in general, were not related to juvenile salmon density. The seasonal mean is a simple, commonly used metric that illustrates similarities and differences across sites. Since it is not necessarily biologically meaningful to stream fish, it does not provide insight into patterns of salmon density here and may not provide much elsewhere. Surprisingly, variation in temperature was not related to density patterns, perhaps because this metric did not necessarily incorporate any physiological reference points. Although intervals from 1 to 6 h were related to age 0 salmon density, intervals more than 6 h were not, probably because these extreme intervals were relatively rare. Here we have shown a set of temperature metrics that are useful and a set that are not. We had a relatively small number of sites, and, as in any field study, there were uncontrolled variables. The percent of the variation explained by temperature clearly indicated that other variables were important. However, the relationship between temperature and salmon density was consistent and measures of temperature were not correlated to other physical factors such width, velocity or substrate size. Our study was not intended to be an examination of all factors that affect salmon. Instead, we asked if summer temperatures can influence patterns of young salmon along a natural north south gradient that crosses physiologically important thresholds. Although we did not derive a single way to look at extreme temperatures, we used an approach that combines statistical exploration and physiologically related benchmarks.

We summarized temperature at three temporal scales (seasonal, daily, and hourly) that can affect the outcome of the analyses (Gardner et al., 2003). Across scales, a tradeoff existed between breadth of information and resolution. Seasonal means provided a single, simple indicator but they lost information about extreme conditions that may be important for cool

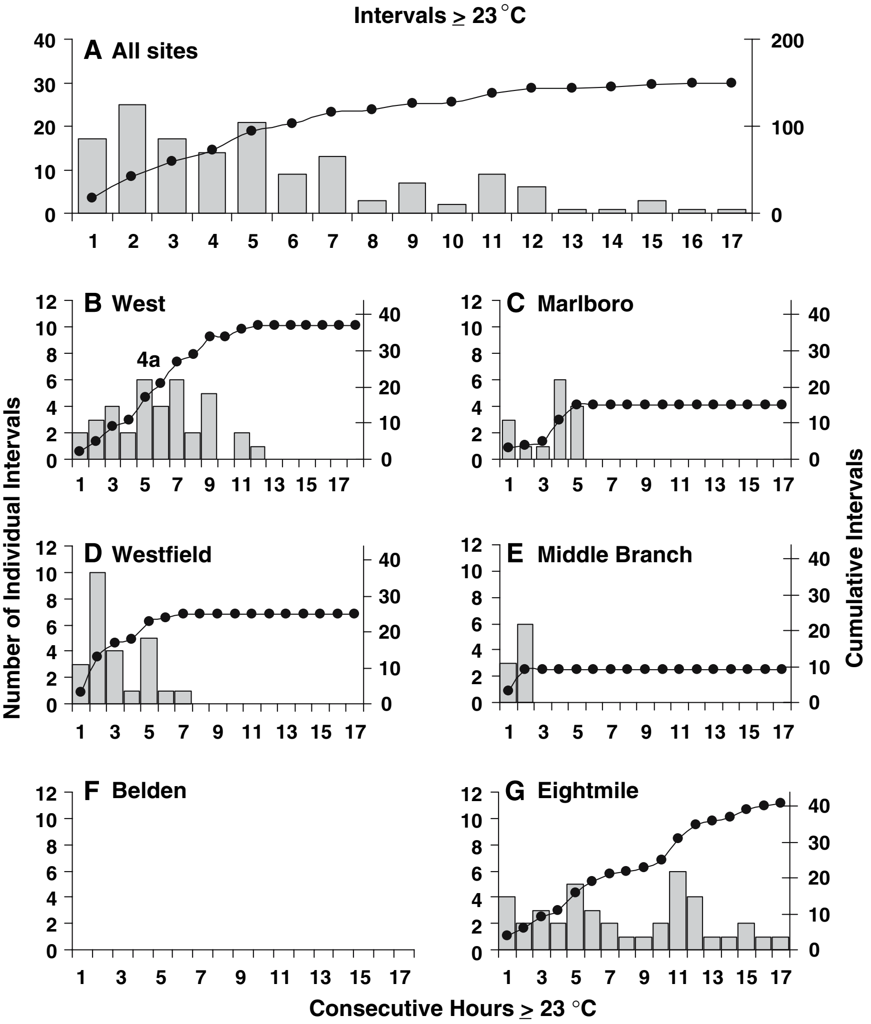

Fig. 5 Number of individual (left Y axis) and cumulative intervals (right Y axis) where maximum daily temperature was ≥23°C. The number of hours per interval is on the X-axis and the frequency of intervals is the response variable. Shown are data for (**A**) All 12 sites (**B**) West 4a, (**C**) Marlboro, (**D**) Westfield Brook, (**E**) Middle Branch of the Westfield, (**F**) Belden, and (**G**) Eightmile

and cold-water fish in summer. These smoothed trends were misleading when extreme values drove important relationships. Daily temperatures provided useful details on across site variation and extreme values. This level of variability, i.e., daily mean temperature in early summer, may be critical to explaining patterns of salmon distribution. Hourly temperature records captured extreme variation and illustrated important differences across sites. Although fish may survive short-term extremes, these events may reduce future fitness. However, the amount of hourly data is voluminous and cumbersome to analyze.

Approaches to assessing thermal tolerance

Relating field water temperatures to natural fish distributions is essential to address environmental impacts and global climate change (Eaton et al., 1995). One approach to evaluate temperature tolerance is to use physiological thresholds derived from controlled laboratory experiments. These methodologies evaluate survival, growth, and other metabolic responses of fish to high temperatures (Fry, 1967; Elliott, 1991; Grande & Andersen, 1991; Elliott & Elliott, 1995). Fish are ectotherms, thus, temperature has the potential to alter many aspects of fish physiology, ecology, and behavior (Schmidt-Nielsen, 1990). Three approaches have traditionally been used to document tolerance to extreme temperatures in the laboratory: incipient lethal temperature, critical thermal maximum, and chronic lethal methodologies (Beitinger et al., 2000). These laboratory-derived thresholds give researchers quantitative temperature benchmarks for reference, but measure different

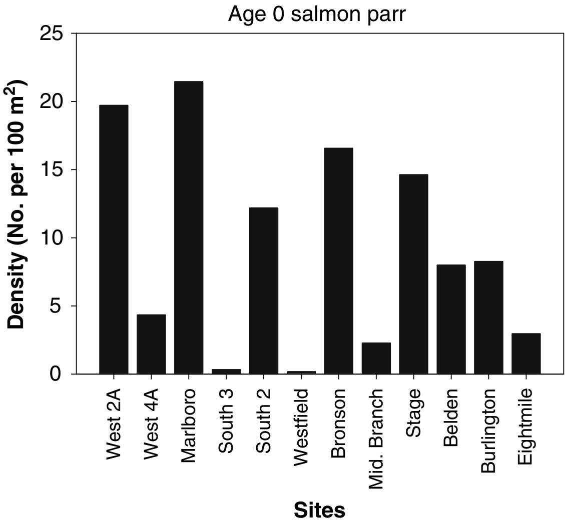

Fig. 6 Density of age 0 Atlantic salmon per 100 m^2 in 1998 at the 12 study sites in the Connecticut River watershed

things (Beitinger et al., 2000). In addition, within a methodology, results can vary. Specifically, upper limits from the different methodologies vary with exposure time (Elliott, 1991), acclimation temperature (Elliott & Elliott, 1995; Beitinger & Bennett, 2000; Currie et al., 2004), and rates of heating (Elliott & Elliott, 1995; Galbreath et al., 2004). Upper lethal temperatures, at which 50% of the test animals survive for some specified time, have been determined for juvenile Atlantic salmon (e.g., Huntsman, 1942; Garside, 1973; Elliott, 1991). However, for juvenile Atlantic salmon acclimated to 15°C, the upper lethal temperature increases from 27.5°C for a 7-day temperature stress to 32°C for a 10-min temperature exposure (Elliott, 1991). In addition, as the acclimation temperature for juvenile Atlantic salmon increases from 5 to 27°C, the upper lethal temperature increases from 24.8 to 27.8°C (Elliott, 1991). Since these methodologies are not necessarily designed to mimic real world events, the regimes these methods test may be artificial relative to real world temperature stressors (Morgan et al., 2001). Our use of field temperatures and field patterns of fish density avoids several of these pitfalls.

Also problematic is that these laboratory measures of high temperatures are typically quantified in the absence of other stressors. Multiple stressors, measured as mortality, changes in behavior, or altered physiological stress responses, could have a greater effect on fish than any single stressor alone (Mesa, 1994; Davis et al., 2001; Bowen et al., 2006). Additional stressors almost always occur in the field. Hypoxia, toxins, low pH, and disease can reduce the extreme temperatures a fish can tolerate (Watenpaugh et al., 1985; Heath et al., 1994). Consequently, lethal temperatures as measured in the laboratory, could overestimate the thermal tolerance of a multiple-stressed juvenile salmon. On the other hand, because laboratory tanks are not a natural habitat, experimental fish at high densities could be more stressed at higher temperatures in the laboratory than those encountered in the field. Although these controlled laboratory methodologies for estimating thermal tolerance are essential, for all of the reasons listed above, they are difficult to apply to the field. New approaches to isolate and quantify complex multiple natural stressors could provide the information we are currently lacking. Our use of natural field patterns incorporates naturally occurring multiple stressors.

Another approach to evaluating temperature tolerance is to relate field temperature records and fish distribution through statistical analysis (Eaton et al., 1995; Welsh et al., 2001; Nelitz et al., 2007; Wehrly et al., 2007). One method is to estimate the maximum temperatures tolerated by fish species in nature using the 95th percentile of weekly mean temperature records at sites where fish and temperature data co-occur (Eaton et al., 1995). Using this FTDMS (Fish Temperature Data Base Matching System) for 30 cold-, cool-, and warm-water species including seven salmonids, values for thermal tolerance were less than the laboratory-based values, but greater than the maximum growth temperatures (Eaton et al., 1995). Another field-based method defines upper thermal tolerance of coho salmon (*Oncorhynchus kisutch)* in tributaries of the Mattole River, CA (Welsh et al., 2001). Logistic regression indicates a significant relationship between maximum temperatures (16.7–18°C) and the presence of coho salmon. However, these maximum temperatures were much lower than predicted by FTDMS and others (23.4°C; Eaton et al., 1995) possibly because of differences in river size, productivity and other site specific features (Welsh et al., 2001). Recently, another field-based method was used to estimate thermal tolerance for brook and brown trout by examining the warmest 5% of the locations present for 11 intervals of 1–63 days using mean and daily maximum temperatures

Table 1 Poisson regression models testing the effect of high summer temperature metrics on juvenile (age 0) Atlantic salmon density. The A. models include overall temperature metrics of mean summer temperature (June–August), standard deviation (SD), daily variation, degree days, and days (D) and hours (H) where the maximum ≥18.5, 20, 23, 25, and 27°C. Also included are: β_1, standard error (SE on β_1), *P*-value, and r_{P}^2. McFadden's pseudo r^2 is calculated as (1−(log deviance full/log deviance intercept)). The B. models test the number of consecutive hours ≥23°C. In both A and B, an α of 0.1 is divided by the number of comparisons (A = 14 models: 0.1/14 = 0.007; B = 12 models: 0.1/12 = 0.008) for a critical α of 0.007 and 0.008, respectively. Marg. = marginal values are 0.008

Model no.	Response variable (Y)	Summer temperature			Evaluation		Significance	Walds 95% CI	
		Metric (X)	β_1	SE	*P*	r_{P}^2		Lower	Upper
A. Overall temperature metrics									
1	Density	Mean	−0.226	0.099	*0.02*	0.08	NS	−0.419	−0.0322
2		SD	−0.277	0.192	*0.15*	0.03	NS		
3		Daily var.	−0.048	0.046	*0.30*	0.02	NS		
4		Degree days	−0.002	0.001	<0.0001	0.26	*	−0.003	−0.001
5		D ≥ 18.5°C	−0.015	0.006	0.007	0.10	*	−0.026	−0.004
6		D ≥ 20°C	−0.011	0.004	0.008	0.10	Marg.	−0.019	−0.003
7		D ≥ 23°C	−0.026	0.008	0.002	0.16	*	−0.042	−0.01
8		D ≥ 25°C	−0.089	0.028	0.001	0.24	*	−0.144	−0.035
9		D ≥ 27°C	−0.082	0.046	0.08	0.06	NS		
10		H ≥ 18.5°C	−0.001	0.0003	0.007	0.11	*	−0.001	−0.0002
11		H ≥ 20°C	−0.001	0.0003	0.020	0.09	NS		
12		H ≥ 23°C	−0.003	0.001	0.014	0.10	NS		
13		H ≥ 25°C	−0.015	0.006	0.015	0.13	NS		
14		H ≥ 27°C	−0.021	0.012	0.08	0.06	NS		
B. Number of consecutive hours ≥23									
1	Density 0	1 H	−0.214	0.072	0.003	0.13	*	−0.356	−0.072
2		2 H	−0.368	0.076	<0.0001	0.62	**	−0.516	−0.220
3		3 H	−0.178	0.065	0.007	0.11	*	−0.306	−0.049
4		4 H	−0.133	0.046	0.004	0.10	*	−0.226	−0.0401
5		5 H	−0.124	0.047	0.008	0.11	*	−0.215	−0.032
6		6 H	−0.268	0.100	0.007	0.13	*	−0.464	−0.073
7		7 H	−0.027	0.052	0.61	0.00	NS		
8		8 H	−0.655	0.254	0.01	0.13	NS		
9		9 H	−0.133	0.088	0.13	0.04	NS		
10		10 H	−0.597	0.293	0.04	0.09	NS		
11		11 H	−0.167	0.080	0.04	0.08	NS		
12		12 H	−0.299	0.128	0.02	0.12	NS		

(Wehrly et al., 2007). The field based approaches utilized by these studies are useful ways to compile temperatures, provide much needed guidelines for the maximum temperatures fish can tolerate, and consider temperature in a more complex environment than laboratory assessments.

However, this statistical field approach has several constraints. First, this approach only looks at extant field patterns, i.e., they do not incorporate any a priori knowledge about physiological endpoints. Thus, they do not have the quantitative rigor of laboratory approaches. Second, this approach does not consider fish behavior such as movements or use of thermal refugia (Eaton et al., 1995). Third, results for the same species can differ across systems because of the interaction of non-temperature stresses and other variables such as predators and competitors. Hence, they may not be universally applicable. Finally, these

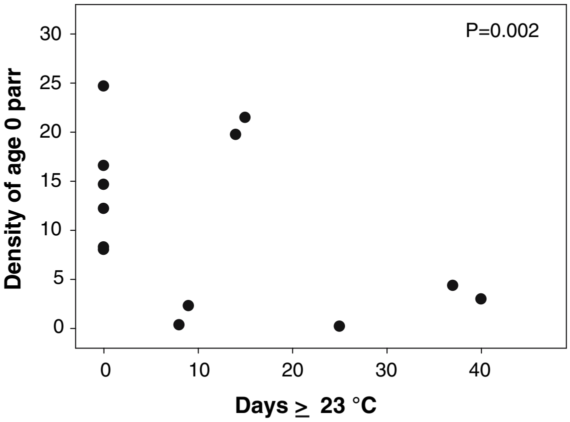

Fig. 7 Based on a Poisson regression, relation of age 0 Atlantic salmon density and number of days where the maximum temperature was ≥23°C at 12 study sites in the Connecticut River watershed in 1998

statistical relationships are typically based on presence absence rather than how change in fish numbers may reflect temperature effects. Our use of physiological thresholds with natural field patterns addresses at least one concern related to statistical relationships. In our study, we combined elements of both approaches, i.e., statistical patterns with physiological-based endpoints to examine the relationships between Atlantic salmon and summer distribution and abundance. However, adding modeling to biological benchmarks and statistical analyses, as was used to predict potential responses of temperature sensitive streams to anthropogenic development (Nelitz et al., 2007), could provide for more detailed predictions.

Temperature reference points and global climate change

Global warming will likely have major effects on freshwater systems (Schindler, 2001; Blenckner, 2005). Climate change is predicted to adversely affect stream salmonids through high temperatures (Gooseff et al., 2005), loss of potential habitat (Eaton & Scheller, 1996; Preston, 2006), and fragmentation of suitable habitat (Flebbe et al., 2006). In the northeastern US, regional climate projections predict increased temperatures, increased droughts, and increased extreme precipitation events (UCS, 2006). Atlantic salmon in the Connecticut River are at the southern edge of their range, making them an ideal species for examining the effects of climate change.

What temperature should be used as a biological guideline for reference? Upper lethal temperatures can be extremely useful for setting an outer bound. However, no researcher or manager would find the endpoints described in these upper lethal experiments, i.e., survival to 10 min or 7 days, acceptable for understanding or managing temperatures in the field. Managers need quantitative standards by which they can judge if certain temperatures will adversely affect fish populations. Researchers also need measures by which they can understand the effects of temperature. In both cases, these quantitative standards need to incorporate physiological and behavioral based information, statistical field based patterns, and the synergistic effect of other stressors that fish encounter in the field. Other abiotic and biotic factors such as reduced habitat, low discharge, increased density, lower food availability, disease, and higher predation can reduce the ability of juvenile salmon to withstand high temperatures. If this is the case, temperature limits used for research and management decisions should be based on the precautionary approach. For juvenile Atlantic salmon, sublethal, molecular heat stress can occur at 23°C in the field (Lund et al., 2002) and behavioral changes can occur at 22–24°C (Cunjak et al., 1993). Thus, 23°C, the upper limit for feeding (Elliott, 1991), may be a conservative benchmark above which juvenile Atlantic salmon could be negatively affected.

In both laboratory and field based statistical approaches, the magnitude and periodicity of temperature change must be considered. Traditional temperature tolerance procedures use a constant temperature challenge while many natural heat stresses are characterized by cycling temperatures in which high temperatures are interspersed with lower temperature refuges. This may elicit a very different response from fish. For example, Bonneville cutthroat trout (*Oncorhynchus clarki utah*) cannot survive a constant temperature more than 24°C, but can survive 6 h above 24°C when these high temperatures are interspersed with cooler temperatures (Johnstone & Rahel, 2003). In the field, this refuge at lower temperatures may provide necessary time for repair of heat-damaged tissue (Meyer et al., 1995). Consequently, multiple stressors, thermal heterogeneity in time and space, and time above and below reference points can aid the interpretation of how extreme temperature affects fish in the field. Although lab and field tools are both useful ways to examine temperature tolerance in both high constant and cycling environments, additional ways to combine biological endpoints and field patterns will provide researchers with greater insights into the effects of temperature. We have tried to illustrate a means by which this can be pursued.

In summary, water temperatures in the Connecticut River basin show both predictable latitudinal trends and unique natural within-site characteristics. Even though the Connecticut River is at the southern edge of the Atlantic salmon's range, most of the watershed has temperatures appropriate for Atlantic salmon. However, as humans continue to modify the landscape through changing land use, water withdrawals, and dams, variation in field temperatures may increase. Consequently, it will be even more important in the future for biologists and environmental managers to have guidelines on both how to interpret complex natural temperature data and how to determine what temperatures are to be avoided.

Acknowledgments We thank Mike Briggs for help with data analysis. This project was funded by the U.S. Forest Service, Northeastern Research Station, Amherst, MA and the U.S. Geological Survey, Northern Appalachian Research Laboratory, and administered through the Massachusetts Cooperative Fish and Wildlife Research Unit and Department of Natural Resources Conservation at the University of Massachusetts, Amherst. The Massachusetts Cooperative Fish and Wildlife Research Unit is a cooperation among the University of Massachusetts, the U.S. Geological Survey, the Massachusetts Division of Marine Fisheries, the Massachusetts Division of Fisheries and Wildlife, and the Wildlife Management Institute. The Vermont Cooperative Fish and Wildlife Research Unit is jointly supported by the U.S. Geological Survey, Vermont Department of Fish and Wildlife, the University of Vermont, and the Wildlife Management Institute. Use of brand names does not confer endorsement by the U.S. federal government. Ryan Butryn and two anonymous reviewers improved the manuscript.

References

Beitinger, T. L. & W. A. Bennett, 2000. Quantification of the role of acclimation temperature in temperature tolerance of fishes. Environmental Biology of Fishes 58: 277–288.

Beitinger, T. L., W. A. Bennett & R. W. McCauley, 2000. Temperature tolerances of North American freshwater fishes exposed to dynamic changes in temperature. Environmental Biology of Fishes 58: 237–275.

Blenckner, T., 2005. A conceptual model of climate-related effects on lake ecosystems. Hydrobiologia 533: 1–14.

Bowen, L., I. Werner & M. L. Johnson, 2006. Physiological and behavioral effects of zinc and temperature on coho salmon (*Oncorhynchus kisutch*). Hydrobiologia 559: 161–168.

Cairns, M. A., J. L. Ebersole, J. P. Baker, P. J. Wigington, H. R. Lavigne & S. M. Davis, 2005. Influence of summer stream temperatures on black spot infestation of juvenile coho salmon in the Oregon Coast Range. Transactions of the American Fisheries Society 134: 1471–1479.

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

Cameron, A. C. & F. A. Windemeijer, 1996. R-squared measures for count data regression models with applications to health-care utilization. Journal of Business and Economic Statistics 14: 209–219.

Campbell, C. A., 1999. Assessing large-scale patterns in the distribution, abundance, and size of juvenile Atlantic salmon in the Connecticut River. M.S. Thesis, University of Massachusetts, Amherst, MA.

Carle, F. L. & M. R. Strub, 1978. A new method for estimating population size from removal data. Biometrics 34: 621–630.

Connecticut River Atlantic Salmon Commission, 1998. Strategic plan for the restoration of Atlantic salmon to the Connecticut River (revised July 1, 1998). Sunderland, MA.

Crozier, L. & R. W. Zabel, 2006. Climate impacts at multiple scales: evidence for differential population responses in juvenile Chinook salmon. Journal of Animal Ecology 75: 1100–1109.

Cunjak, R. A., D. Caissie, N. El-Jabi, P. Hardie, J. H. Conlon, T. L Pollock, D. J. Giberson & S. Komadina-Douthwright, 1993. The Catamaran Brook (New Brunswick) habitat research project: biological, physical, and chemical conditions (1990–1992). Canadian Technical Report of Fisheries and Aquatic Sciences No. 1914.

Currie, R. J., W. A. Bennett, T. L. Beitinger & D. S. Cherry, 2004. Upper and lower temperature tolerances of juvenile freshwater game-fish species exposed to 32 days of cycling temperatures. Hydrobiologia 523: 127–136.

Davis, M. W., B. L. Olla & C. B. Schreck, 2001. Stress induced by hooking, net towing, elevated sea water temperature and air in sablefish: lack of concordance between mortality and physiological measures of stress. Journal of Fish Biology 58: 1–15.

Dunham, J., R. Schroeter & B. Rieman, 2003. Influence of maximum water temperature on occurrence of Lahontan cutthroat trout within streams. North American Journal of Fisheries Management 23: 1042–1049.

Dynesius, M. & C. Nilsson, 1994. Fragmentation and flow regulation of river systems in the northern 3rd of the world. Science 266: 753–762.

Eaton, J. G., J. H. McCormick, B. E. Goodno, D. G. O'Brien, H. G. Stefany, M. Hondzo & R. M. Scheller, 1995. A field information-based system for estimating fish temperature tolerances. Fisheries 20(4): 10–18.

Eaton, J. G. & R. M. Scheller, 1996. Effects of climate warming on fish thermal habitat in streams of the United States. Limnology and Oceanography 41: 1109–1115.

Elliott, J. M., 1991. Tolerance and resistance to thermal stress in juvenile Atlantic salmon. Freshwater Biology 25: 61–70.

Elliott, J. M. & J. A. Elliott, 1995. The effect of the rate of temperature increase on the critical thermal maximum for parr of Atlantic salmon and brown trout. Journal of Fish Biology 47: 917–919.

Elliott, J. M. & M. A. Hurley, 1997. A functional model for maximum growth of Atlantic salmon par (*Salmo salar*), from two populations in northwest England. Functional Ecology 11: 592–603.

Flebbe, P. A., L. D. Roghair & J. L. Bruggink, 2006. Spatial modeling to project southern Appalachian trout distribution in a warmer climate. Transactions of the American Fisheries Society 135: 1371–1382.

Forseth, T., M. A. Hurley, A. J. Jensen & J. M. Elliott, 2001. Functional models for growth and food consumption of Atlantic salmon parr, *Salmo salar*, from a Norwegian River. Freshwater Biology 46: 173–186.

Franco, E. A. D. & P. Budy, 2005. Effects of biotic and abiotic factors on the distribution of trout and salmon along a longitudinal stream gradient. Environmental Biology of Fishes 72: 379–391.

Fry, F. E. J., 1967. Responses of vertebrate poikilotherms to temperature. In Rose, A. H. (ed.), Thermobiology. Academic Press, New York, NY: 375–409.

Galbreath, P. F., N. D. Adams & T. H. Martin, 2004. Influence of heating rate on measurement of time to thermal maximum in trout. Aquaculture 241: 587–599.

Gardner, B., P. J. Sullivan & A. J. Lembo, 2003. Predicting stream temperatures: geostatistical model comparison using alternative distance metrics. Canadian Journal of Fisheries and Aquatic Sciences 60: 344–351.

Garside, E. T., 1973. Ultimate upper lethal temperature of Atlantic salmon, *Salmo salar*. Canadian Journal of Zoology 51: 898–900.

Gooseff, M. N., K. Strzepek & S. C. Chapra, 2005. Modeling the potential effects of climate change on water temperature downstream of a shallow reservoir, Lower Madison River, MT. Climatic Change 68: 331–353.

Grande, M. & S. Andersen, 1991. Critical thermal maxima for young salmonids. Journal of Freshwater Ecology 6: 275–279.

Habit, E., M. C. Belk & O. Parra, 2007. Response of the riverine fish community to the construction and operation of a diversion hydropower plant in central Chile. Aquatic Conservation-Marine and Freshwater Ecosystems 17: 37–49.

Heath, S. T., W. A. Bennett, J. Kennedy & T. L. Beitinger, 1994. Heat and cold tolerance of the fathead minnow, *Pimephales promelas*, exposed to the synthetic pyrethroid cyfluthrin. Canadian Journal of Fisheries and Aquatic Sciences 51: 437–440.

Huntsman, A. G., 1942. Death of salmon and trout with high temperature. Journal of the Fisheries Research Board of Canada 5: 485–501.

Isaak, D. J. & W. A. Hubert, 2004. Nonlinear response of trout abundance to summer stream temperatures across a thermally diverse montane landscape. Transactions of the American Fisheries Society 133: 1254–1259.

Johnson, S. L., 2004. Factors influencing stream temperatures in small streams: substrate effects and a shading experiment. Canadian Journal of Fisheries and Aquatic Sciences 61: 913–923.

Johnstone, H. C. & F. J. Rahel, 2003. Assessing temperature tolerance of Bonneville cutthroat trout based on constant and cycling thermal regimes. Transactions of the American Fisheries Society 132: 92–99.

Jonsson, B., T. Forseth, A. J. Jensen & T. J. Naesje, 2001. Thermal performance of juvenile Atlantic salmon, *Salmo salar* L. Functional Ecology 15: 701–711.

Kangur, A., P. Kangur, K. Kangur & T. Mols, 2007. The role of temperature in the population dynamics of smelt *Osmerus eperlanus eperlanus m. spirinchus Pallas* in Lake Peipsi (Estonia/Russia). Hydrobiologia 584: 433–441.

Keleher, C. J. & F. J. Rahel, 1996. Thermal limits to salmonid distributions in the Rocky Mountain region and potential habitat loss due to global warming: a Geographic Information System (GIS) approach. Transactions of the American Fisheries 125: 1–13.

Kishi, D., M. Murakami, S. Nakano & Y. Taniguchi, 2004. Effects of forestry on the thermal habitat of Dolly varden (*Salvelinus malma*). Ecological Research 19: 283–290.

Lobón-Cerviá, J. & E. Mortensen, 2005. Population size in stream-living juveniles of lake-migratory brown trout *Salmo trutta* L.: the importance of stream discharge and temperature. Ecology of Freshwater Fishes 14: 394–401.

Lund, S. G., D. Caissie, R. A. Cunjak, M. M. Vijayan & B. L. Tufts, 2002. The effects of environmental heat shock mRNA and protein expression in Miramichi Atlantic salmon (*Salmo salar*) parr. Canadian Journal of Fisheries and Aquatic Sciences 59: 1553–1562.

McMenemy, J. R., 1995. Survival of Atlantic salmon fry stocked at low density in the West River, Vermont. North American Journal of Fisheries Management 15: 366–374.

Meeuwig, M. H., J. B. Dunham, J. P. Hayes & G. L. Vinyard, 2004. Effects of constant and cyclical thermal regimes on growth and feeding of juvenile cutthroat trout of variable sizes. Ecology of Freshwater Fish 13: 208–216.

Meisner, J. D., 1990. Effect of climatic warming on the southern margins of the native range of brook trout, *Salvelinus fontinalis*. Canadian Journal of Fisheries and Aquatic Sciences 47: 1065–1070.

Mesa, M. G., 1994. Effects of multiple acute stressors on the predator avoidance ability and physiology of juvenile Chinook salmon. Transactions of the American Fisheries Society 123: 786–793.

Meyer, J. S., D. D. Gulley, M. S. Goodrich, D. C. Szmania & A. S. Brooks, 1995. Modeling toxicity due to intermittent exposure of rainbow trout and common shiners to monochloramine. Environmental Toxicology and Chemistry 14: 165–175.

Meyers, T. F., 1994. The program to restore Atlantic salmon to the Connecticut River. In Calabi, S. & A. Stout (eds), A Hard Look at Some Tough Issues. New England Atlantic Salmon Management Conference, New England Salmon Commission, Newburyport, MA: 11–21.

Moffitt, C. M., B. Kynard & S. G. Rideout, 1982. Fish passage facilities and anadromous fish restoration in the Connecticut River basin. Fisheries 7(6): 2–11.

Morgan, I. J., D. G. McDonald & C. M. Wood, 2001. The cost of living for freshwater fish in a warmer, more polluted world. Global Change Biology 7: 345–355.

Myers, R. H., 1990, Classical and Modern Regression with Applications. Duxbury Press, Pacific Grove, CA.

Nelitz, M. A., E. MacIssac, R. Peterman, 2007. A science based approach for identifying temperature sensitive streams for rainbow trout. North American Journal of Fisheries Management 27: 405–424.

Parrish, D. L., R. J. Benke, S. G. Gephard, S. McCormick & G. H. Reeves, 1998. Why aren't there more Atlantic salmon (*Salmo salar*)? Canadian Journal of Fisheries and Aquatic Sciences 55(Supplement 1): 281–287.

Perry, A. L., P. J. Low, J. R. Ellis & J. D. Reynolds, 2005. Climate change and distribution shifts in marine fishes. Science 308: 1912–1915.

Poff, L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegaard, B. Richter, R. Sparks & J. Stromberg, 1997. The natural flow regime: a new paradigm for riverine conservation and restoration. BioScience 47: 769–784.

Poole, G. C. & C. H. Berman, 2004. An ecological perspective on in-stream temperature: natural heat dynamics and mechanisms of human-caused thermal degradation. Environmental Management 27: 787–802.

Pörtner, H. O. & R. Knust, 2007. Climate change affects marine fishes through the oxygen limitation of thermal tolerance. Science 315: 95–97.

Preston, B. L., 2006. Risk-based reanalysis of the effects of climate change on US cold-water habitat. Climatic Change 76: 91–119.

Quinn, G. P. & M. J. Keough, 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press, Cambridge, UK.

Raffenberg, M. J. & D. L. Parrish, 2003. Atlantic salmon and trout: interactions of species at large scales. Canadian Journal of Fisheries and Aquatic Sciences 60: 279–285.

SAS Institute, 2003. SAS 9.1. Cary, North Carolina.

Schindler, D. W., 2001. The cumulative effects of climate warming and other human stresses on Canadian freshwaters in the new millennium. Canadian Journal of Fisheries And Aquatic Sciences 58: 18–29.

Schmidt-Nielsen, J., 1990. Animal Physiology: Adaptation and Environment. Cambridge University Press, Cambridge, England.

Schrank, A. J., F. J. Rahel & H. C. Johnstone, 2003. Evaluating laboratory-derived thermal criteria in the field: an example involving Bonneville cutthroat trout. Transactions of the American Fisheries Society 132: 100–109.

Stoneman, C. L. & M. L. Jones, 2000. The influence of habitat features on the biomass and distribution of three species of southern Ontario stream salmonines. Transactions of the American Fisheries Society 129: 639–657.

Union of Concerned Scientists (UCS), 2006. Climate Change in the U.S. Northeast UCS Publications, Cambridge, MA.

Wang, L. Z., J. Lyons & P. Kanehl, 2003. Impacts of urban land cover on trout streams in Wisconsin and Minnesota. Transactions of the American Fisheries Society 132: 825–839.

Watenpaugh, D. E., T. L. Beitinger & D. W. Huey, 1985. Temperature tolerance of nitrite-exposed channel catfish. Transactions of the American Fisheries Society 114: 274–278.

Wehrly, K. E., L. Wang & M. Mitro, 2007. Field based estimates of thermal tolerance limits for trout incorporating exposure time and temperature fluctuations. Transactions of the American Fisheries Society 136: 365–374.

Welsh, H. H., F. R. Hodgson, B. C. Harvey & M. F. Roche, 2001. Distribution of juvenile coho salmon in relation to water temperatures in tributaries of the Mattole River, California. North American Journal of Fisheries Management 21: 464–470.

Wheeler, A. P., P. L. Angermeier & A. E. Rosenberger, 2005. Impacts of new highways and subsequent landscape urbanization on stream habitat and biota. Reviews in Fisheries Science 13: 141–164.