Multiple Lines of Evidence for Determining Upper Optimal Temperature Thresholds for Bull Trout

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On November 1, 1999, bull trout were listed as a threatened species throughout its range in the coterminous United States (64 FR 58910) (USFWS 1999). One of the primary factors identified as leading to the decline of bull trout was habitat degradation, often in the form of elevated water temperatures. Elevated water temperatures have been linked to reduced species distribution with populations becoming fragmented and isolated in upper reaches of drainages (Pratt 1992). Water temperature is thought to be a critical element in the persistence or recovery of many bull trout populations (Rieman and Chandler 1999).

A unique and well-documented facet of bull trout biology is the species' requirement for cold water (Rieman and McIntyre 1993). While all salmonids require cold water, bull trout require a narrow range of colder temperature conditions to reproduce and survive. It is probable that if water temperature in bull trout habitat is in optimal condition[1] throughout its range, water temperatures entering downstream habitat for other salmonids such as chinook and steelhead will also be optimal (McCullough 1999).

As part of the EPA Regional Water Temperature Guidance Project, the associated Technical Workgroup was asked to recommend upper optimal temperature thresholds for salmonid species by life stage. The Technical Workgroup recommended 12°C daily maximum temperature for streams where bull trout tributary rearing juveniles occur. Subsequently, temperature threshold

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[1] Optimal temperatures can be considered to be what is optimal for an assemblage of a salmonid species at a place (stream reach) and also what is considered to be optimal for the entire drainage as it affects an entire population. Optimal temperature should consider a variety of key biological effects of temperature, such as to growth rate, reproduction, health, competitive ability, etc. Consideration of what is optimal for an assemblage at a particular reach can draw heavily from laboratory evidence. Obviously, it may be detrimental to a larger population (i.e., downstream cumulative effects) by increasing the temperature in a set of similar headwater reaches so that assemblages there may experience optimal growth temperatures. The best solution for achieving an optimal temperature regime distributed at a stream system scale is to have a regime typical of the long-term natural thermal potential, or that produced in a natural system largely unperturbed by human activities. This spatial distribution would result in extensive downstream distribution of optimal temperatures, an overall abundance of habitat that has maximum summer temperatures that are less than or equal to optimum, and a coincidence of optimal temperature with other habitat requirements of the species (e.g., channel gradient, pool availability, substrate composition, etc.). Consideration of optimality for the population inhabiting a large stream system can make use of a combination of laboratory and field studies.

recommendations were proposed independently by Technical Workgroup members, Mark Hicks, Washington Department of Ecology (DOE) and Don Essig, Idaho Department of Environmental Quality (DEQ). This paper provides additional support for the Technical Workgroup's original recommendation.

This review will focus on two major lines of evidence: laboratory studies on growth optima in relation to water temperature (Selong et al. 2000) and bull trout-temperature distribution relationships (Dunham et al. 2001; Gamett 2002; Haas 1999). These studies were conducted with objectives and results that are directly linked to bull trout temperature requirements. We will also briefly summarize two literature reviews conducted in the context of setting temperature standards supportive of bull trout: Buchanan and Gregory 1997; U.S. EPA 1997.

Emphasis will be given to studies that are available as final manuscripts rather than progress reports. Annual reports for the growth and temperature studies at the USFWS Bozeman Fish Technology Center (McMahon et al. 1998, 1999, and 2000) have been interpreted in various ways to provide rationale for recommended bull trout thresholds; however, these reports were primarily designed to show the project funding sources that progress was being made on the studies. Only the information and results of the studies for the 1998 annual report have been published as a final manuscript (Selong et al. 2000). Much of the controversy over the bull trout temperature thresholds may be related to different interpretations of the annual reports. The final manuscripts may have different interpretations of the results presented in the annual reports discuss and will show more details of the studies (R. Barrows, pers. com).

Uncertainty

Although several lab and field studies are currently in progress, limited information is available describing the temperature requirements of bull trout and Dolly Varden (McCullough et al. 2001). In the paper titled "Scientific issues relating to temperature criteria for salmon, trout, and charr native to the Pacific Northwest," prepared as part of the EPA Region 10 water quality criteria guidance development project, the following guidance is given regarding uncertainty: "Given uncertainty, we are challenged to make decisions based on what we know, while taking adequate precautions to avoid irretrievable or irreversible mistakes. Thus, in moving forward we must be cautious and conservative, especially when actions may affect threatened or endangered species" (Poole et al. 2001).

Uncertainty must also be considered within the context of the information available. In our analysis of evidence useful for recommending upper optimal temperature thresholds we will acknowledge uncertainty in model parameter estimates and uncertainty in the formulation of the evidence.

Temperature metric conversions

The Technical Workgroup originally proposed using the single daily maximum as the temperature metric to describe bull trout thresholds for the following reasons:

- Most commonly used metric in literature describing bull trout distribution and abundance
- Easily understood
- Strong biological implications for acute exposure (describes actual temperature being experienced by the fish)

For ease of comparison with recommended temperatures in the Hicks and Essig papers, and for consistency with the metrics used by the Technical Workgroup for salmon species life stage temperature thresholds, in this paper we will convert the maximum daily maximum temperature (MDMT) to a Maximum Weekly Maximum Temperature (MWMT).

The correlation between different temperature metrics is usually expressed as an average of the differences between the metrics being compared. The regression of one temperature metric on another has been used to derive an average difference between metrics that is applied across the entire range of temperature. Because the relationship between metrics indices is based on an average of the differences, this correlation may not be highly accurate for any single site. In addition, depending on which metrics are used in the regression, there is typically a range of values of, for example, MWMT for every MDMT, despite having a high R^2. Most authors describing the correlation between MDMT and MWMT find an average of about a one degree difference between the two metrics (Hillman and Essig 1998; Haas 1999; Dunham et al. 2001). Dunham et al. (2001) correlated different metrics from data collected at 752 sites. In their analysis, depending on the daily range of temperatures at the sites (expressed as 0-2°C, 2-4°C, 4-6°C, 6-8°C, 8-10°C, 10-12°C, and >12°C) the differences between MDMT and MWMT ranged from 0.44°C to 1.43°C with the greatest difference being found at sites with the greatest range in daily temperatures. In Hillman and Essig (1998), temperatures measured at different sites on the Little Lost River had a range of differences between MDMT and MWMT from 0.4°C to 2.4°C.

MWMT reflects a rolling average of the maximum temperatures over a seven-day period. In the DOE proposed standards this average is expressed as 7DADM (7- day average daily maximum). Averaging temperatures over a week can result in a loss of information. In other words, you "average out" the extremes and may miss those extreme short-term events, such as a maximum daily temperature.

A possible explanation for the level of variation found in correlating the metrics is that streams are not classified according to the level of disturbance from land management impacts. Historically, bull trout streams in many watersheds undoubtedly had a far lower level of disturbance than current conditions. If the relationship between MDMT and MWMT varies with increasing levels of disturbance, the ability to demonstrate that MWMT will provide a good replacement for MDMT diminishes.

The relationships between indices based on daily maxima to those based on average daily values introduce even greater variance. These are not highly precise quantitative conversions--they are not equivalent to converting from English to metric, but are approximations. Less variance might be achieved by deriving conversions from intact stream systems (via screening out those with low diel variation), because an MWMT of a highly disturbed stream likely has a different relationship to a single daily maximum than would an intact stream. Biological implications of day-to-day variation in daily maximum temperature include acclimation of fish to lower temperature and then sudden exposure to higher temperature. The greater the shift in maximum from day to day, the more significant the biological impact if maximum temperatures are at a critical threshold.

Constant temperatures used in laboratory studies are often assumed to be equivalent to an average daily value (over some specified time period). Again, this assumption is correct only when the difference between the mean and maximum is small. For streams having a significant difference between mean and maximum, this assumption may not be reliable.

In summary, the correlation between the metrics is usually expressed as an average of the differences. Different analyses of the relationship between MWMT and MDMT have found a range of conversion factors. In reality the correlation tends to be somewhat site specific, or at least stream condition specific.

The "average" conversion factor from MDMT to MWMT is -1.0°C. For ease of comparison between the three Technical Workgroup papers we will use 11°C MWMT as the recommended bull trout temperature threshold for this paper.

The Assumption that an Optimal, Constant Growth Temperature Would Be an Appropriate Mean Growth Temperature

As stated above, a constant temperature determined in laboratory experiments to be an optimal growth temperature may not be a suitable growth temperature in the field. One reason for this is that in the field food is normally considered to be limiting. If the laboratory-derived optimum is based on satiation feeding, exertion in food capture is minimized, thereby avoiding metabolic stress, and competitive effects are eliminated, the optimum temperature in the field may be considerably lower. In addition, a constant temperature optimum cannot be assumed to also be suitable as a mean temperature in the field that would be equally protective. A mean temperature in a fluctuating temperature environment must be considerably lower than the constant temperature optimum. Also, the amount of the reduction in mean temperature required increases with the amplitude of diel fluctuations. The detrimental influence to growth rate of diel fluctuations that exceed the optimum temperature is illustrated well by Jobling (1997):

> "There are several reports that growth rates of fish and other aquatic organisms may be increased by exposure to fluctuating temperature regimes (Biette and Geen 1980, Spigarelli, Thommes, and Prepejchal 1982, Diana, 1984, Konstantinov and

> Zdanovich 1986, Vondracek 1982, Diana 1984, Konstantinov and Zdanovich 1986, Vondracek, Wurtsbaugh and Cech 1988, Berg et al. 1990, Miao 1992), the acceleration effect of fluctuating temperatures being known as the Kaufmann effect (Cossins and Bowler 1987). The growth acceleration resulting from exposure to fluctuating temperatures is usually assessed by comparing the rate of growth observed under conditions that cycle regularly between two temperatures with that obtained at the 'mean' temperature (Table 2).
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> The apparent growth-promoting effect of thermocycling is not universal, and there are also reports that growth rate is either depressed or unaffected by fluctuating temperature regimes (Hokanson, Kleiner and Thorslund 1977, Cox and Coutant 1981, Vondracek, Cech and Buddington 1989, Woiwode and Adelman 1991). The extent to which growth rate will be either depressed or accelerated, or be unaffected by a fluctuating temperature regime, will depend both upon the amplitude of the thermocycle and the 'mean' temperature about which the temperature fluctuates (for discussion see Cossins and Bowler 1987). The nature of rate-temperature curves leads to the expectation that growth promotion will be greatest when cycles fluctuate around a low 'mean' temperature (Fig. 3). This is in fact, the case. Growth is generally accelerated by temperatures that fluctuate around a low 'mean', thermocycling has less effect on growth when the 'mean' is close to the optimum temperature, and growth is markedly depressed when temperatures fluctuate around temperatures above the optimum (Fig. 3; Table 2)."

The diagram by Jobling (1997) (Figure 1; his Fig. 3) illustrates that growth rates increase with constant temperature for fish to a maximum and then decline as temperatures rise above this optimum temperature. This generalized illustration based on review of numerous fish species is based on feeding to satiation. By determining growth rate under constant vs. fluctuating temperatures, where each thermocycle has a mean equal to the constant temperature and varies by ±2°C to ±3°C around the mean, the ratios of growth under cyclic/constant temperatures can be plotted against temperature (°C). Although in his figure, growth rate is maximized at approximately 20°C, the crossover point where the growth rate ratio cyclic:constant equals 1.0 is 16°C. As maximum temperature increases above the optimum temperature, a fluctuating temperature regime underperforms the constant temperature regime. Fluctuating regimes with larger amplitudes of variation provide lower growth rates than fluctuating regimes with less variation and the magnitude of impairment increases with extent of exceedance of the growth optimum. Another way to look at this diagram is that to achieve parity in growth rates under fluctuating and constant regimes, the fluctuating regime must have a mean less than the growth optimum at constant temperatures.

Pre-1995 and Pre-1997 Bull Trout Temperature Reviews

During the Oregon Department of Environmental Quality's (ODEQ) Triennial Water Quality Standards Review (ODEQ 1995), a temperature technical advisory committee was formed to assist in the water quality standards review. The committee concluded that temperature standards should not be based on lethal levels but on sublethal temperature effects such as growth, species interactions, disease resistance, and reproduction. Temperature requirements for each life history stage and each monthly time period for bull trout were summarized from both field observations and laboratory studies. The temperature committee recommended a bull trout standard that was adopted by ODEQ along with other narrative criteria for bull trout habitat. The final adopted standard includes "an absolute numeric criteria of 10°C (50°F) based on a moving 7-day average maximum daily temperature for waters...determined to support or to be necessary to maintain the viability of native bull trout."

In 1997, EPA published its Final Rule (July 31, 1997; 62 FR 41162) for Water Quality Standards for Idaho. This rule was supported by the July 21, 1997 Administrative Record review, which provided the technical basis for promulgation of Idaho's water quality standard. Based on this review of literature and data for juvenile bull trout growth and rearing at associated temperatures, EPA established a criterion of 10°C expressed as a consecutive seven-day average of daily maximum temperatures for June, July, August, and September.

Juvenile Bull Trout Growth and Temperature Laboratory Studies

Bull trout growth and survival temperature study: Selong et al. (2001) (year one)

In 1998, temperature studies on growth and survival of juvenile bull trout were initiated at the U.S. Fish and Wildlife Service's Fish Technology Center in Bozeman, Montana. These studies were designed to aid in the development of thermal standards for juvenile bull trout (Selong et al. 2001). Results of the 1998 studies have been published (Selong et al. 2001). Results from subsequent studies are not yet available except in annual reports. The authors of these annual reports have cautioned against using information in the annual reports to guide or influence management decision determining bull trout temperature thresholds (T. McMahon, pers.com; R.Barrows, pers.com). The annual reports were designed primarily to show the project funding sources that progress was being made on the studies. Manuscripts may have different interpretations of the results and will show more details of the studies.

In the 1998 laboratory study, Selong et al. (2001) investigated lethal and sublethal effects of temperature. They found that small bull trout will stop feeding when temperatures exceed 22°C. Over 60 days, half of the bull trout exposed to constant temperatures of 21°C died. In these trials fish were fed at satiation rations with a feed specifically designed for bull trout. This feed was very palatable to bull trout, low in moisture content, and very high in caloric value (R. Barrows, pers. com.). Fish were fed by automatic feeders and kept in covered tanks in order to minimize stress. The goal of this feeding regime was to increase feed consumption as much as possible and to maximize the gross energy being consumed by the fish each day. Field fish biologists from Montana report that age 1+ bull trout in the Bozeman lab are much larger than same age fish in the wild (R. Barrows, pers.com.).

These studies also examined growth of juvenile bull trout in relation temperature. Using regression analysis the peak growth was estimated to occur at 13.2°C. The 95% confidence interval of the peak growth temperature yielded a maximum-growth range of 10.9-15.4°C. This range of nearly 4°C reflects the uncertainty that occurs under even very controlled conditions. 13.2°C was the mathematical average for the optimum growth temperature.

Bull trout growth and survival temperature study: Annual reports 1999 (year two) and 2000 (year three)

The set of consecutive annual reports by McMahon et al. (1998, 1999, 2001) provide much needed information. However, in their current annual report format, there are many issues that are not described fully enough to form a scientific basis for making management decisions, especially when some of the conclusions contradict classic fish bioenergetics literature. The authors of the annual reports acknowledge the preliminary nature of these reports and the omission of detailed information regarding the studies. They also acknowledge that the published manuscripts may have different conclusions and information than the annual reports (R. Barrows, pers. com). Some of the controversy within the EPA Technical Workgroup regarding the optimal temperature thresholds for bull trout is related to different interpretations of these reports.

Relying solely on information provided in the annual reports (McMahon et al. 2000 and 2001) could lead to an interpretation of the data and graphs that is contradictory to similar bioenergetics studies for other salmonids. As an example of the dangers of relying on a single piece of evidence to form a conclusion, especially when that evidence is in a preliminary form, we will provide a detailed analysis of sections in the McMahon et al. annual reports (2000, 2001) that demonstrate growth optimum remaining essentially constant as food rations are reduced, and compare that conclusion to the prevailing literature, which demonstrates a significant decrease in optimal growth temperature as ration size declines. Examples of studies on salmonids showing that the optimum growth temperature declines with food limitation include studies for sockeye (Brett and Shelbourn 1975, Shelbourn et al. 1973), chinook (Brett et al. 1982), brown trout (Elliott 1994), and coho (Edsall et al. (1999) (Figures 2, 3, 4, and 5, respectively).

Among the preliminary analyses in the McMahon et al. reports, the method for measuring food consumption appears to offer error in its estimate. The reports provide scant information on the actual consumption rates at satiation feeding as temperature increases. No information is given on metabolic losses or loss in weight under starvation conditions. Setting aside the areas of doubt in methodology, caused probably by insufficient explanation in their current form as annual reports, the basic conclusions that were made by the authors or drawn by interpretation by technical members that the optimal temperature for growth remains constant (or declines no more than about 1°C) when food ration is severely reduced, can be contrasted with the preponderance of evidence available in the literature.

Upon careful analysis, the difference between the results of McMahon et al. (2001) on bull trout feeding relative to temperature and ration vs. classic research on this subject is due largely to the manner by which rations were calculated. As stated by McMahon et al. (2001):

> "In earlier studies, fish were fed a fixed ration based on body size, whereas in our study and that of Elliott and Hurley (1999), rations were fed as a fixed proportion of satiation or maximum energy intake (satiation). Results obtained using the two different approaches appear to be contradictory, but are only different due to the way that a restricted ration was determined."

As stated by Elliott and Hurley (1999):

> **"When fixed quantities of energy are used, the optimum temperature decreases with decreasing C_{IN}. [i.e., daily energy intake as calories.] However, when C_{IN} is expressed as a proportion, p, of the maximum energy intake, the optimum temperature increases with decreasing energy...These different conclusions are not contradictory because they are based on the same model and the same data set, but they illustrate well the need to define clearly the units for energy intake in comparative studies."**

In McMahon et al. (2001), when ration was 100% (i.e., of satiation), growth rate peaked at 13.2°C, but shifted downward to 12.3°C when ration was 11% of satiation. Rather than this small decrease in peak growth at lower rations being some new scientific information regarding the effect of different ration size on growth at different temperatures that only seems to apply to bull trout and that is truly different from what has been found in all previous studies, the results are merely a different way to plot data (R.Barrows, pers.com.). That is, if the bull trout data had been plotted in the conventional manner, a strong decline in optimum temperature with declining ration would be the likely result. The work of Elliott and Hurley (1999) (Figure 6) indicates that the optimum growth temperature for bull trout would actually decline as ration is decreased because the two methods for plotting the results are totally complementary. The decline in optimum growth temperature with decreasing ration is based on an actual decline in calories ingested. That is, if the temperature is 13°C for juvenile bull trout (the approximate optimum growth temperature under satiation feeding), growth rate will decline for bull trout if this ration is reduced to 80% ration and will decline again if the caloric intake is decreased to 60% ration from that at 13°C. The relationship between lower caloric intake (calories/gram fish weight/day) and lower optimal temperature for bull trout will be demonstrated in the manuscript that is currently being written for publication based on the 1999 Mc Mahon et al. study (R.Barrows, pers.com).

In contrast to the bull trout data, the optimum growth temperature established for brown trout at satiation, a species much more tolerant of warmer waters, was 13.9°C (Elliott and Hurley 1999). The work on brown trout represents one of the most intensive, thorough bioenergetic investigations ever done on any fish species. For brown trout feeding at a daily caloric intake 57% of that needed to produce optimal growth at 13.9°C, the optimal growth temperature declined to 11.5°C. If rations were reduced to 29%, optimum growth temperature would decline to 7.3°C based on the figures presented in Elliott and Hurley (1999)(Figure 6). Given the more rigorous cold temperature requirements of bull trout and the predominant expectation that feeding in the field would be at less than satiation, one should expect that realistic optimum growth temperatures would be considerably less than 13°C. One could then seriously question whether 13°C would represent the upper end of optimal or might be a substantial exceedance of optimal.

The importance of understanding peak growth temperature at less than satiation rations is related to evidence that there often is food limitation in natural streams. Bull trout tend to spawn and rear in headwater streams and these streams in the Pacific Northwest are characterized by low levels of primary and secondary productivity (Gregory et al. 1987). Salmon fry, eggs, and decomposing carcasses historically were an important source of food and nutrients in streams. With the recent decline of Pacific salmon, productivity of Northwest streams has been further diminished. (Cederholm et al. 2000). Filbert and Hawkins (1995) recently reviewed a set of papers that reported food limitation for stream salmonids from several geographic areas. Papers in their review reporting food limitation in the Pacific Northwest included Murphy et al. 1981, Hawkins et al. 1983, Wilzbach 1985, Baker 1989, and Intermountain West (Binns and Eiserman 1979).

In conclusion, if caloric intake is restricted from that which would produce the optimum growth rate, growth rate will be reduced and, in addition, the temperature producing the optimum growth rate at that energy intake will decline. This result is mathematically true for bull trout, just as it is for chinook, coho, sockeye, and brown trout (see Elliott and Hurley 1999).

Although there is additional information on bull trout growth in a laboratory setting, most of this information has not been published. Some of the information from these annual reports could be used in support of bull trout temperature recommendations. However, use of this information would require a very critical, in-depth review of the data since the information in the reports is preliminary. We will respect the authors caution against using the reports until the information is more fully presented and analyzed when accepted as a manuscript for publication.

Bull Trout Temperature and Distribution Field Studies

The most current and extensive database and analysis of juvenile bull trout distribution relative to temperature is provided in Dunham et al. (2001). This database of thermograph records throughout the current range of bull trout in the United States included both data from U. S. Forest Service Rocky Mountain Research Station surveys of bull trout and stream temperature and data received from other biologists in the region (Rieman and Chandler 1999). These data, presented as a graph of predicted probability of occurrence vs. maximum daily temperature for bull trout <150 mm indicate that probability of occurrence declines steadily as temperatures increases from 10 to 20°C. At a maximum daily temperature of 15°C the probability of occurrence is approximately 60%. When the maximum daily temperature is 11-12°C the probability of occurrence is approximately 80%. This represents a substantial difference in distribution. This pattern of distribution could reflect sublethal influences of temperature (Dunham et al. 2001). To the extent that waters are naturally capable of achieving temperatures of 12°C maximum daily temperature rather than 15°C maximum daily temperature, achieving the lower temperature will substantially reduce the risk of extirpation or displacement of juvenile bull trout from the reach.

At colder temperatures (i.e., <10°C) the extrapolation of probability of occurrence values using logistic regression is less robust. Reasons for this might be related to sampling efficiency for bull trout at the colder temperatures. Bull trout become more secretive as temperatures decline (i.e., effectively hide in the substrate or banks) and are very difficult to observe via snorkeling (Thurow and Schill 1996) . This causes sampling efficiency to be reduced, increasing the cases of non-observance at low temperatures. Given that growth rates of 50-g brown trout at 8°C are still 50% of optimal, where optimal growth temperature at satiation is 13°C (Elliott and Hurley 1999), it seems reasonable that bull trout, a species requiring much more colder temperatures, could do well at temperatures below 10°C. That is, there is no reason to assume that temperatures in the range 8-10°C would limit distribution. Assuming that the tendency to hide in the substrate does not vary significantly between 12 and 15°C, it would seem that sampling efficiency within this temperature range would remain fairly constant. Consequently, one would conclude that the large reduction in probability of occurrence is highly correlated with maximum daily temperature.

Haas (2001) examined maximum temperature and its effect on the associations of bull trout and rainbow trout. Mean daily maximum water temperatures of about 12°C or less were good predictors of bull trout presence, numerical dominance, and higher condition factor. Rainbow trout were numerically dominant and had higher condition factor at maximum water temperatures above 14°C. In sympatry bull trout were dominant in sites with maximum temperature <13°C. Although bull trout were able to maintain healthy populations at temperatures up to a daily maximum temperature of 13°C, Haas felt that this study and other data indicated 12°C as a better and more representative maximum temperature (G. Haas pers com). Haas (2001) also examined the correlation for different temperature metrics and in his analysis this 12°C maximum temperature limit roughly corresponds to a maximum daily average temperature of 10.7°C, a maximum weekly maximum temperature of 11.6°C, and a maximum weekly average temperature (MWMT) of 10.2°C.

The relationship between summer water temperature and bull trout distribution and abundance in the Little Lost River presents an example from a field study of the relationship of species composition, ration size (in this case stream productivity), and bull trout optimum temperature (in this case high abundance). Gamett (2002) reported that all sites with high densities of bull trout (>20 fish/ 100 m^2) had only bull trout present or bull trout with very few rainbow. Also, most of the sites with densities >20 fish/ 100 m^2 were in an area perturbed by a very intense fire in 1988, which also burned the riparian area. Following this fire there was a big increase in primary productivity. In the Little Lost River basin nearly the entire Smithie Fork drainage burned in the 1988 fire. Of all the sample sites in the Gamett study, Smithie Fork drainage had the highest productivity for bull trout. (Gamett, pers.com). Although bull trout were influenced by fire in the short term, due to factors such as multiple age class outmigrating they were able to recolonize and reach their current abundance in these post-fire highly productive streams.

Using Multiple Lines of Evidence: An Example, Using Coho and Bull Trout, of Integrating Field and Lab Study Results

In order to understand the logic behind using multiple lines of evidence to establish bull trout temperature requirements, it may be instructive to provide an example using a similar process for another species, coho. Comparable types of data are available for coho as are being relied upon most heavily for bull trout criteria --i.e., optimum growth temperature and distribution. For coho the water temperature providing optimum growth conditions under satiation feeding on a diet of minced alewives was 15°C (Edsall et al. 1999). When feeding rate was reduced to 2% of wet body wt/d the optimum temperature for growth declined to 10°C. By contrast, bull trout (*Salvelinus confluentus*), feeding on a specially formulated high calorie feed of krill and with vitamins/minerals to satiation in the Selong et al. (2001) study, had an optimum growth temperature of 13.2°C. This optimum growth temperature at satiation is comparable to that of lake trout (*Salvelinus namaycush*), (12.5°C) (Edsall and Cleland 2000), brown trout (*Salmo trutta*) (13.9°C)(Elliott and Hurley 1999), and Arctic char (*Salvelinus alpinus*) (14°C) (Jobling 1983).

A major difference between the Edsall et al. study and that of Selong et al. is in the food. The Selong et al. study used a food that had approximately a 5-fold increase in caloric content over conventional salmon feeds. Because the ability to grow is a function of the balance between growth rate and metabolic rate as well as of the total calories ingested, the ability to divert excess assimilated energy to growth increases when ingested food has a high calorific content. Satiation feeding under such conditions may provide far greater caloric intake/day than under most studies where feeding to satiation occurs on lower quality food. This means that even at a feeding rate of 20% of satiation on the high calorie diet, the caloric intake would be equal to what is normally termed satiation feeding level in conventional feeding studies. Caloric intake under field conditions may then be far different than under laboratory conditions where super-rich food is available and there is little metabolic cost involved in catching the food.

Juvenile coho freshwater distribution data relative to water temperatures are available from Welsh et al. (2001). These authors presented a logistic regression of coho salmon presence/absence in 21 tributaries of the Mattole River in relation to the maximum weekly maximum temperature (MWMT). The 21 tributaries provided a range of MWMT values from 12 to 27°C. Streams supporting juvenile coho salmon had temperature regimes characterized by MWMT values of ≤18°C. None of the 10 streams having MWMT >18.0°C had coho. Of the 11 streams with MWMT <16.3°C, nine of them had juvenile coho. The only ones not to have coho were a stream having access problems at low flow and another stream that had had herbicide treatments.

Dunham et al. (2001) found a high probability of occurrence of bull trout juveniles (approx. 75%) with temperatures (MDMT) of 12°C (Figure 7). High probability of occurrence was also found with temperatures between 6 and 12°C. When maximum daily temperature was 18°C the probability of occurrence was approximately 33% of that at 12°C.

These data indicate that bull trout have an optimal growth temperature at satiation that is equivalent to that of other *Salvelinus* species as well as brown trout and Arctic char. Its optimal growth temperature is also approximately 2°C less than that of coho. If rations are reduced from what might be considered the satiation level of feeding in the field, one might assume that the temperature that would produce optimum growth would be reduced by 2-3°C. This amount of reduction in optimum growth temperature appears to be most probable based on studies of Edsall et al. (1999) on coho and Elliott (1994) on brown trout. To keep the temperature high while reducing food availability would result in high metabolism and reduced growth. In addition, maximum daily temperatures of <12°C produce a high probability of occurrence for bull trout as well as for coho. Temperatures of 18°C result in very substantial reductions in occurrence in bull trout and virtual elimination of coho. (Note: the database for coho cited was much less extensive than that for bull trout but it was determined near the southern geographic limit to coho distribution). Given the greater known sensitivity of bull trout to warm water than both coho and brown trout, it appears that optimum conditions in the field for both growth rate and distribution are where maximum daily temperature is <11°C.

Heat Shock Protein Evidence

Not all evidence should be considered as being of equal importance when determining optimal temperatures for bull trout in an ecosystem context. Weber (2001) examined the heat shock induction temperature for bull trout in order to provide an independent assessment of the thermal limit of bull trout. Initially two heat shock proteins found in chinook salmon were tested for the experiment with bull trout. Following preliminary experiments only one of the heat shock proteins provided useful results and was chosen for the experiment. If the discarded indicator had been used, a higher induction level would have been suggested. Other untested heat shock proteins are likely found in bull trout and these may prove to be even more sensitive. Heat shock protein information has the potential to be an early warning monitoring procedure for resource specialists, but depending on which one is selected it can only be inferred that a threshold value indicating biochemical stress is at least as low as that indicated by the test.

The results of the experiment with induction of a heat shock protein provide new information on a biochemical level of temperature effects when other stressors, such as competition and limited ration, are not present. This biochemical information can be added to the information about temperature effects from other levels in the biological hierarchy, such as feeding or competition, that are not expressed at a biochemical level. If such biochemical stress were indicated at a temperature lower than provided by other lines of evidence, there might be good reason to exert special caution. Early warning monitoring indicators are useful when higher order biological processes appear to be insensitive or statistically significant differences in higher order processes (e.g., changes in community composition, changes in decomposition rates) are difficult to discern. However, when a single biochemical indicator suggests a higher temperature threshold for effect than other lines of evidence, it would be inappropriate to simply average in a value from a less sensitive test to derive a mean for all separate lines of evidence. When weighing evidence we must balance all the different levels of information on temperature effects to the fish - from molecular to community and ecosystem and possibly emphasize the most sensitive ones.

Conclusion and a Recommendation

Our understanding of thermal effects on bull trout is based on a combination of laboratory and field evidence. It is important to evaluate the strengths and weaknesses of these different lines of evidence as well as to a conduct a critical evaluation of the study methods, statistical analysis, and confidence intervals for results.

The laboratory studies described in this paper are useful in determining certain cause and effect relationships within the controls of the study; i.e., increased peak growth temperature as ration size (calories/gram fish weight). However, it is impossible for laboratory studies to duplicate the complex ecological setting that individual fish experience. Some of the limitations of using the results of a lab study such as Selong et al. (2001) in developing temperature standards that will be applied to fish in a natural setting are feeding unlimited rations of specially designed bull trout food very high in calories, lack of energy expended by the fish to obtain food, lack of predators or competitors, and lack of multiple stressors found in nature.

Results of field studies may be difficult to interpret due to "noise" from the environmental variation found in nature. Other limitations may result from difficulty of obtaining precise field measurements and the associated sampling errors, difficulty of replication, difficulty of matching the actual fish distribution with the measured thermal regime at a given time or location, and effects of competitors.

Dunham et al. (2001) provide a good description of factors to consider when combining results from field and lab studies recently conducted on bull trout temperature requirements:

> "Model predictions from distributions in the field (Figure 2) imply that bull trout may be present at potentially lethal temperatures, but that probability of occurrence is relatively low (e.g., <0.50) until maximum daily temperatures

> decline to approximately 14-16°C. Probability of occurrence is not high (e.g., >0.75) until maximum daily temperatures decline to approximately 11-12°C. These patterns could reflect sublethal influences of temperature. For example, Selong et al. (2001) found that growth of bull trout on unlimited rations in the laboratory was maximized at 13.2°C. If rations are limited, the temperature at which maximum growth is realized can be shifted to lower temperatures (T. McMahon, Montana State University, personal communication). More detailed field investigations of growth, behavior, and other responses are needed to better understand the sublethal responses of bull trout to temperature."

The EPA Technical Workgroup recommended 12°C MDMT, which is approximately equivalent to 11°C MWMT, as the upper optimal temperature threshold for bull trout. The stream temperature that will support juvenile bull trout is not a single number but rather a range of numbers with associated risks to the fish. Dunham et al. (2001) provides an analysis of an extensive database with bull trout occurrence and temperatures from across the range of bull trout linked to the expected probability of occurrence for bull trout. This analysis gives managers options for temperature thresholds based on risk expressed as a probability of occurrence. Because cold water is so important to bull trout conservation, a protective approach would be to require 11°C MWMT in those waters that are capable of attaining this temperature, either in their current condition or with restoration, and that are necessary for bull trout recovery.

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Figures

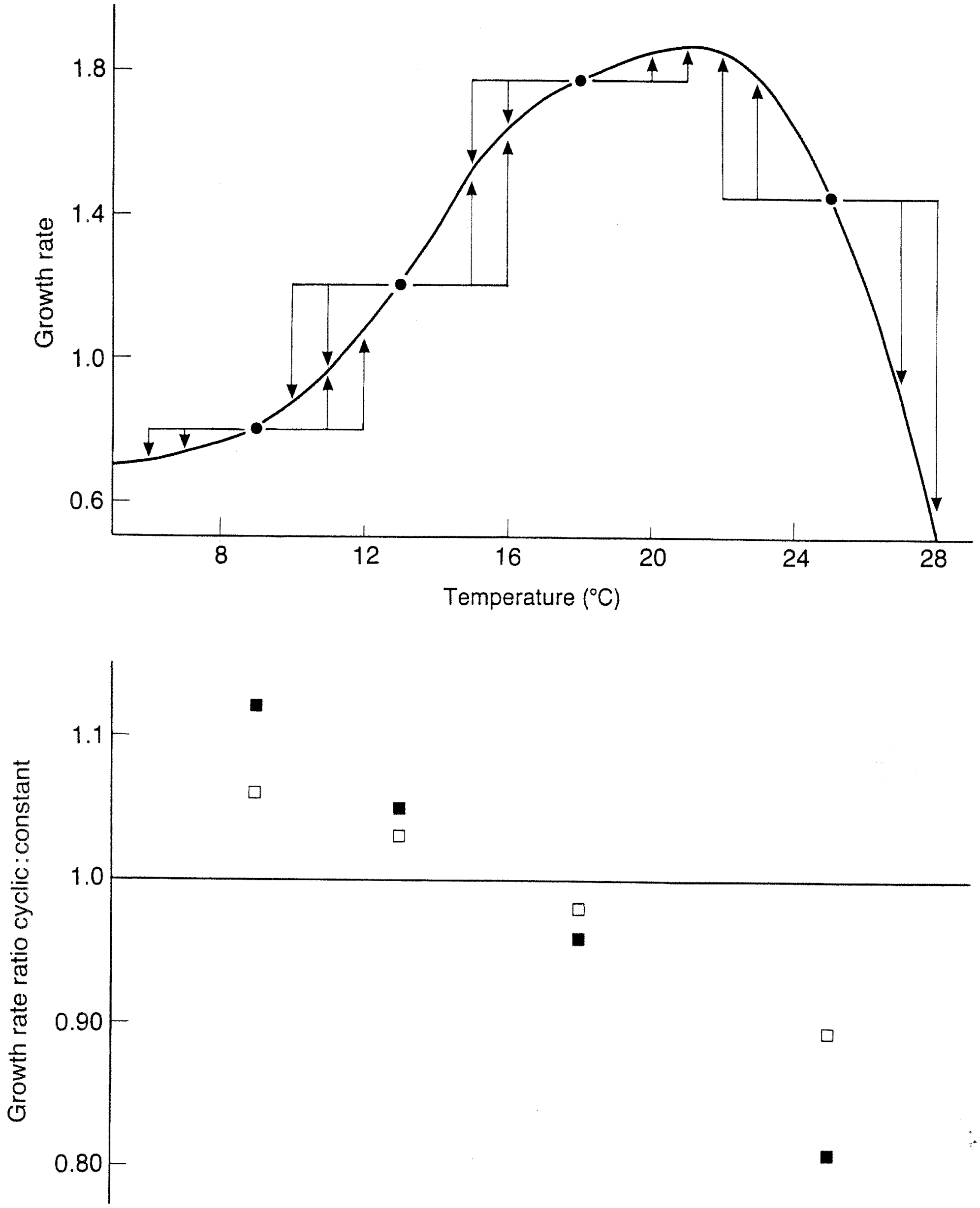

Fig. 3. Rate–temperature curve illustrating growth rates at different constant temperatures (●) and the possible influences of thermocycling (↑ ↓) upon rates of growth. The growth rate ratio refers to the rate of growth observed under thermocycling conditions relative to that attained under constant temperature at the cycle 'mean'. Comparisons were made using growth rate data for different constant temperatures and thermocycles of 'mean' ± 2 °C (□) and 'mean' ± 3 °C (■).

Figure 1. Influence of constant and fluctuating temperatures on growth rates. Jobling (1997).

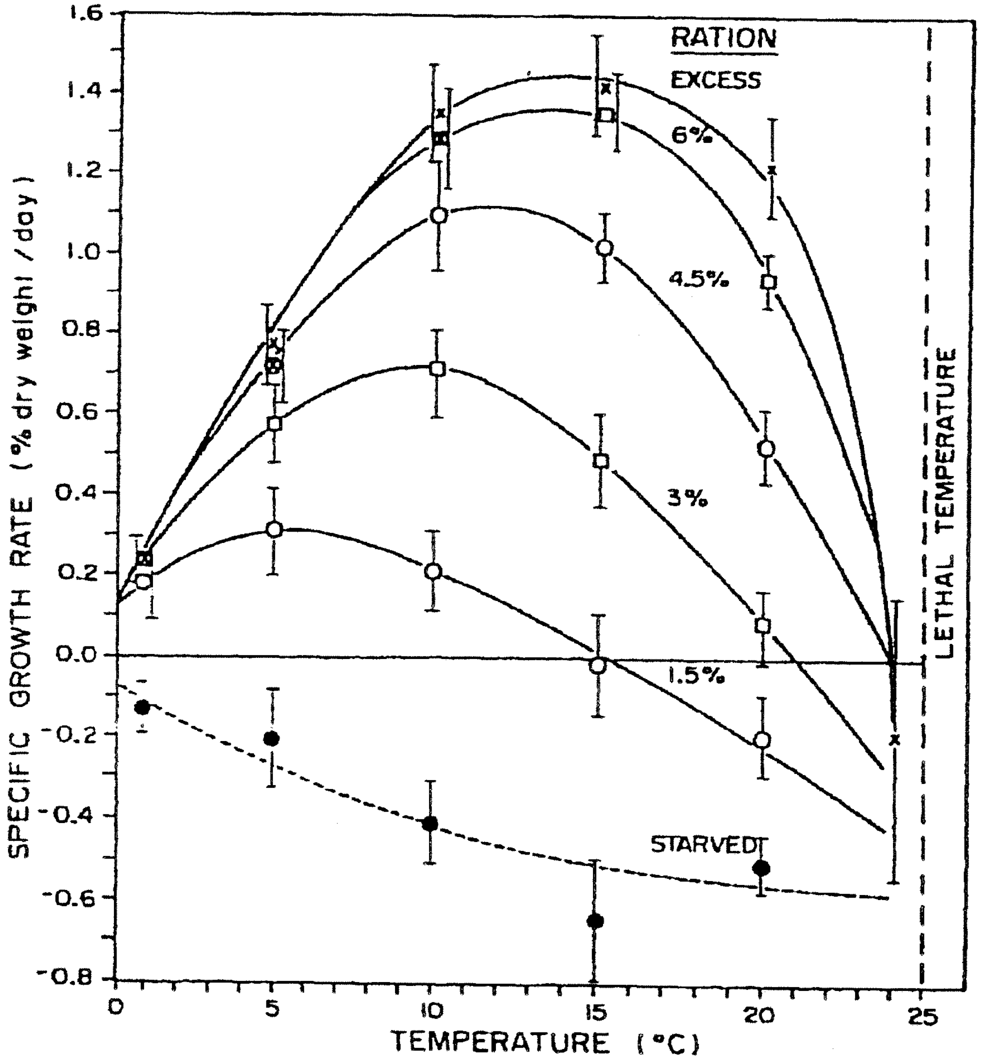

Figure 3.6

Effect of reduced ration on the relationship between growth rate (±2SE) and temperature for 7- to 12-month-old sockeye salmon. Points for excess ration or where a prescribed ration turned out to be excessive are marked with an X. The broken line for starved fish is a provisional interpretation. The similar variance for most points reflects the absence of competition for food in this schooling species. (From Brett et al. 1969)

Figure 2. Growth rate of sockeye salmon relative to temperature and food ration. Brett et al. (1969).

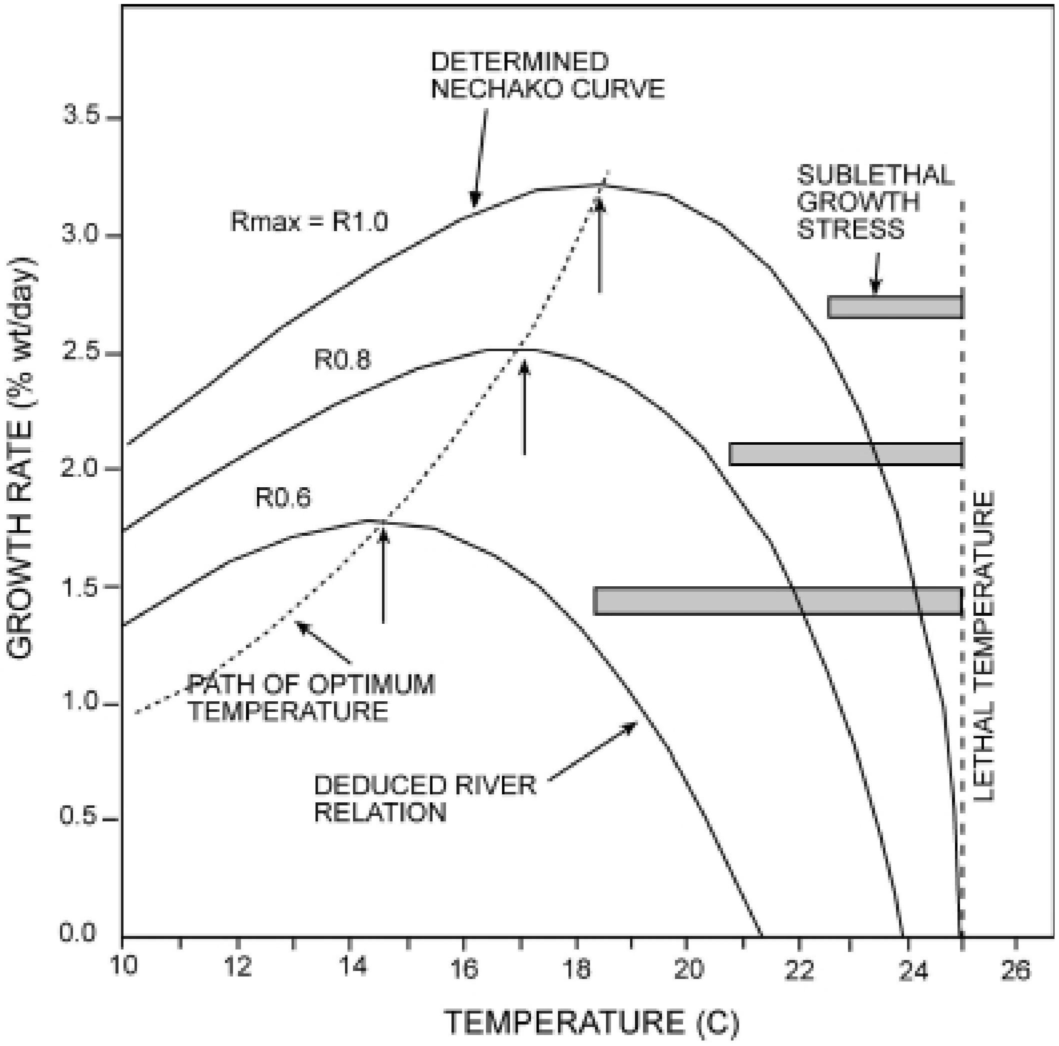

Figure 3. Growth rate of chinook relative to temperature and food ration. Brett et al. (1982).

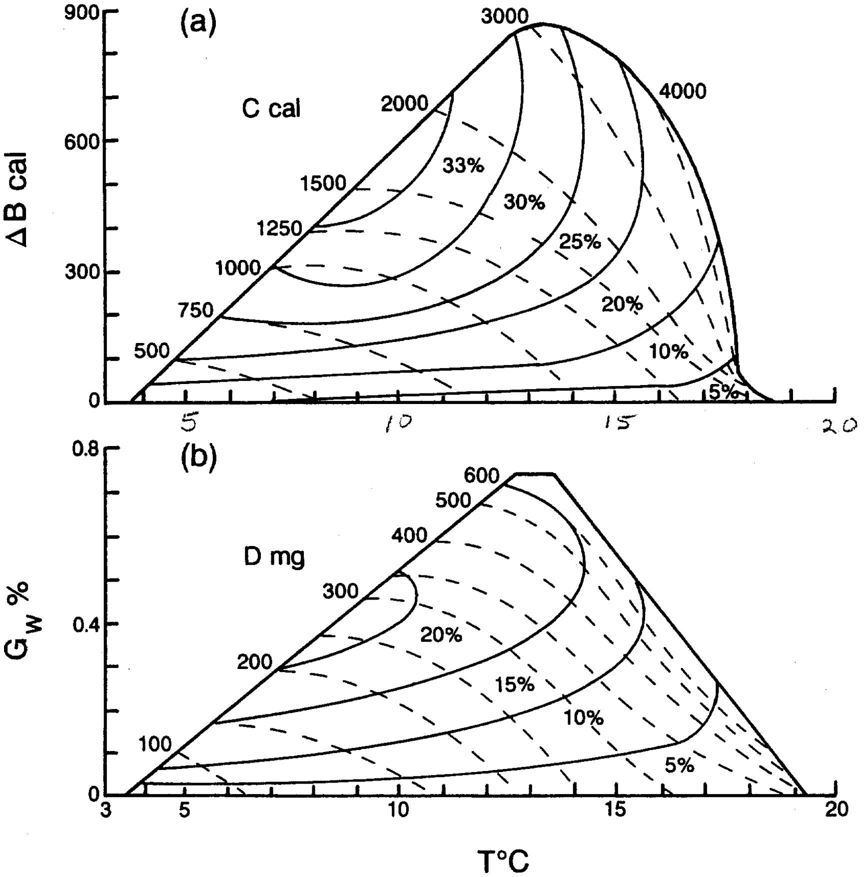

Fig. 4.14 Gross efficiency isopleths (%) for trout of initial weight close to 50 g. Percentage efficiency isopleths are drawn over the curves relating growth to temperature at fixed ration levels in terms of: (a) energy values (from Elliott 1976*c*); (b) wet weight (from Elliott 1975*d*).

Figure 4. Growth rate of brown trout relative to temperature and food ration. Elliott (1994).

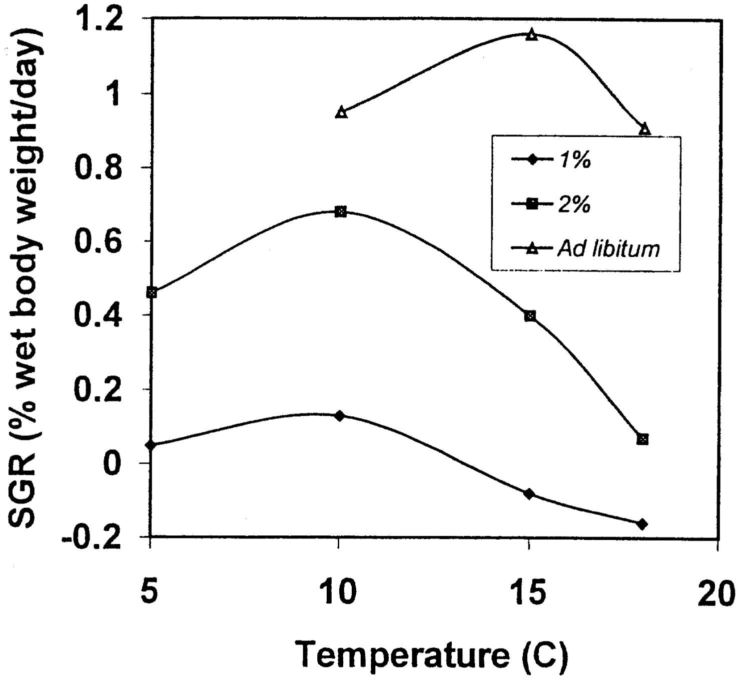

FIG. 2. Specific growth rate (SGR) of juvenile coho salmon at different ration levels and temperatures. Curves fitted by Excel 97 smoothing function.

Figure 5. Growth rate of coho relative to temperature and food ration. Edsall et al. (1999).

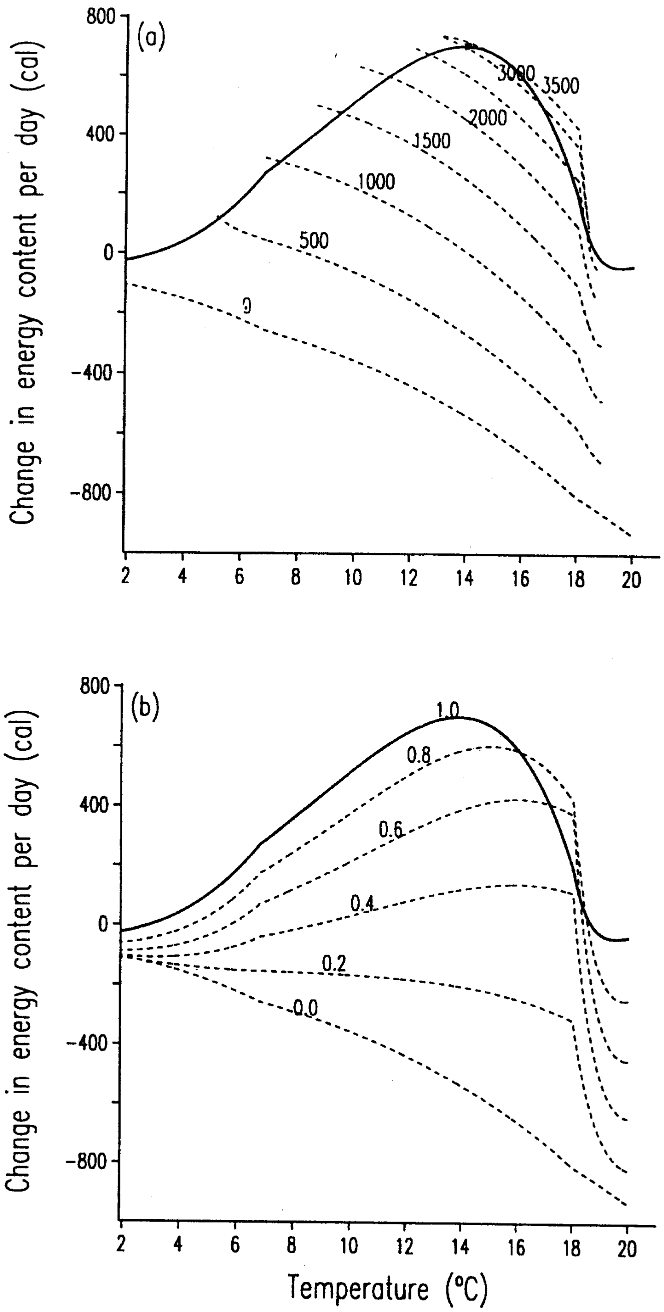

Fig. 4 Relationship between the mean daily change in the total energy content (C_G, cal) of a 50-g brown trout and the water temperature (T, °C); the solid curve shows the values of C_G for fish on maximum rations and the isopleths show the relationship for different ration levels with daily energy intake (C_{IN}, cal) expressed as: (a) fixed quantities of energy; and (b) a proportion (p) of the maximum energy intake.

Figure 6. Effects of rations on growth rates at various temperatures for brown trout. Elliott and Hurley (1999).

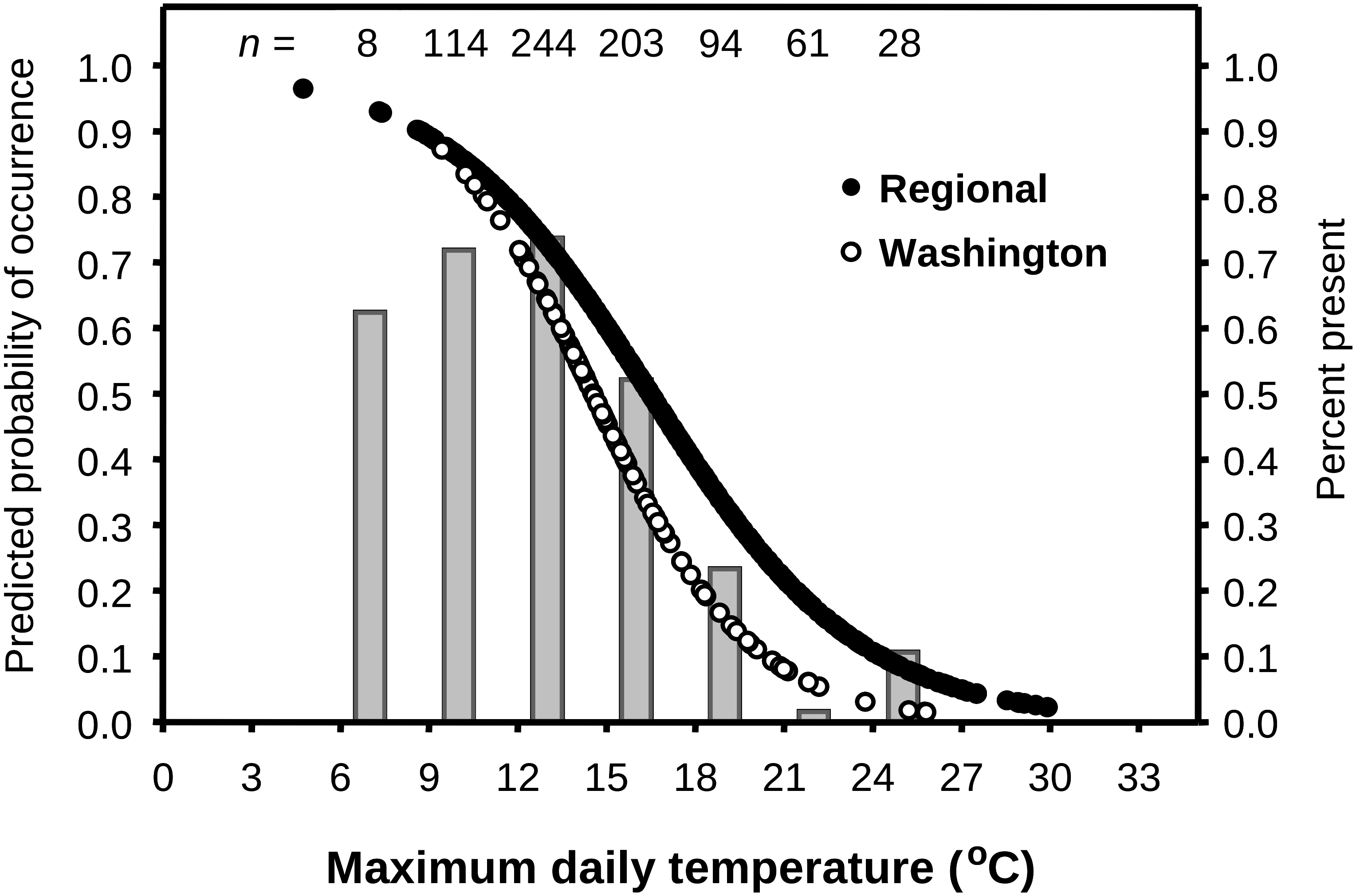

Figure 7. Logistic regression estimates of probability of occurrence for bull trout relative to maximum daily temperature. Dunham et al. (2001).