ASSESSING CUMULATIVE THERMAL STRESS IN FISH DURING CHRONIC EXPOSURE TO HIGH TEMPERATURES

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Abstract

As environmental laws become increasingly protective, and with possible future changes in global climate, thermal effects on aquatic resources are likely to receive increasing attention. Lethal temperatures for a variety of species have been determined for situations where temperatures rise rapidly resulting in lethal effects. However, less is known about the effects of chronic exposure to high (but not immediately lethal) temperatures and even less about stress accumulation during periods of fluctuating temperatures. In this paper we present a modeling framework for assessing cumulative thermal stress in fish. The model assumes that stress accumulation occurs above a threshold temperature at a rate depending on the degree to which the threshold is exceeded. The model also includes stress recovery (or alleviation) when temperatures drop below the threshold temperature as in systems with large daily variation. In addition to non-specific physiological stress, the model also simulates thermal effects on growth.

Introduction

The impact of power plants on the thermal regimes of aquatic ecosystems has been a concern for decades. As environmental laws become increasingly protective and with possible future changes in global climate, thermal effects on aquatic resources are likely to regain the attention it received in the 1970's. Power plant thermal effects typically result from either the discharge of heated water used for cooling at fossil fuel and nuclear plants or changes in flow regimes and reservoir operations in the case of hydropower plants.
Operating licenses often include articles with criteria designed to protect aquatic resources, particularly fish, from unnatural thermal impacts. These criteria vary in both complexity and effectiveness, and rarely take into account temporal and cumulative aspects of thermal exposure on fish. Typical criteria include one or several of the following (listed in order of increasing complexity): 1) a single maximum temperature that may not be exceeded, 2) a time-averaged (daily or longer) mean temperature that may not be exceeded, or 3) criteria (like 1 or 2 above) that vary monthly (or seasonally) to account for acclimation to the average seasonal temperature and variable susceptibility by different species and life stages.

These criteria are often established based on experimentally determined Critical Thermal Maxima (CTM) which measure an acute response (e.g., loss of equilibrium or death) to a rapid increase in temperature. A 2°C safety margin is usually included when using CTM results to establish thermal criteria. In some cases, the Upper Incipient Lethal Temperature (a measure of long-term exposure effects) and reproductive effects on spawning adults and early life stages are also considered. These measures of thermal response are typically determined for different acclimation temperatures, but rarely include the additional effect of chronic exposure to sub-lethal temperatures that can be stressful but not lethal. It is common knowledge that the recent thermal history of a fish acclimates it to higher temperatures, thereby extending its tolerance limit (Parker and Krenkel 1969, Jobling 1994). However, beyond a certain point, acclimation benefits are exceeded, and prolonged exposure to non-lethal temperatures causes physiological stress which can reduce a fish’s tolerance of high temperatures and ultimately affect population success.

Not only do the most standard criteria fail to consider chronic effects, but they also do not account for stress recovery during periods of fluctuating temperature when temperatures periodically drop below stressful levels. Large daily fluctuations in water temperature as a result of either natural conditions or industrial operations can result in significantly different impacts than constant temperatures on which most regulatory criteria are based. In thermally fluctuating environments, it is likely that a single maximum temperature criterion would be exceeded repeatedly for short durations rather than continuously for a long period. It is also possible that mean temperatures could remain below criteria based on average conditions that are presumed to be safe, but exposure to short-term temperature peaks could still be detrimental. The dynamics of stress recovery in fish is poorly understood, but may be an important factor in thermal effects in many situations.

Because of the poor understanding of thermal stress in fish in thermally dynamic environments and the uncertainty associated with the establishment of regulatory criteria, there is a high likelihood that many existing criteria are either under- or over-protective. From an environmental perspective, it is usually better to be over-protective; however, from a power production perspective it is obviously not desirable to spend unnecessarily for nonessential mitigation. A better understanding of the cumulative nature of thermal stress along with stress recovery dynamics is crucial in establishing regulatory criteria that are protective of the environment while at the same time not overly conservative.
The purpose of this paper is to describe a model framework which we have developed to assess both the temporal aspects of thermal exposure and the dynamics of cumulative stress and recovery in fish exposed to fluctuating temperature regimes.

It is common for many streams (both natural and impacted) to experience daily fluctuations of $>4^\circ\text{C}$ during the summer (Figure 1), and some may fluctuate as much as $10^\circ\text{C}$. Although the amount of daily fluctuation in ambient air temperature is probably the most important factor in dictating water temperature fluctuation, other factors such as the size of the water body, amount of flow, degree of mixing, and exposure to solar radiation are also important. Figure 1 illustrates features of a typical thermal regime that probably affect cumulative thermal stress in fish. The temperature at which stress begins to occur is largely dependent on a fish's prior exposure history or acclimation. For example, typical seasonal acclimation allows fish to be more tolerant of high temperatures in the summer than in the winter. Even with acclimation there is a temperature beyond which stress occurs regardless of previous acclimation at sub-stressful temperatures. One aspect of stress accumulation of which little is known is stress recovery when exposure to high temperature is removed. The temperature at which recovery occurs, the rate of recovery, and the length of time for full recovery are largely unknown. The model framework we have developed includes these aspects of thermal stress and recovery.

![Figure 1. Factors that affect thermal stress accumulation in fish in fluctuating environments.](image)

**Methods and Results**

The thermal effects model was designed in a systems dynamics framework using commercially available Stella® software. This system is user friendly and allows for easy manipulation of

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input parameters and state variables. The model described here was parameterized for rainbow trout (i.e., the bioenergetics parameters and temperature thresholds) but is easily transferable to other species where basic physiological parameters are known. Below, we describe the thermal stress component of the model first and then describe the entire thermal effects model.

**Thermal Stress Component**

The direct thermal stress component of the model is similar to damage-repair models developed for ecotoxicology investigations (Breck 1988, Meyer et al. 1995). Figure 2 shows the relationship among those factors that affect stress accumulation and recovery including:

- the magnitude of high temperature exposure,
- the duration of high temperature exposure,
- acclimation history (both short- and long-term),
- stress recovery during periods of reduced temperature, and
- size- and species-specific effects on threshold temperatures.

![Figure 2. Diagrammatic representation of direct thermal stress submodel.](image-url)
The basic equation of this thermal stress submodel is:

\[
\text{Thermal Stress}(t) = \text{Thermal Stress}(t - dt) + (\text{Accumulation} - \text{Recovery}) \times dt, \quad (1)
\]

where \(t\) is the current time step and \(dt\) is the size of the time step.

The model (i.e., equation 1) tabulates an index of thermal stress which has yet to be directly related to actual physiological stress or other health effects. In the model, thermal stress is accumulated as temperature exceeds a threshold level and at a rate that depends on acclimation history and the size and species of the fish. For the simulations presented here, the base threshold temperature was set at 21°C. Recovery occurs when temperatures drop below a threshold at a rate that depends on duration and magnitude below the threshold. For now, we assume that recovery occurs at a rate 25% slower than stress accumulation.

To demonstrate how the model works we applied it to a two-month record of temperatures from the Madison River in Montana (Figure 3). We used temperatures from two locations below a hydropower dam that have different degrees of daily temperature fluctuation (1-2°C at site A versus 4-5°C at site B) even though the daily mean temperatures at the two sites are similar (19.9°C at site A versus 20.3°C at site B). Site A is about 2 miles downstream of the dam and reflects the thermal dampening effects of the impoundment. Site B is 9 miles downstream of the dam. See Bevelhimer et al. (1997) for a detailed description of thermal issues on the Madison River.

![Graphs showing thermal stress index and fish weight over time](image)

**Figure 3.** Model predictions of thermal stress (top right panel) and growth (bottom right panel) for fish exposed to two thermal regimes (left panels) of similar mean temperature but different daily variability.
Model results indicate that, on average, a fish at the downstream site (B) would have a stress index that is 2 to 3 times greater than a fish at site A even though the difference in mean temperature is only 0.4°C. Until the stress index is related to actual health effects, such as physiological performance, via laboratory experimentation, it is difficult to assign a biological meaning to these results.

**Multiple Effects Model**

The complete thermal effects model also includes the effects on growth (as determined by a bioenergetics sub-model) and condition factor (a ratio of length:weight that indicates general state of health) (Figure 4). Reduced growth or physiological condition are long-term effects of chronic high temperature exposure that can result in greater susceptibility to other sources of mortality, such as disease and predation. The bioenergetics sub-model has become a common tool in fisheries science (Adams and Breck 1990) and provides a means to assess growth as the difference between the caloric intake (i.e., food consumption) and energetic costs (i.e., respiration, activity, egestion, and excretion). Most of the relationships included in the bioenergetics model are sensitive to changes in temperature.

The basic equation of the growth portion of the model is:

\[
\text{Growth}(t) = \text{Growth}(t - dt) + \left( \text{Food Consumption} - \text{Food Processing Costs} \right) - \left( \text{Egestion} - \text{Excretion} - \text{Respiration} \right) * dt
\]

Just as there are differences in estimated thermal stress realized by fish at the two sites, the model also predicts differences in growth (Figure 3). Fish at site A, which had less daily variation, had about 50% greater growth than fish at site B by the end of the two-month simulation.

**Discussion**

The effects of fluctuating temperature regimes on temperature tolerance, thermal stress accumulation and recovery, and growth is still largely a mystery. Developing a model that assesses these effects will require a basic understanding of the relationships between fluctuating temperature and tolerance, stress, and growth. These relationships have been investigated in a variety of laboratory experiments although few definitive conclusions have been drawn. For example, studies by Otto (1974), Heath et al. (1993), and Bennett and Beitinger (1997) all found that fluctuating temperature regimes increased a fish's tolerance of high temperatures, but Currie et al. (in press) found no such enhancement in similar studies.

The effects caused by fluctuating conditions can also be quite complex and not always easily explained. Greater growth under conditions of greater daily temperature fluctuation as predicted by the model (see Figure 3) has also been observed in laboratory studies (Cox and Coutant 1981,
Konstantinov and Zdanovich (1987). However, the difference in growth under these conditions is not necessarily just a function of the amount of variability, but might also be a function of how near the mean temperature is to stressful levels. Hokanson et al. (1977) found that temperature fluctuations within the preferred temperature range resulted in greater growth than constant temperatures with the same mean, but when the mean of the fluctuating regime exceeded the optimal temperature range, constant conditions resulted in greater growth than did the fluctuating regime.

Figure 4. Diagrammatic representation of complete thermal stress model.
One of the reasons for developing this model is to provide a tool that can be used to reduce the impact of power plant operations on fish populations. In order to be both protective and cost efficient, mitigative measures must become more responsive to short-term changes in plant operations and environmental conditions. For such a system to be effective, real-time monitoring must provide adequate warning for mitigative measures to be invoked prior to environmental impact. We believe this model, once fully developed and tested, will be able to forewarn of impending thermal effects before they occur and also serve as a basis for implementing effective regulatory criteria.

The model as currently configured still requires groundtruthing to assign biological meaning to the thermal stress index. We are currently performing laboratory experiments to better understand cumulative thermal stress and the relationships between the magnitude and duration of high temperature exposure and fish health effects. These experiments are variations on the standard CTM experiments, and the information derived from them will be used to calibrate the model and refine existing relationships.

The results derived from the laboratory experiments and model will provide a better understanding of the thermal ecology of fishes and better assessment of temperature effects at thermal outfalls and dam tailwaters resulting in (1) better temperature criteria development and (2) more accurate and timely monitoring. This tool will allow users to more precisely determine potential environmental effects and thus design and implement corrective measures that directly address specific problems.

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