

EFFECTS OF ELEVATED WATER TEMPERATURE ON FISH AND MACROINVERTEBRATE COMMUNITIES BELOW SMALL DAMS

JOANNA L. LESSARD* and DANIEL B. HAYES

Natural Resources Building, Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI 48824, USA

ABSTRACT

Many studies have investigated the ecological changes that occur below dams that release cold, hypolimnetic water, but very few studies have looked at the effects of the release of warm, surface waters. The effect of small, surface release dams on downstream thermal regimes is a major habitat concern for many cold-water systems, however. The objective of this study was to examine the effects of summer temperature increases due to impoundment on downstream fish and macroinvertebrate communities in cold-water streams. We sampled fish, macroinvertebrates and habitat upstream and downstream of dams on ten rivers during the summers of 1998 and 1999. Changes in mean summer temperature downstream varied from a cooling of 1 °C to an increase of more than 5 °C. Increasing temperatures downstream coincided with lower densities of several cold-water fish species, specifically brown trout (*Salmo trutta*), brook trout (*Salvelinus fontinalis*) and slimy sculpin (*Cottus cognatus*) while overall fish species richness increased downstream. Density of mottled sculpin (*Cottus bairdi*), another cold-water species, was not related to temperature changes below the dams. Macroinvertebrates showed shifts in community composition below dams that increased temperature. This study provides information useful for determining the extent of impact of these small, surface release dams, which are abundant across the country. Copyright © 2003 John Wiley & Sons, Ltd.

KEY WORDS: dams; water temperature; fish community; brook trout; brown trout; smily sculpin; macroinvertebrates; cold-water streams

INTRODUCTION

Dams provide many benefits to society (e.g. hydroelectric power, flood control, water level regulation), but they also have the potential to alter populations of aquatic organisms. Changes in fish populations due to impoundments are well documented, and occur through a variety of mechanisms. The best-known mechanism is the reduction in upstream migration that occurs where dams do not have adequate fish passage facilities (Holden, 1979; Ward and Stanford, 1987). Effects on fish migration are most obvious for anadromous fishes, and can greatly reduce or even extirpate local populations (Brooker, 1981; Ward and Stanford, 1987). Dams also affect downstream populations by changing water quality and habitat conditions. Changes in water quality and river habitat affect the biota in many ways, and can impact stream-resident fishes as well as migratory species.

Aquatic macroinvertebrates are also affected by habitat changes caused by dams (Armitage, 1979, 1984; Fraley, 1979; Harding, 1994). Effects of dams on macroinvertebrate communities are important because of the role that macroinvertebrates play in stream ecosystem function (Cummins, 1979; Cummins and Klug, 1979; Merritt *et al.*, 1984). In contrast to fish, aquatic insects have winged adult stages that allow for movement between stream sections. Direct impacts by dams on aquatic macroinvertebrate communities, therefore, may be principally due to alteration of habitat, while impacts on fish also include migration blockage.

The creation of an impoundment can alter numerous physical and chemical factors such as stream substrate, dissolved oxygen and water temperature (Cummins, 1979; Stanford and Ward, 1979; Ward and Stanford, 1979; Waters, 1995; Hayes, 1999). Dams affect substrate by acting as a sink for fine sediments (Ward

* Correspondence to: JoAnna L. Lessard, Department of Entomology, 243 Natural Science Building, Michigan State University, East Lansing, MI 48824, USA. E-mail: lessard4@msu.edu

Received 16 August 2001

Revised 23 March 2002

Accepted 29 April 2002

and Stanford, 1983a, 1987; Waters, 1995). Deep release dams often draw water from anoxic hypolimnion causing dissolved oxygen reductions downstream (Ward and Stanford, 1987). Depth of release also affects downstream temperature regime. Reduction in temperature below deep release dams has been thoroughly investigated (Stanford and Ward, 1979; Ward and Stanford, 1979, 1987; Armitage, 1984; Jensen, 1987). Even though the majority of dams in the United States are small surface release dams (National Research Council, 1992; Collier *et al.*, 1996), few studies have investigated the effects of the release of warm epilimnetic water on downstream communities.

Increased temperatures can have important consequences for stream organisms. Bioenergetic studies indicate a strong positive relationship between feeding rates and metabolism with temperature for both fish and insect communities (Gibbons, 1976; Wotton, 1995). Increased metabolic rate carries with it a need for increased levels of food quantity or quality in order to maintain growth and survival rates (Wotton, 1994). Also, temperatures must not exceed the biological preferences of typical cold-stenotherms (i.e. 20 °C) if cold-water fauna are to prosper downstream (Allan, 1995; Giller and Malmqvist, 1998; Taniguchi *et al.*, 1998).

This research documents how increases in stream temperature below small dams impact fish and macroinvertebrate communities. Our major objectives were to: (1) characterize how temperature increases due to impoundment affect the population density of selected cold-water fishes including: brown trout (*Salmo trutta*), brook trout (*Salvelinus fontinalis*), slimy sculpin (*Cottus cognatus*) and mottled sculpin (*Cottus bairdi*); and (2) characterize how the downstream fish and macroinvertebrate communities change with increasing temperatures. We hypothesized that densities of cold-water fish would be lower below dams that increased downstream temperatures, and that this decrease would be accentuated as temperatures rose above the physiological optimum of most cold-water fish and macroinvertebrates.

STUDY AREA

Three streams were sampled during the summer of 1998 and seven streams during 1999 (Table I). The study streams were broadly distributed throughout Michigan's lower peninsula (Figure 1) and were selected based on the following criteria: (1) a dam was present; (2) there was a resident trout population; (3) there was no operational fish ladder (to allow independent comparisons of upstream and downstream populations); and (4) all streams were wadable. The majority of streams were sampled at six sites, three upstream and three downstream of the dam. Two streams (Cedar Creek and White River) had only two downstream sites because the water was too deep for an additional site, resulting in a total of 58 sites. When possible, distances of 1

Table I. Mean summer temperature (°C), and impact of dams on temperature (above–below). Fish and macroinvertebrate community characteristics, and changes in community composition across stream reaches as indicated by Sorenson's similarity index

Stream	Temperature (°C)		Dam impact	Fish richness		Sorenson's similarity	Macroinvertebrate richness		Sorenson's similarity	EPT richness	
	Above	Below		Above	Below		Above	Below		Above	Below
Boardman	14.7	18.7	−4.0	4	13	0.47	22	20	0.71	12	11
Cedar	13.8	17.6	−3.8	5	10	0.00	20	17	0.54	10	7
Dowagiac	20.2	22.1	−1.8	20	14	0.53	21	23	0.59	12	8
Fish	23.0	25.0	−2.0	22	25	0.60	26	19	0.76	13	10
Manton	13.0	18.5	−5.5	7	18	0.48	21	22	0.51	12	10
Maple	16.8	15.8	1.0	21	11	0.63	31	26	0.84	12	11
Middle Branch	14.3	18.2	−3.9	15	16	0.77	26	20	0.65	12	8
Prairie	18.7	19.1	−0.4	14	15	0.90	19	21	0.85	11	11
Sugar	17.9	21.0	−3.1	13	22	0.46	24	20	0.55	10	9
White	15.6	19.0	−3.4	10	15	0.64	16	17	0.55	7	8
Mean	16.8	19.5	−2.7	13.1	15.9	0.55	22.6	20.5	0.65	11.1	9.3

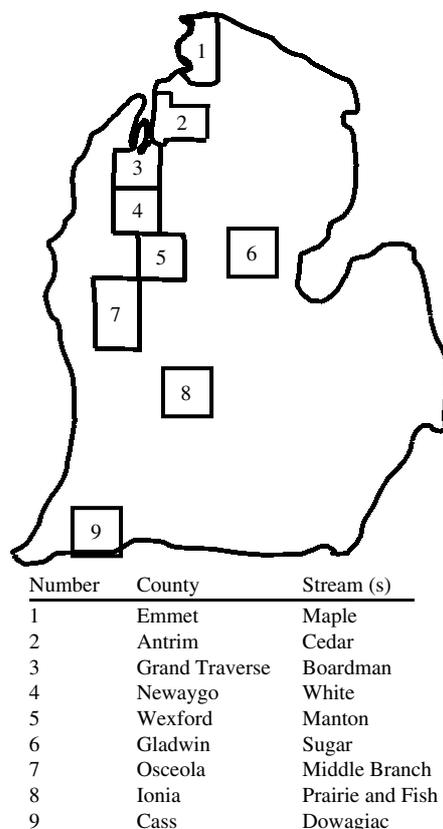


Figure 1. Counties in Michigan's lower peninsula where study streams are located

to 3 river kilometres separated sites, and no sites were selected within the impoundment. The first site below each dam was generally placed approximately 100 m downstream of the plunge pool.

METHODS

Study sites were 60 to 80 m long, generally ending at the boundary between two mesoscale habitat units (e.g. at the juncture of a riffle and a pool). Each site contained an upstream, downstream and middle transect. At each transect, wetted width, water depth and substrate size composition (Kondolf and Li, 1992) were measured. At the middle site above and below each dam (i.e. sites 2 and 5) water flow velocity was recorded.

Several water quality parameters also were measured at each site. Stream temperature, dissolved oxygen and conductivity were recorded on the day of biological sampling using a Yellow Springs Instruments (YSI) meter. Water samples were taken at each site for laboratory analysis of total phosphorus concentrations. Total phosphorus concentrations were determined by persulphate digestion (Valderrama, 1981) followed by ascorbic-molybdate colorimetry (Murphy and Riley, 1962). In 1999, Onset[®] temperature loggers were placed at the upstream and downstream sites proximal to the dam in each river. Hourly temperature readings were recorded from May to October for all ten streams.

Fishes were sampled at 56 sites and macroinvertebrates at all 58 sites. Fishes were sampled in deeper streams using a barge electroshocking unit and a backpack unit was used in shallower streams. To keep fish from moving in or out of the site while sampling, block nets were placed at the upstream and downstream boundaries. A multi-pass removal method was used to estimate the population size of our target species with a minimum of three passes (Van Deventer and Platts, 1983). All fishes caught were identified to species, and target species were counted. Generally three passes were sufficient to reduce the catch of trout in the

third pass to 50% or less than catch in the previous pass. If this wasn't the case, then additional passes were made until consecutive passes yielded a 50% or more reduction in trout. It was difficult to get a significant reduction in either species of sculpin, so total catch from all passes combined was used as a relative index of abundance for these species.

Three macroinvertebrate samples were collected from cobble and/or gravel substrates in riffles at each site using a modified Hess sampler (20 cm diameter with 250 μm mesh catch bag) (Merritt *et al.*, 1996). Invertebrates were washed from stream substrates into the sampler for two minutes, to standardize samples across substrate types. Samples were fixed with ethanol and transported to the laboratory for processing where one sample was randomly selected from each site (six per stream). These samples were dyed with rose bengal and passed through a 1 mm sieve. Samples were picked under a 10 \times magnifying lense, sorted and identified to the family level.

Data analysis

Mean summer temperature upstream and downstream of each dam was determined by first computing the mean summer temperature from the sites with the data loggers from 1 June to 31 August. Mean summer temperatures at sites without loggers were obtained via extrapolation from point measurements and loggers (Lessard, 2000). Mean summer temperature above and below each dam was calculated as the mean of all three sites in that section.

Habitat (physical and chemical) differences above and below the dams for each stream were estimated using a general linear model analysis. Analysis of habitat differences over all study streams as well as differences in macroinvertebrate family richness, Ephemeroptera, Plecoptera, Trichoptera (EPT) richness, and fish species richness, comparing above and below sections, was done using a mixed model analysis of variance (ANOVA), where stream was treated as a random effect and position was treated as a fixed effect.

$$y = \alpha + \beta x + b + e \quad (1)$$

where y is the parameter of interest, α is the intercept and overall mean, β is the slope and fixed effect of position, x is an indicator variable for position, b is the random effect of stream, and e is the error term.

A correlation analysis was run to investigate how each individual habitat parameter was related to macroinvertebrate, EPT and fish species richness. Next, stepwise regression (MaxR) (Hocking, 1976) was used to determine which habitat parameter(s) was the best predictor of each community parameter. To see what could be driving community changes downstream, another stepwise regression (MaxR) was run on macroinvertebrate and fish community differences and changes in select habitat parameters between sections.

To investigate the impact of the dams on fish and macroinvertebrate community composition, Sorensen's similarity index values (Sorensen, 1948) were computed comparing stream sections using the following equation:

$$QS = 2C/(A + B) \quad (2)$$

where QS is the index of community similarity, A is the number of taxa upstream, B is the number of taxa downstream, and C is the number of taxa common in both stream sections. Species level of taxonomic resolution was used for the fish community and family level was used for macroinvertebrates. Stepwise regression (MaxR) was used to see which habitat changes, if any, were related to fish and macroinvertebrate community similarity.

Population abundances of the two trout species (brown and brook) were estimated using Microfish (Van Deventer and Platts, 1985), a software program for removal methods. The population abundance for the two sculpin species (slimy and mottled) were estimated using total catch. Population densities (fish per hectare) for each species were calculated for each site. Preliminary analyses indicated that the mean density data were not linear and the variance was not homogeneous, therefore a \log_e transformation on the density estimates ($\text{Ln}(\text{density} + 1)$) was used to correct these problems. A correlation analysis was run and Pearson r -values were calculated for the transformed data and each habitat parameter. Using this analysis as a guide, stepwise

regression analysis (MaxR) was run to determine which habitat parameter(s) were most related to the mean $\ln(\text{density} + 1)$ of each species (referred to as brook, brown, slimy, and mottled).

A predictive model was developed for each species' density and the most related habitat parameter(s) (if there was a significant relationship) using a mixed modelling analysis of covariance (ANCOVA), where stream was treated as a random effect and position and habitat covariates were treated as fixed effects. Analyses were done on average densities within each position (above or below the dam).

RESULTS

Physical habitat characteristics varied widely among study streams with mean values ranging as follows: width (5.3 to 20.3 m), average depth per transect (11.7 to 65.3 cm), and discharge (0.4 to 21.8 m³ s⁻¹) (Lessard, 2000). Longitudinal habitat conditions followed predictable downstream trends including a widening and deepening of the channel and an increase in stream substrate size. The substrate in most of the study streams was dominated by sand and gravel in upstream reaches and sand, gravel, cobble mixtures in downstream reaches.

The chemical environment also varied substantially among study streams with phosphorus ranging from 9.4 to 61.7 µg L⁻¹, conductivity from 252 to 541 µS, and dissolved oxygen from 7.6 to 11.9 mg L⁻¹ (Lessard, 2000). Mean phosphorus and conductivity values did not show significant longitudinal trends between stream sections. Dissolved oxygen concentrations were always >80% saturation in our study streams and were not significantly different below the dams.

Mean summer water temperatures varied significantly between stream sections across all study streams. Temperatures ranged from 13.0°C to 23°C in upstream sections and from 15.8°C to 25°C in downstream sections (Table I). Averaging across all streams, downstream temperatures increased significantly from 16.8°C to 19.5°C. On a site by site basis, mean summer temperature increased below the dams and did not show a return to upstream temperatures, even at the site farthest downstream. Differences in temperature above and below dams ranged from a 1.0°C cooling downstream in the Maple River to a 5.5°C warming downstream in Manton Creek (Table I).

Fish species richness was generally higher downstream of the dams than upstream (Table I). Fish species richness was most correlated with mean summer temperature (Table II), but conductivity, total phosphorus, stream discharge, and modal substrate size were also strongly correlated with richness. Stepwise regression, however, indicated that temperature was the best single predictor of fish species richness ($p = 0.0001$, $R^2 = 0.49$, $n = 56$). Stepwise regression analysis on the relationship between changes in fish species richness between stream sections and changes in habitat showed that changes in richness were most related to the amount of warming downstream of the dams ($p = 0.003$, $R^2 = 0.79$, $n = 10$) (Figure 2).

Fish community similarity, comparing above and below sections, was 0.55 on average and ranged from 0 (Cedar Creek) to 0.90 (Prairie Creek) (Table I). Stepwise regression indicated that changes in mean depth, not temperature, were most related to fish community similarity ($p = 0.027$, $R^2 = 0.59$, $n = 10$). Streams that

Table II. Pearson's correlation coefficients (r) and corresponding p -values between fish species richness and stream habitat conditions

Habitat variable	Fish species richness		
	Pearson's r	P -value	Sample size(n)
Mean summer temperature	0.68	0.0001	56
Conductivity	0.58	0.0001	56
Total phosphorus	0.44	0.0015	49
Stream discharge	0.44	0.0160	30
Substrate mode	0.31	0.0192	56
Stream width	0.27	0.0478	56
Water depth	0.03	0.8242	56
Dissolved oxygen	-0.25	0.0690	56

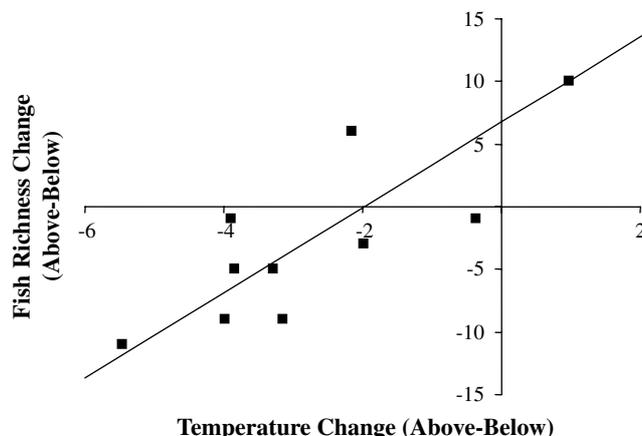


Figure 2. Regression of differences in fish species richness on differences in mean summer temperature (dam impact) between above dam and below dam reaches ($R^2 = 0.79$). Square symbols indicate where the data plot from the ten study streams

were significantly deeper downstream had lower similarity values. There was not a significant relationship between similarity and the difference in stream temperature between above and below stream sections. The data were highly variable, however, potentially obscuring an underlying relationship.

Across all streams, total trout density averaged 906 fish ha⁻¹ upstream and 268 fish ha⁻¹ downstream, a 70% decrease (Table III). Brook trout were present in six of the ten study streams and were not found below the dams in three of those streams. Brook trout density decreased from a mean of 346 fish ha⁻¹ above the dams to 12 fish ha⁻¹ below the dams. Brown trout were present in all ten streams and were not found below three of the dams. Brown trout density decreased from 560 fish ha⁻¹ above to 256 fish ha⁻¹ below. Slimy sculpin were present in four of the study streams and were not found below the dams in two of those streams. Slimy sculpin catch decreased from 569 fish ha⁻¹ above to 127 fish ha⁻¹ below. Mottled sculpin were caught in eight of the study streams and were not found below the dams in three of those streams. Mottled sculpin catch decreased from 329 fish ha⁻¹ above to 74 fish ha⁻¹ below.

Temperature was the most highly correlated habitat variable for both brook and brown trout density (Table IV). Based on the results of stepwise regression analysis, the best variable for predicting brook trout and brown trout density and slimy sculpin catch also was mean summer temperature ($p = 0.0001$, $R^2 = 0.57$;

Table III. Densities (in fish per hectare ± 1 standard error), for the four target fish species above and below the dams

Stream	Brook trout		Brown trout		Slimy sculpin		Mottled sculpin	
	Above	Below	Above	Below	Above	Below	Above	Below
Boardman	234 (44)	18 (13)	585 (125)	342 (111)	1124 (432)	277 (144)	0 (0)	0 (0)
Cedar	191 (76)	0 (0)	872 (185)	0 (0)	2264 (981)	0 (0)	0 (0)	0 (0)
Dowagiac	0 (0)	0 (0)	73 (67)	0 (0)	0 (0)	0 (0)	1079 (540)	0 (0)
Fish	0 (0)	0 (0)	23 (23)	0 (0)	0 (0)	0 (0)	52 (47)	0 (0)
Manton	2416 (1113)	19 (19)	2878 (466)	598 (162)	1475 (307)	0 (0)	11 (11)	22 (22)
Maple	497 (408)	84 (9)	147 (147)	749 (615)	824 (337)	990 (339)	0 (0)	4 (4)
Middle Branch	4 (4)	0 (0)	214 (62)	37 (37)	0 (0)	0 (0)	556 (164)	29 (15)
Prairie	0 (0)	0 (0)	76 (38)	55 (29)	0 (0)	0 (0)	482 (277)	347 (248)
Sugar	0 (0)	0 (0)	558 (306)	0 (0)	0 (0)	0 (0)	60 (34)	0 (0)
White	115 (68)	0 (0)	170 (59)	782 (372)	0 (0)	0 (0)	1049 (186)	338 (21)
Mean	346	12	560	256	569	127	329	74
Standard error	236	8	272	105	258	100	139	45

Table IV. Pearson's correlation coefficients (r) between Log_e transformed densities (fish per hectare) of the four target fish species, stream habitat conditions, and macroinvertebrate family richness. The number of sites (N) and the P -value for each relationship are also reported

Habitat variable	N	Brook trout		Brown trout		Slimy sculpin		Mottled sculpin	
		r	P -value	r	P -value	r	P -value	r	P -value
Mean summer temperature	56	-0.66	<0.001	-0.64	<0.001	-0.56	<0.001	-0.06	0.63
Conductivity	56	-0.61	<0.001	-0.44	<0.001	-0.62	<0.001	0.27	0.05
Total phosphorus	49	-0.49	<0.001	-0.48	<0.001	-0.42	<0.001	0.19	0.20
Stream discharge	30	-0.29	0.12	-0.55	<0.001	-0.23	0.23	-0.29	0.12
Substrate mode	56	-0.20	0.13	-0.28	0.04	-0.23	0.09	-0.03	0.82
Stream width	56	-0.20	0.15	-0.24	0.08	-0.02	0.86	-0.16	0.25
Water depth	56	-0.16	0.25	-0.34	0.01	0.03	0.83	-0.31	0.02
Macroinvertebrate richness	56	0.26	0.06	0.19	0.17	0.26	0.05	-0.02	0.90
Dissolved oxygen	56	0.35	0.01	0.28	0.04	0.35	0.01	-0.16	0.26

$p = 0.0001$ $R^2 = 0.43$; $p = 0.0001$ $R^2 = 0.45$ respectively). Mottled sculpin catch was not related to temperature or any of the habitat variables we measured.

Results from the mixed ANCOVA relating summer temperature to brook trout, brown trout and slimy sculpin density indicated that position (above or below the dam) was non-significant, so a reduced model was selected for all three species. The final mixed model relating temperature (T) to brook trout density was:

$$\text{Log}_e(\text{density} + 1) = 17.9 - 0.915(T) \quad (3)$$

No brook trout were found in sites with mean summer temperatures $>19^\circ\text{C}$ (Figure 3).

For brown trout, the relationship was:

$$\text{Log}_e(\text{density} + 1) = 14.73 - 0.602(T) \quad (4)$$

Brown trout were found at sites ranging up to 25°C , although few sites were sampled with temperatures greater than 25°C .

The relationship between slimy sculpin catch and temperature was:

$$\text{Log}_e(\text{catch} + 1) = 13.89 - 0.655(T) \quad (5)$$

Similar to brook trout, slimy sculpin were not found in sites with mean summer temperature $>20^\circ\text{C}$. For brook trout and brown trout the regression lines fit the data well, but it appears that other factors are likely also to play a role in determining slimy sculpin abundance (Figure 3).

Macroinvertebrate family richness was similar in stream reaches above and below dams (Table I). Correlation analysis indicated that none of the habitat parameters, including temperature, were significantly related to macroinvertebrate richness. Stepwise regression also was unable to reveal a model with any significant relationships. The EPT richness was significantly reduced ($p = 0.034$, $n = 58$, effect size = 1.8 families) downstream of the dams. Stepwise regression indicated that EPT was most related to stream size (width and depth) with wider, deeper sites having fewer families; high variability in the EPT data resulted in a model with low predictive power ($R^2 = 0.15$), however.

Macroinvertebrate family similarity between sections was 0.65 on average and ranged from 0.54 in Cedar Creek to 0.84 in the Maple River (Table I). Macroinvertebrate similarity was significantly related to mean summer temperature change ($R^2 = 0.64$, $p = 0.0057$, $n = 10$) (Figure 4). Larger increases in downstream temperatures coincided with lower macroinvertebrate community similarity between stream sections.

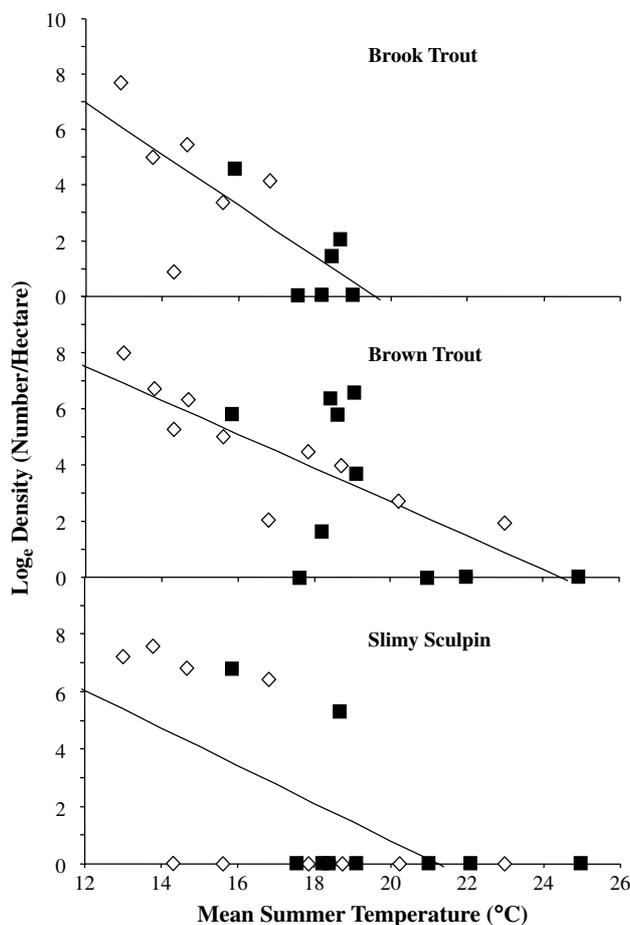


Figure 3. Mixed modelling analysis relating the \log_e transformed brook trout, brown trout and slimy sculpin population densities to mean summer temperature ($^{\circ}\text{C}$). Upstream (open diamonds) and downstream (closed squares) samples are indicated, but position was not significant. Brook trout model is based on the six streams that contained brook trout and the brown trout and slimy sculpin models are based on all ten study streams

DISCUSSION

Stream regulation (i.e. damming) alters the natural longitudinal flow of energy and materials, thereby altering the physical and chemical characteristics of downstream reaches and the biological community (Ward and Stanford, 1983a,b; Stanford and Ward, 2001). The serial discontinuity theory (Ward and Stanford, 1983a; Stanford and Ward, 2001) offers a hypothesis for the impact that a dam will have on downstream habitat and biota. This theory, however, was developed with the assumption that dams operate via hypolimnetic draw, and thus many of the conclusions, especially those involving predictions about water quality and biotic changes, run contrary to what we observed. In our streams, water quality variables that are often changed downstream of deep release dams, such as total phosphorus, conductivity and dissolved oxygen, were not significantly altered by the dams in our study.

Temperature increases below dams have been given little attention, and primarily have focused on impacts on the macroinvertebrate community (Fraleay, 1979; Ward and Stanford, 1979; Armitage, 1984; Harding, 1994; Wotton, 1995). It has been suggested that impacts on temperature are restricted to the area of stream directly below the impoundment and that temperatures quickly equilibrate with the air (Brooker, 1981). Without some cooling factor (e.g. groundwater recharge) downstream, however, reaches with increased summer temperatures are not able to shed added heat during the summer, but continue to warm according to normal stream processes

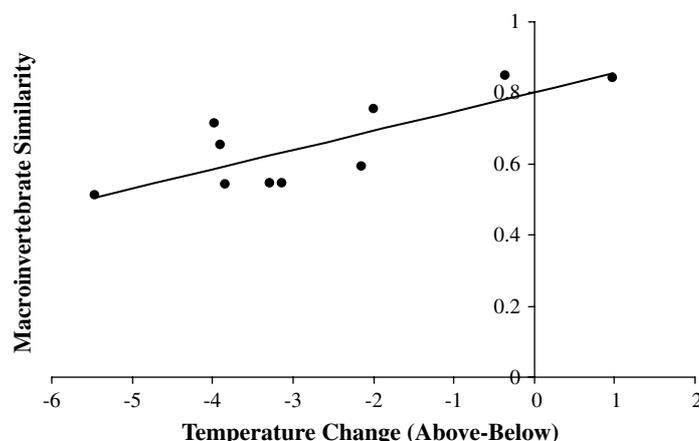


Figure 4. Regression of macroinvertebrate similarity between above and below sections on mean summer temperature change (i.e. dam impact) ($R^2 = 0.64$). Circle symbols indicate where the data plot from the ten study streams

(Boon and Shiers, 1976; Vannote *et al.*, 1980). This heat loading has the potential to maintain downstream temperatures above the range that cold-water stenotherms prefer. Fraley (1979) found significant summer temperature increases in the Madison River, Montana, that never returned to upstream temperatures even 56 km downstream of a surface release dam.

We focused on increases in mean summer temperature below dams, and how it related to alterations in downstream communities. Dams alter temperature in other ways (e.g. reduced diel fluctuation) and in other seasons, but it is during the summer that temperatures reach a maximum. Studies of trout densities and growth in relation to annual temperature parameters found significantly stronger relationships using summer versus winter mean temperatures (Hinz and Wiley, 1997). Fraley (1979) found that both temperature and diurnal temperature fluctuation were altered below a surface-release dam, but that diurnal temperature fluctuation returned to upstream values with increasing distance downstream of the dam. Temperature change, therefore, may be a more consistent indicator of thermal alteration for longer distances downstream.

Factors influencing temperatures below dams include the size of impoundment (specifically depth and surface area), residence time, whether or not the impoundment stratifies, and the release depth (Ward and Stanford, 1979; Brooker, 1981; Wotton, 1995). Although it was not a goal of our study to predict the amount of temperature impact for individual streams, the impacts we observed were likely due to differences in surface area, depth and residence time. Another important factor is the amount of groundwater coming in upstream and downstream of the dam (Allan, 1995; Giller and Malmqvist, 1998). These data, however, were not available for this study. A few of the dams in this study that had less of an impact on temperature, also tended to have warmer upstream temperatures. This was most likely due to the fact that these also were larger streams with more thermal inertia than smaller, cold, headwater streams (Vannote *et al.*, 1980).

Mean summer temperature was the best predictor of density for both trout species. Brook and brown trout are cold-water stenotherms that have positive growth between 4 and 20 °C, with upper lethal limits around 25 °C (Elliott, 1994; Allan, 1995; Marod, 1995). Brook trout catch and movement patterns have been related to the number of days temperature exceeded 16 °C (Marod, 1995), and in our study streams brook trout were never found above 19 °C. Brook trout were eliminated below the dams more often than brown trout. The former showed a 96% downstream decrease across all streams, while the latter were reduced by 54% downstream.

Both slimy and mottled sculpin are typically found in cold, shallow stream habitats and are usually associated with brook trout, although slimy sculpin are more consistently considered a headwater species (Scott and Crossman, 1973). Stream substrate and temperature together are considered the primary determinants for sculpin habitat suitability (Scott and Crossman, 1973). In this study, temperature was the best predictor of slimy sculpin abundance, but we were unable to determine what drives mottled sculpin abundance. Other

research investigating mottled sculpin abundance and habitat in Michigan was also unable to detect any significant relationships (Newman, 1999).

Position with respect to the dam was not an important factor in determining trout or sculpin abundance, indicating that the presence of a dam alone did not negatively impact these species. Instead, it was the alteration of downstream habitat away from biological preferences that appeared to be detrimental for these populations during the summer. Seasonal movement and distribution of these species throughout the year within each stream section (above or below) needs to be investigated to determine the importance of tributaries as thermal refugia in these types of streams. Under suboptimal thermal conditions, brook trout move into colder, headwaters or tributaries and then return to middle reaches in the fall and winter (Scott and Crossman, 1973; Marod, 1995). As emphasized by Hayes *et al.* (1998) cold headwater streams provide thermal refugia for brook trout in streams where lower reaches warm above 20 °C during the summer. Use of these refugia can enhance the overall growth and production for the stream as a whole. Brown trout also show behavioural movements in response to temperature (Elliott, 1994) but are able to remain competitive at warmer temperatures than brook trout (Taniguchi *et al.*, 1998). This may be why brown trout persisted in main channel, downstream reaches more often than brook trout in our streams. From our results and these other studies, it appears that a dam that increases downstream summer temperatures above 19 °C can be expected to severely limit brook trout populations, and if mean temperatures are increased above 20 °C all three species (brook trout, brown trout and slimy sculpin) are likely to be significantly reduced.

Diversity in streams is expected to increase as one moves from headwater areas to middle reaches and then decrease again toward the mouth (Vannote *et al.*, 1980). Ward and Stanford (1983a) postulated in the serial discontinuity theory that biotic diversity below a dam would decrease either from reduced detrital transport in headwater streams or from reduced temperature fluctuation in middle reaches. The pattern we observed in fish species richness did not follow this model. Fish species richness was almost always highest below the dams, particularly in streams with more warming (i.e. higher impact of the dam). Higher impact streams had significantly lower fish species richness upstream compared to downstream sections, while lower impact streams had similar numbers of species both above and below the dams. Viewing increased temperature as a disturbance, as defined by the intermediate disturbance hypothesis (Ward and Stanford, 1983b), these dams could be considered 'moderate disturbances' of the downstream community. This was because temperatures did not rise into the lethal range for most cool- and warm-water fish species, thereby allowing for an increase in richness downstream. So while the influence of these dams on cold-water fish populations was clearly detrimental, the impact on the fish community from a richness standpoint may be less so.

In a study of low-head barriers, Dodd (1999) observed that fish species richness peaked just below barriers and then declined with increasing distance downstream, toward what was observed for uninterrupted streams. These barriers did not alter habitat and the peak below was attributed to a pooling of fish species at the barrier (Dodd, 1999). Aggregation of fish species attempting to move upstream may have played a role in our study streams as well, but the fact that fish species richness remained elevated with increasing distance downstream, particularly in higher impact streams, indicated that temperature was probably more important. Considering the strong relationship between temperature and fish richness, it seems reasonable to conclude that changes in mean summer temperature below these types of dams are critical in determining how diverse the fish community downstream will be.

Studies comparing rivers across the globe have shown macroinvertebrate family richness to be linearly related with stream temperature, with diversity increasing with increasing temperature (Jacobsen *et al.*, 1997). Macroinvertebrate community similarity, however, was significantly related to differences in mean summer temperature and richness was not. The fact that macroinvertebrate richness was not significantly different between stream sections suggested that it was not a change in richness downstream causing lower similarity, but rather a replacement of taxa. The relationship between similarity and level of impact points to temperature as the primary reason for this replacement. Macroinvertebrates, however, often show shifts in habitat preferences along environmental gradients within a family, and so identification to the species level may have shown a different relationship (Fraleley, 1979; Hauer *et al.*, 2000). Fraleley (1979) found a decrease in macroinvertebrate genus diversity directly below a surface release dam, and then increases in diversity, toward upstream levels, at sites further downstream.

SUMMARY AND CONCLUSIONS

Stream habitats change from headwater reaches to the mouth, and dams are known to alter certain habitat parameters so that the normal continuum is disrupted. Mean summer temperature was the only stream habitat parameter that was significantly different between upstream and downstream sections away from what would be predicted for unregulated streams. In general, mean summer temperature was substantially increased downstream by these small, surface release facilities. These increases in temperature were maintained at least 2–3 km below the dams. Downstream communities responded to warming below dams with shifts in the macroinvertebrate community, increased fish species richness, and reductions in brown trout, brook trout and slimy sculpin population densities.

In order to retain viable cold-water fisheries downstream of these types of dams, alteration of the dam operation appears necessary. Releasing water from the metalimnion or hypolimnion, in stratified reservoirs is one option. Many of these dams, however, are small facilities, with reservoirs that may not stratify. Another complication is that dams require frequent upkeep to retain their physical integrity and public safety. Many communities nationwide are facing decisions about the future of their local dams as these types of facilities deteriorate with age and come up for re-licensing. During these processes, the removal of such dams should be seriously considered. Communities need to consider the environmental and economical costs when making decisions about dam maintenance, fishery management, and dam removal.

ACKNOWLEDGEMENTS

The authors thank the Michigan Department of Natural Resources for funding support. Special thanks to Dr Richard W. Merritt for his advice throughout this project and assistance with macroinvertebrate identification as well as for reviewing earlier drafts which improved this paper greatly. The helpful reviews of J. D. Allan and an anonymous reviewer are gratefully acknowledged.

REFERENCES

- Allan JD. 1995. *Stream Ecology: Structure and Function of Running Waters*. Chapman and Hall: London.
- Armitage PD. 1979. Stream regulation in Great Britain. In *The Ecology of Regulated Streams*, Ward JV, Stanford JA (eds). Plenum Press: New York; 257–272.
- Armitage PD. 1984. Environmental changes induced by stream regulation and their effect on lotic macroinvertebrate communities. In *Regulated Rivers*, Lillehammer A, Saltveit SJ (eds). Oslo University Press: Oslo, Norway; 139–165.
- Boon PJ, Shiers SW. 1976. Temperature studies on a river system in North-East England. *Freshwater Biology* **6**: 23–32.
- Brooker MP. 1981. The impact of impoundments on the downstream fisheries and general ecology of rivers. *Advances in Applied Biology* **6**: 91–152.
- Collier M, Webb RH, Schmidt JC. 1996. *Dams and rivers: a primer on the downstream effects of dams*. US Geological Survey Circular 1126: Tucson, AZ.
- Cummins KW. 1979. The natural stream ecosystem. In *The Ecology of Regulated Streams*, Ward JV, Stanford JA (eds). Plenum: New York; 7–24.
- Cummins KW, Klug MJ. 1979. Feeding ecology of stream invertebrates. *Annual Review of Ecological Systems* **10**: 147–172.
- Dodd HR. 1999. The effects of low-head lamprey barrier dams on stream habitat and fish communities in tributaries of the Great Lakes. M S Thesis, Michigan State University: East Lansing MI.
- Elliot JM. 1994. *Quantitative Ecology and the Brown Trout*. Oxford University Press: New York.
- Fraley JJ. 1979. Effects of elevated stream temperatures below a shallow reservoir on cold-water macroinvertebrate fauna. In *The Ecology of Regulated Streams*, Ward JV, Stanford JA (eds). Plenum: New York; 257–272.
- Gibbons JW. 1976. Thermal alteration and the enhancement of species populations. In *Thermal Ecology II*, Esch GW, McFarlane RW (eds). ERDA Symposium Series (CONF-750425).
- Giller PS, Malmqvist B. 1998. *The Biology of Streams, Rivers*. Biology of Habitats No. 4. Oxford Press: New York.
- Harding JS. 1994. Variations in benthic fauna between differing lake outlet types in New Zealand. *New Zealand Journal of Marine and Freshwater Research* **21**: 417–427.
- Hauer FR, Stanford JA, Giersch JJ, Lowe WH. 2000. Distribution and abundance patterns of macroinvertebrates in a mountain stream: an analysis along multiple environmental gradients. *Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie* **27**: 1485–1488.

- Hayes DB. 1999. Issues affecting fish habitat in the Great Lakes Basin. In *Great Lakes Fishery Policy and Management: a Binational Perspective*, Taylor WW, Ferreri CP (eds). Michigan State University Press: East Lansing, MI; 209–237.
- Hayes DB, Taylor WW, Drake MT, Marod SM, Whelan GE. 1998. The value of headwaters to brook trout (*Salvelinus fontinalis*) in the Ford River. In *Headwaters: Water Resources and Soil Conservation. Proceedings of Headwater '98, the Fourth International Conference on Headwater Control*, Merano, Italy, Haigh MJ, Krecek J, Rajwar GS, Kilmartin MP (eds). Oxford and IBH Publishing Co: New Delhi, India; 175–185.
- Hinz LC, Wiley MJ. 1997. Growth and production of juvenile trout in Michigan streams: influence of temperature. Fisheries Division Research Report No. 2041.
- Hocking RR. 1976. The analysis and selection of variables in linear regression. *Biometrics* **32**: 1–50.
- Holden PB. 1979. Ecology of riverine fishes in regulated stream systems with emphasis on the Colorado River. In *The Ecology of Regulated Streams*, Ward JV, Stanford JA (eds). Plenum: New York; 57–74.
- Jacobsen D, Schultz R, Encalada A. 1997. Structure and diversity of stream invertebrate assemblages: the influence of temperature with altitude and latitude. *Freshwater Biology* **38**: 247–261.
- Jensen AJ. 1987. Hydropower development of salmon rivers: Effect of changes in water temperature on growth of brown trout (*Salmo trutta*) psmolts. In *Regulated Streams Advances in Ecology*, Craig JF, Kemper JB (eds). Plenum Press: New York; 207–218.
- Kondolf GM, Li S. 1992. The pebble count technique for quantifying surface bed material size in instream flow studies. *Rivers* **3**: 80–87.
- Lessard JL. 2000. Temperature effects of dams on cold-water fish and macroinvertebrate communities. MS Thesis, Michigan State University, East Lansing, MI.
- Marod SM. 1995. The influence of temperature and discharge on movement patterns of brook trout, *Salvelinus fontinalis*, in the Ford River, Dickinson County, Michigan. MS Thesis, Michigan State University, East Lansing MI.
- Merritt RW, Cummins KW, Burton TM. 1984. The role of aquatic insects in the cycling of nutrients. In *The Ecology of Aquatic Insects*, Resh VH, Rosenberg DM (eds). Praeger Publishers: New York; 134–163.
- Merritt RW, Resh VH, Cummins KW. 1996. Design of aquatic insect studies: Collecting, sampling and rearing procedures. In *An Introduction to the Aquatic Insects of North America* (second edition), Merritt RW, Cummins KW (eds). Kendall/Hunt: Dubuque, Iowa; 12–28.
- Murphy J, Riley LP. 1962. A modified single solution method for the determination of phosphate in natural waters. *Analytica Chimica Acta* **27**: 31–36.
- National Research Council. 1992. *Restoration of aquatic ecosystems: science, technology, and public policy*. National Academy Press: Washington, DC.
- Newman KR. 1999. Effects of changing land cover and human development on the fish and hydrology of the Huron River watershed. PhD Dissertation, Michigan State University, East Lansing, MI.
- Scott WB, Crossman EJ. 1973. *Freshwater Fishes of Canada*. Bulletin of the Fisheries Research Board of Canada No. 184.
- Sorenson T. 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content. *Kongelige Danske Videnskaberne Selskabs Skrifter* **5**: 1–34.
- Stanford JA, Ward JV. 1979. Dammed rivers of the world: symposium rationale. In *The ecology of regulated streams*. In *The Ecology of Regulated Streams*, Ward JV, Stanford JA (eds). Plenum: New York; 1–6.
- Stanford JA, Ward JV. 2001. Revisiting the serial discontinuity concept. *Regulated Rivers: Research and Management* **17**: 303–310.
- Taniguchi Y, Rahel FJ, Novinger DC, Gerow KG. 1998. Temperature mediation of competitive interactions among three fish species that replace each other along longitudinal stream gradients. *Canadian Journal of Fisheries and Aquatic Science* **55**: 1894–1901.
- Valderrama JC. 1981. The simultaneous analysis of total nitrogen and total phosphorus in natural waters. *Marine Chemistry* **10**: 109–122.
- Van Deventer JS, Platts WS. 1983. Sampling and estimating fish populations from streams. *Transactions of the North American Wildlife and Natural Resources Conference* **48**: 349–354.
- Van Deventer JS, Platts WS. 1985. A computer software system for entering, managing, and analyzing fish capture data from streams. US Department of Agriculture, Forest Service. Intermountain Forest and Range Experimental Station Research Note INT-352: Ogden, UT.
- Vannote RL, Minshall GW, Cummins KW, Sedell JR, Cushing CE. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Science* **37**: 130–137.
- Ward JV, Stanford JA. 1979. Ecological factors controlling stream zoobenthos with emphasis on thermal modification of regulated streams. In *The Ecology of Regulated Streams*, Ward JV, Stanford JA (eds). Plenum: New York; 35–56.
- Ward JV, Stanford JA. 1983a. The serial discontinuity concept of lotic ecosystems. In *Dynamics of Lotic Ecosystems*, Fontaine TD, Bartell SM (eds). Ann Arbor Science: Ann Arbor, MI; 29–42.
- Ward JV, Stanford JA. 1983b. The intermediate-disturbance hypothesis: An explanation for biotic diversity patterns in lotic ecosystems. In *Dynamics of Lotic Ecosystems*, Fontaine TD, Bartell SM (eds). Ann Arbor Science: Ann Arbor, MI; 347–356.
- Ward JV, Stanford JA. 1987. The ecology of regulated streams: Past accomplishments and directions for future research. In *Regulated Streams Advances in Ecology*, Craig JF, Kemper JB (eds). Plenum Press: New York; 391–409.
- Waters TE. 1995. *Sediment in Streams: Sources, Biological Effects and Control*. American Fisheries Society: Bethesda, Maryland.
- Wotton RS. 1994. Particulate and dissolved organic matter as food. In *The Biology of Particles in Aquatic Systems*, Wotton RS (ed.). Lewis: Boca Raton, FL.
- Wotton RS. 1995. Temperature and lake-outlet communities. *Journal of Thermal Biology* **20**: 121–125.