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[Note]

Do Brown Trout Choose Locations with Reduced Turbulence?

ALINE J. COTEL*
Department of Civil and Environmental Engineering, University of Michigan, Ann Arbor, Michigan 48019, USA

PAUL W. WEBB
School of Natural Resources and the Environment, University of Michigan, Ann Arbor, Michigan 48019, USA

HANS TRITICO
Department of Civil and Environmental Engineering and School of Natural Resources and the Environment, University of Michigan, Ann Arbor, Michigan 48019, USA

Abstract.—The physical habitat requirements of cover, depth, and current speed for brown trout *Salmo trutta* are associated with high shear zones in stream flows, which in turn result in high turbulence. Observations were made on current speeds and turbulence intensity (TI) in a sand-bed trout stream. Exemplary transects showed that current speeds ranged from 0 to 60 cm/s and that TI ranged from 0 to 0.7. Turbulence intensity was inversely related to current speed. Brown trout were usually found in the lower 5 cm of the stream, where shear forces result in high turbulence. Locations occupied by brown trout had lower TI than similar locations without brown trout but higher TI than is typical of an average stream.

Current velocity, water depth, substrate, cover, and shade are major features used to codify the physical habitat requirements for many species of salmonids as indicated, for example, by habitat suitability indices (HSI), habitat diversity criteria (HSC), and the habitat probabilistic index (HPI) (Raleigh 1982; Raleigh et al. 1986; Baker and Coon 1995; Girard et al. 2003; Guay et al. 2003; Williams et al. 2004).

Turbulence is also a physical characteristic of streams (Hawkins et al. 1993). As seen in laboratory situations locations chosen by fishes are affected by the levels of turbulence (Pavlov et al. 1982, 1983, 2000; Shtaf et al. 1983; Pavlov and Tyurukov 1988; Odeh et al. 2002; Enders et al. 2003; Liao et al. 2003). Smith (2003) and Smith et al. (2005) showed that trout, while apparently attracted to shear zones, chose locations with reduced turbulence. However, there are relatively few observations on turbulence in streams or on the effects of turbulence on the choice of locations by trout in their natural habitat.

The present research, addresses two questions to determine whether turbulence affects habitat choice by brown trout *Salmo trutta* in a sand-bed stream (Table 1). First, is turbulence lower in locations occupied by brown trout than in otherwise similar locations unoccupied by brown trout? Second, how do levels of turbulence in locations occupied by brown trout compare with those in other sections available within the same stream? The second question is an essential corollary to the first because hydrodynamic theory suggests that optimal habitat requirements (HIS, HSC, and HPI) place brown trout in high turbulence situations. As such, there may be limited choices, if any, for brown trout to avoid turbulence in natural settings.

Methods

Stream habitat.—Observations were made within a 500-m reach of the west branch of the Maple River in Emmet County, Michigan, during July and August 2002, 2003, and 2004. The West Maple River is a third-order, cold-water stream, with substantial input of cold groundwater supplemented with surface input from wetlands (Wiley et al. 2002; Zorn et al. 2002). The predominant land cover is mixed hardwood, with aspen *Popolus tremuloides*, red pine *Pinus resinosa*, and beech *Fagus grandifolia* shading much of the stream.

Stream habitat composition (Bain and Stevenson 1999) was based on detailed analysis of a 50-m stretch of stream 6–12 m in width within the 500-m reach studied in 2002. Observations were made at grid points occurring at 2-m intervals along the thalweg, and 1-m intervals along transects from bank to bank at each 2-m intervals. At each point, substrate, cover, usually occurring as instream large woody debris (LWD), and the presence of aquatic plants (primarily *Vallisneria americana*) were recorded. In addition, water depth and mean current speed were measured. Mean current speed in the water column was measured at 60% of the total depth from the water surface by means of a Marsh-McBirney electromagnetic flowmeter (model

* Corresponding author: acotel@umich.edu

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TABLE 1.—Summary of observations and methods used to determine turbulence intensity in brown trout habitat to compare current speed and turbulence intensity (1) between locations with and without fish and (2) between locations with fish and typical stream locations; ADV = acoustic Doppler velocimetry.

Measurement(s)	Fish versus no fish 2002	Fish versus no fish 2003	Fish versus streamwide (2004)
Measurement of turbulence intensity (TI) and current speed (u) at the nose of brown trout in natural habitat locations. Water depth, temperature, cover, presence of aquatic plants (primarily *Vallisneria americana*), local bathymetry, and substrate also recorded.	Using Marsh-McBirney flowmeter	Using Marsh-McBirney flowmeter	Using ADV
Measurement of TI and u at similar locations in which no trout were seen.	Using Marsh-McBirney flowmeter	Using Marsh-McBirney flowmeter	
Measurement of u and TI throughout the water column at 1-m intervals across the stream to determine typical ranges for a small sand-bed trout stream.			Using ADV
Calculation of discharge from measurement of mean current speed at 60% of depth at 1-m intervals across the stream.	At three locations using Marsh-McBirney flowmeter	At three locations using Marsh-McBirney flowmeter	Obtained from ADV data for whole water column
Stream habitat composition recorded at 2-m intervals along the thalweg and 1-m cross-stream intervals for a typical 50-m reach. Mean current speed at 60% of depth, water depth, temperature, cover, presence of aquatic plants, local bathymetry, and substrate recorded.	Current speed recorded using Marsh-McBirney flowmeter		

2000). Current speed was sampled at 20 Hz for a 2-min period. The Marsh-McBirney flowmeter sensor head was 35 mm in diameter and was precise to ± 2% of mean current speed. The flowmeter was deployed on a wading pole and oriented upstream, avoiding possible interference of the pole on the flow near the sensor. These data were used to describe the coarse-scale stream features at each grid point: run, riffle, shallow sandbar and shallow margin (Bain and Stevenson 1999).

Discharge.—Discharge was determined for each year. In 2002 and 2003, the mean current speed was measured as described above at 1-m intervals across three stream cross-sections. In 2004, the current speeds were determined by means of an acoustic Doppler velocimeter (ADV, Sontek Field ADV Serial Number A525). We took measurements throughout the water column at 1-m intervals across the stream at two locations. These measurements were needed to determine the range of turbulence intensity (TI) and current speed available within a stream as described below. The mean current speeds at 60% of the water depth were summed for the 1-m intervals across the stream to obtain discharge (Bain and Stevenson 1999).

Turbulence.—Turbulence is most commonly quantified in studies using fishes in terms of a nondimensionalized measure of variation in velocity magnitude relative to the local average speed where the measurement is made (Sanford 1997; Pavlov et al. 2000; Odeh et al. 2002). This statistical measure of turbulence is defined as the turbulence intensity, TI, which is derived from the following equation:

$$TI = \sigma / u_{\mathrm{local}}, \tag{1}$$

where σ = the standard deviation of the instantaneous velocity and u_{local} = the average local current speed.

As mentioned above, we switched to using the ADV in 2004 to measure current velocity and its variation. The ADV is used in field situations to sample velocities from 0.1 to 250 cm/s within a standard cylindrical sampling volume with a diameter of 6 mm and a height of 9 mm (e.g., Kraus et al. 1994; Nikora and Goring 1998, 2000; Nikora et al. 2002a, 2002b). The ADV uses the principle of the Doppler effect to measure velocity, detecting changes in wave characteristics caused by the flow of the water relative to a 10 MHz carrier wave. The typical noise level is 1% of the velocity range when transmitting data at 25 Hz, as in this application. At this rate we recorded more than 1,800 instantaneous measures of velocity from the ADV for each sample location. Mean velocity was determined at each location and TI was calculated from equation (1). The ADV was supported on a tripod, and oriented in the direction of the overall stream flow. The tripod was arranged with two upstream legs, spread maximally to be as far as possible from the flow incident to the sensor volume. Therefore, there was no interference between the sampling volume and the legs of the tripod. Data from the ADV were filtered (Wahl 2000) to reduce signal to noise ratios (SNR) by removing measurements less than 15 and were despiked with the phase space de-spiking method described by Goring and Nikora (2002).

Fish.—Brown trout were located by snorkeling.

Two snorkelers moved side-by-side slowly upstream over the 500-m stream length (Smith 1994; Dolloff et al. 1996; McMahon et al. 1996). Some brown trout darted into cover, but most did not appear to notice the snorklers.

When a brown trout was found, it was observed for at least 2 min to ensure that it was holding station at that location and was not affected by the observer's presence. Brown trout were often found at the same locations on successive days, but data were only obtained once. Total length (TL) was estimated to about the nearest 2 cm (Dolloff et al. 1996). The accuracy of estimates was determined using fish-shaped objects of known length in typical stream situations. The positions of the noses of the brown trout relative to the location in the stream were recorded. Water depth, temperature, cover, local bathymetry and substrate also were recorded. Measurements of current velocity and its variation were made as described above while the snorkelers continued upstream to locate another brown trout.

Fish locations (2002 and 2003 observations).—The question of whether brown trout were found in locations with lower turbulence than similar locations lacking fish was addressed by measuring TI at the nose positions of brown trout and comparing these with minimal values measured in similar no-fish locations. Observations were made over 7 d in July 2002 and 14 d in July–August 2003. A brown trout location was sampled only once.

When a brown trout was located by snorkelers, the Marsh-McBirney flowmeter was deployed at the position of the fish's nose, and current speed (u_{nose}) and TI were measured. Water depth, temperature, stream cover (e.g., large woody debris [LWD]), the presence of aquatic plants (primarily *V. americana*), local bathymetry and substrate also were recorded.

All brown trout occupied substratum dips over a sandy bottom with some gravel, at locations that were shaded and had instream cover, usually as LWD, but lacking aquatic plants. Differences occurred among brown trout locations in u_{nose}, TI, water depth and brown trout length. Multiple regression with TI as the dependent variable was used to show that alternative or confounding factors, such as length and water depth, were not key explanatory factors for our experimental design. The relationship between current speeds and TI was best described as a power function, so that log-transformed current speed and TI were also examined using regression analysis. Only u_{nose} proved to have a significant effect on TI and the best fit relationships between these two variables was determined using nonlinear regression analysis.

No-fish locations (2002 and 2003 observations).—During the sampling period each year, snorkelers also identified locations that were as similar as possible to the occupied locations but lacking brown trout. Before using data from these no-fish locations, repeated observations were made to ensure that trout were absent from these sites. At no-fish sites, u_{local} and TI were measured using the Marsh-McBirney flowmeter at several positions, each of which was typical of locations chosen by brown trout. We conservatively report the smallest TI values for these no-fish locations. Water depth, temperature, stream cover, presence of aquatic plants, local bathymetry, and substrate also were recorded. Relationships among variables differing among no-fish sites were examined as described above for fish sites.

Comparisons of fish and no-fish locations (2002 and 2003 observations).—While multiple regression showed relationships among variables within the fish and no-fish sites, differences between brown trout and no-brown-trout locations were further tested for significance by means of analysis of covariance (ANCOVA; Zar 1997) with current speed and depth as covariates.

TI variation for exemplary stream transects (2004).—Two transects were found that included the range of habitat features typical of the trout stream as determined from the stream survey in 2002. Measurements of u_{local} and TI were made at 1-m intervals across the stream at each transect, and at heights above the substratum of 1, 3, 5, 10, 15, 20, 30, 40, and 50 cm, as applicable. No measurements were made within 10 cm of the water surface as the volume needed to measure velocity by the ADV lies 10 cm below the transducers. These data were also used to determine the mean water-column current speed at 60% of the water depth at 1-m intervals in order to calculate discharge as described above (Bain and Stevenson 1999). These measurements were made for three stream cross-sections in 2002 and 2003, and two stream cross-sections in 2004.

TI variation and fish locations (2004 observations).—Brown trout were located as described above for 2002 and 2003. Values for u_{nose} and TI for 17 brown trout were compared with data from the years 2002 and 2003.

The relationships between TI, u_{local}, and u_{nose} also were analyzed and compared as described above for fish and no-fish locations.

Results

Stream Habitat

The 500-m length of stream was comprised of pools and runs, shallow sandbars often supporting patches of *V. americana*, and edge habitat. In the intensively sampled 50-m length of stream, pools occupied 35% of the reach area, with mean water column current speed

(60% of depth averaging 13.5 ± 0.2 cm/s [mean ± 2 SEs]) and depths averaging 49.0 ± 0.4 cm. Depths for runs were smaller, averaging 33.3 ± 0.5 cm while average current speeds for the water column were larger averaging 24.3 ± 0.2 cm/s. The runs represented 33% of the 50-m reach area. Shallow areas with *V. americana* represented 24% of the reach area, with water-column mean current speeds of 14.2 ± 4.2 cm/s and depth 22.2 ± 0.4 cm. Shallow edge habitat, which was a shallow, mucky area of the stream lacking aquatic plants, totaled 8% of the sampled reach area. Mean current speeds for the water column of edge habitat were 10.0 ± 0.7 cm/s and mean depth was 10.9 ± 0.6 cm. Large woody debris was present in 20% of locations sampled. Overall, the stream was typical of other Michigan sand-bed streams (Wiley et al. 2002; Zorn et al. 2002).

Fish

Three species of trout were found in the West branch of the Maple River: brown trout, brook trout *Salvelinus fontinalis*, and rainbow trout *Oncorhynchus mykiss*. Data are reported here only for the most abundant species, brown trout. Mottled sculpin *Cottus bairdii* and Johnny darter *Etheostoma nigrum* also were observed.

Over the 3 years of sampling, observations were made on brown trout ranging in total length from 5 to 25 cm. Brown trout were found in water with depths ranging from 16 to 57 cm and values of u_{nose} ranging from 1 to 37 cm/s with a mean of 14 ± 3 cm/s. All locations where brown trout were present were shaded and had cover in the form of LWD. No brown trout were found in locations with aquatic plants. Physical attributes generally were within the range considered optimal in use-based and bioenergetics-based HSC (Baker and Coon 1995).

All brown trout were found in dips in the substratum, which were predominantly comprised of sand but which sometimes contained small amounts of gravel. Of these brown trout, 40% were seen on the upstream slope, 27% at the deepest point of a dip, 13% on ledges created by embedded solid materials on the side of a dip, 10% associated with LWD located above the streambed, and 10% were found in various other locations. The few brown trout swimming at increased heights above the bottom were seen within logjams. The distance between the ventral surface of the brown trout and the stream bottom ranged from 0 to 15 cm, with a mean of 2.3 cm, and a modal height of 0 cm. The noses of the brown trout were from 1 to 16 cm from the bottom. Eighty-five percent of these nose-points were within 5 cm of the bottom. Thus, brown trout were found in habitats where shear rates were expected to be high.

Most brown trout (80%) swam with steady undulations of the body and caudal fin, even when in contact with the bottom. The remaining brown trout rested on the bottom in the parr posture (Arnold et al. 1991) without swimming motions. One brown trout was observed using the Kármán gait (Liao et al. 2003) and another sat on the bottom, leaning against LWD, a stabilizing posture seen in laboratory situations (Eidietis et al. 2002). All these behaviors are typical in our observations of healthy fishes in other field situations.

Fish Locations (2002 and 2003 Observations)

All sampled sites occupied by brown trout were typical of a sand-bed stream, in that fish were found in substratum dips over a sandy bottom with some gravel. Sites were shaded and instream cover was present usually as LWD, but *V. americana* was absent.

Current speed at the nose, TI, and other habitat variables (Table 1) were measured for 20 brown trout in 2002 and 14 in 2003 with the Marsh-McBirney flowmeter. Brown trout were solitary, except in 2002 when one group of three and another of four brown trout were found sharing a habitat. In these situations, u_{nose} and TI were measured for lead (upstream) brown trout.

At each location we also measured and noted the variability in water depth and brown trout length. Multiple regression using TI as the dependent variable showed no significant relationships between TI and brown trout length and water depth (multiple linear regression, $P > 0.65$). In addition, brown trout length was not correlated with u_{nose}, water depth, or other physical variables (Table 1) (multiple linear regression, $P > 0.5$ and Pearson Correlation followed by Bonferroni test for significance, $P > 0.1$). Thus brown trout location varied with TI and u_{nose}.

For 2002 and 2003, TI ranged from 0.03 to 11 while u_{nose} ranged from 1 to 29 cm/s. Standard deviation increased with u_{nose}, with a value of 0.6 cm/s for u_{nose} of 1.6 cm/s for the three lowest u_{nose} values in 2002 and a value of 1.3 cm/s at u_{nose} of 24 cm/s for the top three values of u_{nose}. The TIs for these data were 0.41 and 0.06, respectively. Thus TI was relatively lower at higher current velocities; that is, the variation in current velocity increased at a slower rate than that of current velocity itself.

The TI was significantly related to u_{nose} ($P < 0.01$), the relationship for both 2002 and 2003 being best described (maximum R^2) by a negative power function. Thus TI decreased with u_{nose} according to the following equations (Figure 1a, b):

$$2002: TI = (0.71 \pm 0.26) u_{\text{nose}}^{-0.64 \pm 0.24} \quad R^2 = 0.877, P < 0.01; N = 20 \tag{2}$$

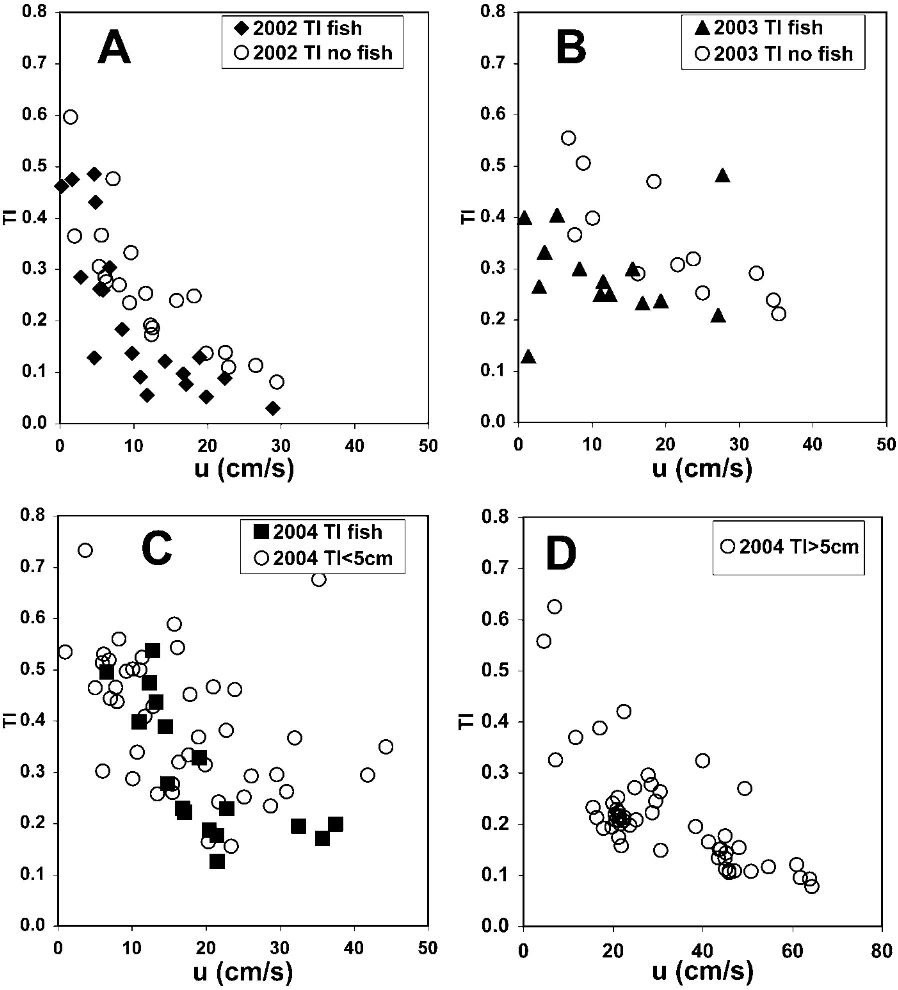

FIGURE 1.—Relationships between turbulence intensity (TI) and current speed (u) for various locations with brown trout and similar locations with no fish. The relationships between TI and the current speed at the fish's nose are shown by solid symbols for **(A)** 2002, **(B)** 2003, and **(C)** 2004; open symbols show the relationships between TI and average local current speed for the sites without fish in 2002 and 2003 as well as those for TI values within 5 cm of the bottom at sandy sites with large woody debris in 2004. The relationships were significantly lower for locations with fish than for those without fish (ANCOVA; $P <$ 0.001). Panel **(D)** shows the relationship between TI and average local current speed more than 5 cm from the bottom at sandy sites with large woody debris in 2004.

$$2003: TI = (0.39\pm0.06)u_{\text{nose}}{}^{-0.15\pm0.08} \quad R^2 = 0.9827, P<0.01; N = 14. \tag{3}$$

No-Fish Locations (2002 and 2003 Observations)

By design, we selected no-fish locations that had physical features as similar as possible to those of the sites occupied by brown trout (i.e., sandy dips with occasionally some gravel that were shaded and had LWD cover but lacked *V. americana*).

For no-fish sites, the minimal values of TI declined with u_{local} (Figure 1a, b) in the same way as between u_{nose} and TI, that is,

$$2002: TI = (0.65\pm0.14)u_{\text{local}}{}^{-0.43\pm0.12} \quad R^2 = 0.947, P<0.01; N = 21 \tag{4}$$

$$2003: TI = (1.16\pm0.47)u_{\text{local}}{}^{-0.44\pm0.15} \quad R^2 = 0.982, P<0.01; N = 12. \tag{5}$$

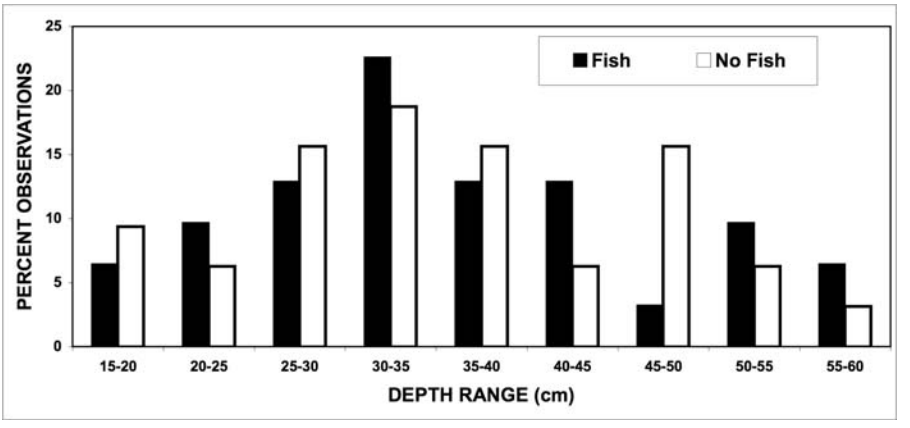

FIGURE 2.—Depth distribution of the locations occupied by fish and the chosen locations without fish sampled in 2002 and 2003.

Comparisons of Fish and No-Fish Locations (2002 and 2003 Observations)

Fish and no-fish sites were chosen to share the categorical features described above but were different in terms of current speeds and depth. The depths at fish and no-fish locations spanned the same range (Figure 2), and were not significantly different (unpaired *t*-tests, $P = 0.95$). Current speeds spanned the same range (Figure 1).

The values of local current speed and TI were lower in 2002 than in 2003 for both fish and no-fish locations. This presumably reflects differences in discharge (0.47 m3/s in 2002 and 0.67 m^3/s in 2003).

After taking into account the range of current speeds and depths typical of brown trout habitat for 2002 and 2003, the TI values for fish locations were significantly smaller than those in no-fish locations (ANCOVA; $P < 0.001$). Thus, brown trout chose lower turbulence locations over those meeting similar preferred physical habitat features.

TI Variation for Exemplary Stream Transects (2004)

The TI was measured for exemplary transects that were chosen to include typical habitat features as determined in the 2002 detailed survey of a 50- m reach. The first transect (Figure 3) included LWD upstream of and along the sampled cross-section (high LWD transect), creating a run area to the left, and a large central pool. The second transect (Figure 4) was characterized by a predominantly sandy-bottomed run (sandy transect) with an eroded dip, and a shallow sandbar with *V. americana*. Discharge was 0.80 m^3/s in 2004.

Current speeds in both the high LWD and sandy transects were typical of streams, the maximum u_{local} being found toward the center of the stream and the water surface and lower values being found near the boundaries (Figures 3, 4). In the high LWD density transect, u_{local} ranged from 0 to 60 cm/s. The highest u_{local} occurred at the center of the stream where LWD constricted and hence accelerated flow (a in Figure 3). In contrast, u_{local} was reduced by 20–30 cm/s downstream of LWD (b in Figure 3). The lowest u_{local} occurred at the streambed (c in Figure 3) and where LWD was dense (d in Figure 3). In contrast, in the sandy transect, the maximum u_{local} of 45 cm/s (e in Figure 3) was lower than in the high LWD transect because the sandy transect had a larger cross-sectional area (Figure 3) and few obstructions to channel the flow. Instead, u_{local} was reduced to about half the maximum as the depth gradually decreased towards the shoreline in an area with LWD oriented parallel to the current just upstream of the transect (f in Figure 3). However, the sandy transect differed from the high LWD transect in that there was a more extended velocity transition zone over the mid-stream region. Current speed was similarly reduced in a dip, a shallow depression towards the center of the transect (g in Figure 4). The lowest u_{local} occurred near the streambed, as in the high LWD transect, and also in a patch of *V. americana* (h in Figure 4) in the sandy area.

The TI was lowest towards the high-velocity portions of the stream in both transects (o in Figures 3, 4). The TI was higher downstream of the LWD than upstream in the high LWD transect, taking values of 0.3–0.4 (p in Figure 3). However, the largest values of TI, around 0.6, occurred where stream edges combined with LWD (r in Figure 3). Where LWD was least prevalent in the high LWD transect, the TI value was

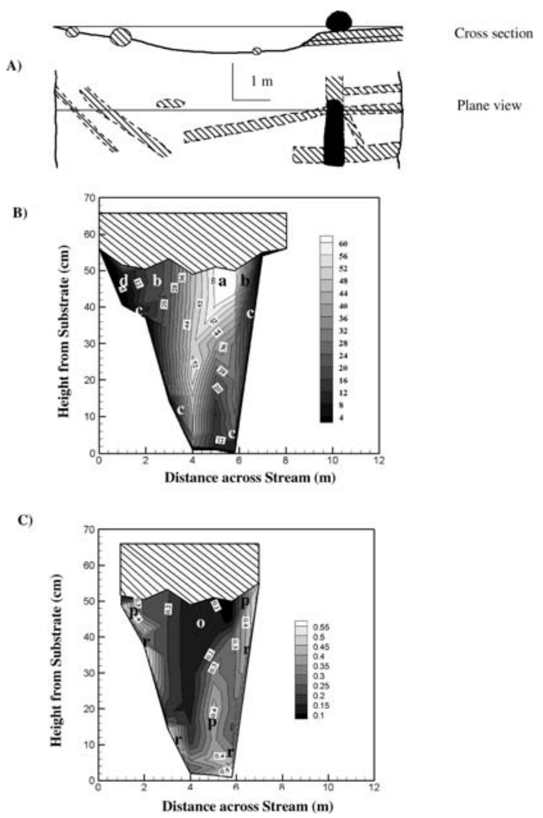

FIGURE 3.—**(A)** Sketch map and **(B–C)** flow characteristics of a cross-stream transect with large accumulations of large woody debris (LWD). The cross-section faces upstream, into the flow. In panel (A), emergent LWD is indicated by shading and submerged LWD by diagonal shading. For clarity, only major pieces of LWD are shown, but these pieces will have created logjams of smaller items. Panel (B) presents contour plots showing the variation in current velocity (cm/s) over the cross-section, panel (C) contour plots showing the variation in turbulence intensity. The large cross-hatched sections represent areas of the water column that were too close to the surface for velocity to be measured.

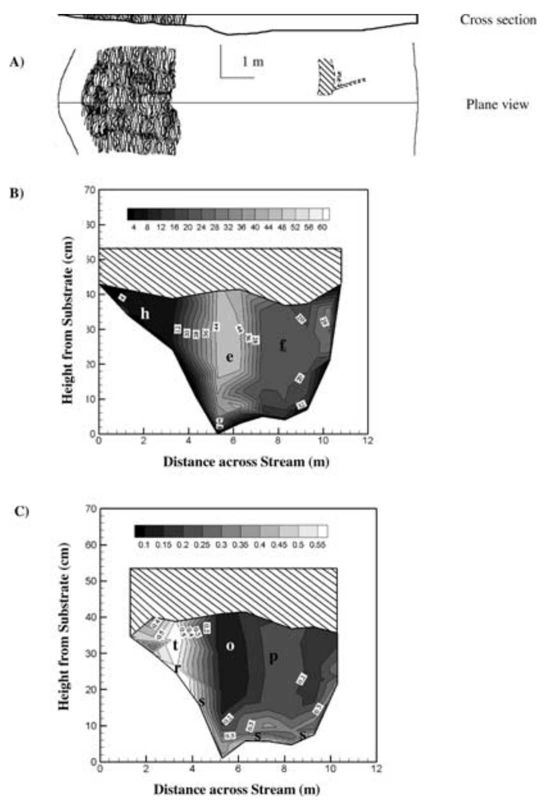

FIGURE 4.—**(A)** Sketch map and **(B–C)** flow characteristics along a cross-stream transect over a sandy area of stream bed with little in-flow structures. In panel (A), irregular hatching denotes a macrophyte bed. Other features of the figure are as described in the caption to Figure 3.

about 0.35 at the streambed, higher than TI in the water column, but lower than TI in the presence of LWD (s in Figure 4).

In the sandy transect, TI values that occurred immediately downstream of the LWD (p in Figure 4) were somewhat higher than the midstream minimum. These values were similar to values resulting from the presence of LWD in the high LWD transect. Similarly, TI values increased near the streambed of the sandy transect (s in Figure 4), with elevated values near the streambed downstream of in-flow structures, such as *V. americana* (r in Figure 4). However, the largest TI in either transect occurred at the edge of the *V. americana* patch (t in Figure 4).

Combining observations from both transects, TI varied from 0.08 to 0.73 over a range of u_{local} from 1 to 64 cm/s. As found for the fish and no-fish locations (equations 2 through 5), TI was inversely related to u_{local}, the relationship being best described by the power function

$$TI = (0.86 \pm 0.14) u_{\text{local}}{}^{-0.36 \pm 0.06}$$
$$R^2 = 0.899,\ P < 0.001;\ N = 118. \qquad (6)$$

As 85% of brown trout were located no more than 5 cm from the stream bed, the relationship between TI and u_{local} was determined for measurements at depths no more than 5 cm. For these data, $\text{TI}_{\le 5\ \text{cm}}$ and $u_{\le 5\ \text{cm}}$ were related as follows:

$$TI_{\le 5cm} = (0.73 \pm 0.16) u_{\le 5\text{cm}}{}^{-0.26 \pm 0.09}$$
$$R^2 = 0.919,\ P < 0.001;\ N = 44. \qquad (7)$$

The $\text{TI}_{\le 5\ \text{cm}}$ was larger for a given u_{local} than TI for greater heights above the bottom (Figure 1D). This is not surprising as flow close to the bottom is within the shear zone where u_{local} changes rapidly with height, and hence where turbulence is likely to be high.

TI Variation and Fish Locations (2004 observations)

In addition to our systematic measurement of TI and u_{local}, we measured TI and u_{nose} for 17 brown trout using ADV in 2004 (Figure 1c). The TI in the fish locations varied from 0.18 to 0.53, covering much of the range of TI in the stream. However, for flow within 5 cm of the bottom where most brown trout were located, TI ranged from 0.16 to 0.73, so that brown trout occupied locations toward the lower end of the TI range.

As with the brown trout locations sampled in 2002 and 2003, TI was related to u_{nose} by a power function, namely,

$$TI = (0.39 \pm 0.26) u_{\text{nose}}{}^{-0.64 \pm 0.24}$$
$$R^2 = 0.877, P < 0.01; N = 14. \quad (8)$$

Similarly, other physical habitat features were not correlated with TI in locations occupied by brown trout (multiple linear regression [$P > 0.5$] and Pearson correlation followed by Bonferroni test for significance [$P > 0.1$]). Finally, TI at u_{nose} for the brown trout was significantly lower than TI at $u_{\leq 5cm}$ (ANCOVA; $P < 0.028$).

Discussion

This study quantified turbulence in terms of the statistical variation in current speed relative to the average velocity at given locations and considers higher levels of TI to be associated with greater control challenges to stability (Webb 1998; Pavlov et al. 2000; Odeh et al. 2002; Enders et al. 2003). Turbulence intensity decreased as a power function with increasing speed, suggesting that stability challenges would rapidly decrease at higher current speeds. In contrast, Smith et al. (2005) suggested absolute values of standard deviation would be a better a measure of the challenges of dealing with turbulence. In this view, if standard deviation were constant over all current speeds, TI would decrease linearly with current speed, but the stability challenges faced by a fish would be independent of current speed.

Stability, which involves the ability to control posture and location in the water column, is not a simple function of perturbation magnitude. Dynamic stability also depends on the momentum and kinetic energy of the system, these being functions of speed. Thus, the ability to achieve dynamic stability, such as for a fish exposed to turbulence, depends on both perturbations associated with velocity variation and the mean current speed faced by the fish. As speed increases, the momentum of a fish increases. This promotes stability. As a result, dynamic stability can be sustained at a higher velocity in the face of larger perturbations (Webb 2006). This idea can be visualized from the experience of riding a bicycle. At very slow speeds, stability is difficult to achieve, and small perturbations can cause failure – i.e., loss of control. At high speeds, not only do such small perturbations become negligible, but stability can be achieved over a much larger range of perturbations.

Thus, we suggest that TI is an appropriate measure of turbulence effects in terms of the impact on fishes. The TI takes into account the speed-dependence of control and the ability to achieve stability over a larger range of turbulent velocity fluctuations as mean velocity increases. The physical analysis could directly consider momentum or even kinetic energy fluctuations rather than velocity fluctuations. However, the same numerical result as determined by equation (1) will be realized because the additional terms cancel out.

When choosing a location in their natural habitat fish make compromises among many interacting physical and biotic factors. Our observations were made during the day, and presumably reflect brown trout's choice of resting nonfeeding locations. At other times, factors, such as feeding and size-dependent choice of prey, also could affect location choices,that are associated with patterns of flow that are different from those that we studied. Nevertheless, in our study, brown trout were found in locations with lower TI than similar unoccupied sites, even though these fish in the West Maple River were found with cover, near the bottom, and at intermediate current velocities, factors that tend to promote turbulence. Brown trout were not found in the lowest TI because low values were found with the fastest currents in mid-stream and towards the water surface (Figures 3, 4). At the same time, the highest TI was avoided because this occurred in shallow water containing *V. americana* patches.

Turbulence arises as a result of shear owing to viscous effects in velocity gradients, which are largely created by interactions between the flow and instream structures of the stream bed or protuberances (Carling 1992; Atkinson 1999; Smith 2003; Roy et al. 2004; Smith et al. 2005). Fishes are found in currents where shear forces often tend to be high, so that it is especially noteworthy that brown trout choose lower TI locations from among those available. However, such turbulence-creating features are not unique to trout streams. In other waters fish are typically found in the lower regions of the water column near the bottom or near or among protruding structures such as rocky materials, LWD, macrophytes and corals (Fausch and White 1981; Puckett and Dill 1985; Matthews and

Heins 1987; Allan 1995; Matthews 1998; Enders et al. 2003; Standen et al. 2004; Fulton and Bellwood 2002). Additional research should focus on understanding the importance of turbulence in these nonstream habitats.

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