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ARTICLE

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Abstract
Habitat, water chemistry, and water temperature requirements and preferences have been well documented for stream-dwelling Brook Trout *Salvelinus fontinalis*, but fisheries managers rarely know what factors limit Brook Trout abundance in their jurisdictions. We measured various habitat (width, depth,% pool, and wood abundance), water chemistry (pH and conductivity), and water temperature metrics and estimated Brook Trout biomass at 33 stream reaches in northeastern Vermont to determine what factors were most strongly related to Brook Trout biomass, with the ultimate goal of predicting whether adding wood to these streams could be expected to increase Brook Trout abundance. We fit generalized additive models to investigate potential linear and nonlinear relationships between Brook Trout biomass and the various habitat, chemistry, and temperature metrics. Akaike's information criterion was used to rank candidate models. The top-ranked model included the duration of water temperatures exceeding 20°C, total wood density, and maximum riffle depth, and it predicted that Brook Trout biomass could be expected to increase with increasing woody habitat as long as water temperature does not exceed 20°C for 200 h or more per summer. The model also predicted that the benefits of adding woody habitat would be more pronounced in streams with deeper riffles. The absence of stream pH and pool area from the top-ranked models was surprising. Our results highlight the importance of evaluating the local relationships between fish biomass and stream habitat as well as the important influence of study design on the results and conclusions.

The concept of limitation is fundamental to ecology (Shelford 1913), and much of our effort in the fields of fish ecology and fisheries management has been devoted to identifying the factors that limit fish production. In streams, the availability of suitable habitat is widely acknowledged as a common limiting factor for fish production and abundance (Poff and Huryn 1998; Rosenfeld 2003; Rosenfeld and Taylor 2009; Minns et al. 2011), but the term "habitat" can encompass many elements of the stream environment. The specific habitat features limiting fish production and abundance can vary within and across streams, which creates the need for regionally focused habitat assessments. There are, however, a number of metrics which consistently arise as important features in a stream (e.g., pools, habitat complexity, cover, and thermal conditions), and determining which features are important within given regions is necessary for an overall understanding of the relationship between fish production and the stream environments in which they live.

We were particularly interested in the degree to which instream woody habitat relates to fish abundance in these systems. Wood in streams can benefit fish by increasing pool frequency, pool size, and habitat complexity (Montgomery et al. 1995; Sundbaum and Näslund 1998; Crook and Robertson 1999; Gurnell et al. 2005). Large wood and large wood jams are key structural elements in forested streams (Gurnell et al. 2002, 2005; Gregory et al. 2003), and wood input to streams is expected to

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increase across northeastern North America as a result of both natural processes and anthropogenic activities. As riparian forests mature and recover from historic land use and forests shift from the stem-exclusion phase to a more complex gap-dynamic phase of stand development, wood loading to streams across the eastern USA will increase (Keeton et al. 2007; Warren et al. 2009). Warming climate conditions, which allow invasive species such as the hemlock wooly adelgid *Adelges tsugae* and the emerald ash borer *Agrilus planiplennis* to move north, will also promote wood loading to streams across the region through the mortality of host trees (Evans et al. 2011). In addition to natural increases in stream wood, restoration efforts often add wood to increase habitat complexity and enhance stream recovery (Roni et al. 2002; Kail and Hering 2005; Nagayama et al. 2008; Nagayama and Nakamura 2010). While a number of studies—both observational and experimental—have found significant positive relationships between in-stream wood and fish abundance (Burgess and Bider 1980; Flebbe and Dolloff 1995; Solazzi et al. 2000; Roni and Quinn 2001; White et al. 2011), increasing wood does not necessarily lead to an increase in fish, and in many streams the benefits of wood for stream fish remain equivocal (Thompson 2006; Stewart et al. 2009; Antón et al. 2011). This uncertainty in wood function is particularly relevant in the northeastern USA, where glaciation has left an abundance of coarse material that can create large pools even when wood is absent (Warren and Kraft 2003).

Beyond physical structures in the stream environment, the term "habitat" can also encompass the chemical and thermal conditions of a stream (Baker et al. 1996; Todd et al. 2008; Chu et al. 2010; Waco and Taylor 2010; McKenna and Johnson 2011). Limits imposed by these two factors—temperature and chemistry—can reduce fish populations independent of the availability of structural elements (Baker et al. 1996; Siitari et al. 2011). For example, low pH conditions (chronic or episodic acidification) in many headwater streams in the eastern USA can substantially reduce fish diversity and abundance (Baker et al. 1996; Baldigo and Lawrence 2000; Warren et al. 2010). Temperature regimes may affect fish at both low and high extremes. Stress associated with elevated stream temperatures can decrease abundance via direct mortality and emigration in search of thermal refugia (Baird and Krueger 2003; Xu et al. 2010a, 2010b; Wenger et al. 2011). In contrast, particularly low temperatures can decrease fish abundance directly via reduced growth rates and fecundity of individual fish and indirectly through a reduction in overall ecosystem productivity (Mullner and Hubert 2005; Coleman and Fausch 2007a, 2007b). Given the potential for chemical and thermal conditions to limit fish production in streams, our habitat assessment explicitly included these factors along with the physical structure of the stream environment.

Our goal was to determine which physical habitat (width, depth,% pool, and wood abundance), water chemistry (pH and conductivity), and water temperature metrics were most strongly related to Brook Trout *Salvelinus fontinalis* abundance in northeastern USA streams. We were particularly interested in wood and whether a focus on the addition of wood in habitat restoration is appropriate in these streams given the numerous other factors that can affect fish abundance. Although the relationship between fish abundance and stream habitat has been evaluated elsewhere in this region (van Zyll De Jong et al. 1997; Kocovsky and Carline 2005; Waco and Taylor 2010; Warren et al. 2010; McKenna and Johnson 2011), this study is unique in two primary ways. First, we quantified fish abundance and stream habitat across a high number of sites within a relatively small area that encompassed a range of gradients and substrate types. We assessed low-gradient tributaries in addition to the boulder-dominated headwater streams that are often considered "typical" for the region. This high-resolution field analysis controlled for regional variability in climate, stocking histories, fish communities, and underlying geological conditions, which allowed us to focus specifically on local habitat and its influence on stream fish. Second, we used a statistical approach that allowed us to assess both linear and nonlinear relationships between habitat features and fish abundance.

METHODS

All of the 33 stream reaches were within or just outside of Essex County, Vermont, which is the least populated county in the state (Figure 1). Stream reaches ranged in length from 21 to 94 m (Table 1). The land cover is largely dominated by northern hardwood forests, with pockets of spruce–fir forest. The physiographic region is known as the Northeastern Highlands, and the underlying bedrock is mostly granite. The area has a long history of logging, including heavy clear-cutting and log driving on the major rivers. Logging remains a major land use in the area, but large portions of land have been conserved by the Vermont Agency of Natural Resources and the U.S. Fish and Wildlife Service.

Assessments of fish abundance, water temperature, water chemistry, and habitat occurred in the summer and fall of 2011. Brook Trout abundance was estimated during July and August with multiple-pass depletion and a maximum likelihood estimator (Carle and Strub 1978). Electrofishing was conducted using either battery-powered backpack units or gasoline-powered generators stationed on shore or in a canoe. Captured Brook Trout were measured and weighed before being returned to the stream.

Water temperatures were monitored using Onset HOBO temperature loggers. The loggers were deployed in May and retrieved in late September, with water temperatures being recorded every 30 min. Temperature data were used to calculate two metrics taken from Butryn (2010): duration over 20°C and 22°C, which were simply the amount of time (in hours) that water temperatures exceeded the threshold values of 20°C or 22°C. These two temperature thresholds were chosen because Brook Trout prefer temperatures less than 20°C (Jobling 1981) and exhibit a heat-shock response at 22°C and above (Lund et al. 2003).

Water chemistry metrics were measured during low-flow conditions in July and August and included conductivity, pH,

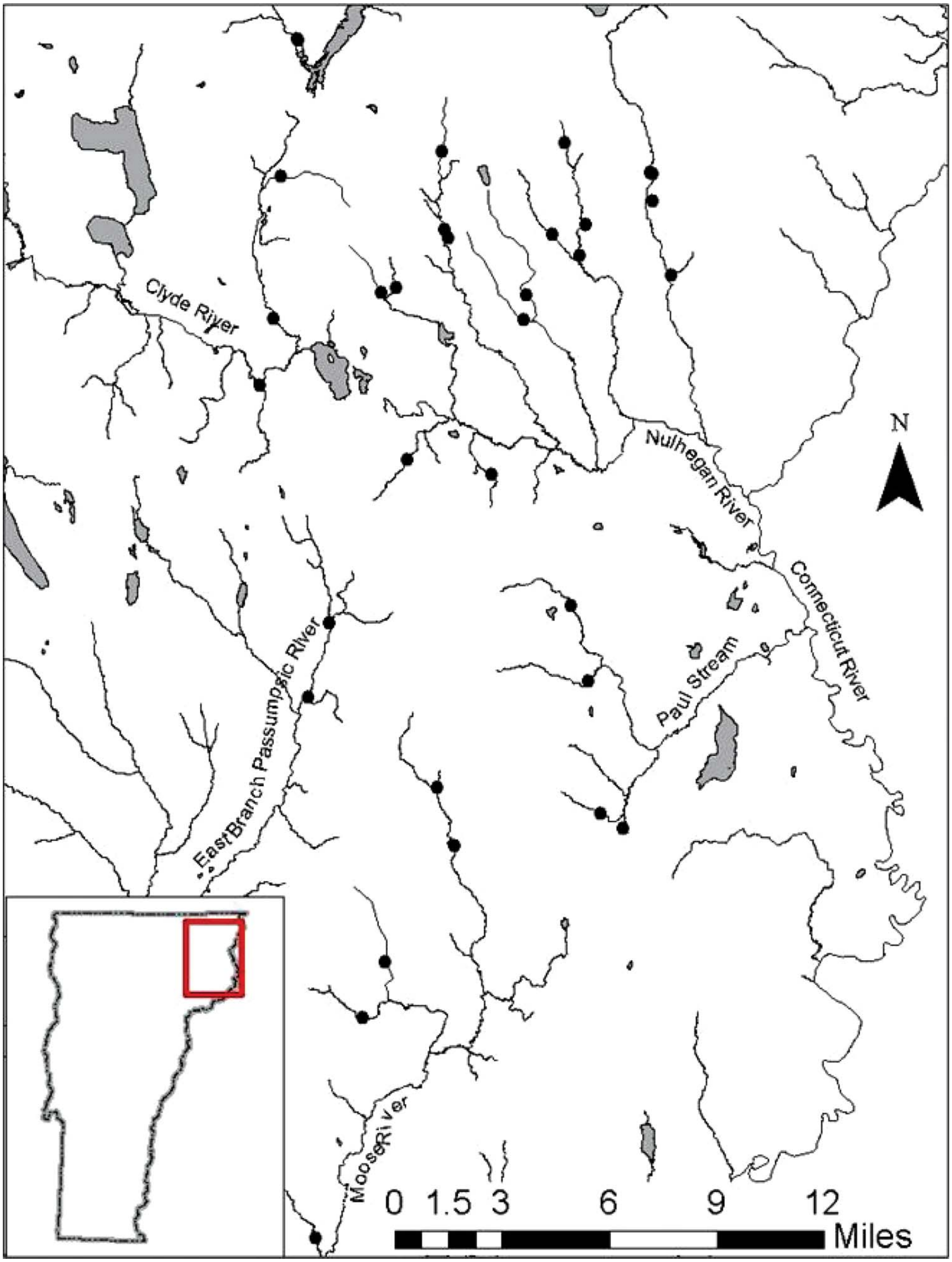

FIGURE 1. Locations of the 33 stream reaches sampled to evaluate Brook Trout biomass and habitat relationships in northeastern Vermont. [Figure available in color online.]

TABLE 1. Summary of fish, temperature, chemistry, and physical habitat metrics measured for 33 reaches in northeastern Vermont. Not all of the metrics were utilized in the generalized additive models.

Metric	Description	Mean	SD	Minimum	Maximum
BKT	Brook Trout biomass (kg/ha)	22	22	0	123
dur20	Duration of water temperatures over 20°C (h)	75	124	0	586
dur22	Duration of water temperatures over 22°C (h)	16	37	0	184
cond	Conductivity (μS)	47	26	16	148
pH		7.3	0.5	5.8	8.2
alk	Alkalinity (mg/L $CaCO_3$)	17	11	2	40
L	Reach length (m)	49	16	21	94
wetW	Mean wetted width (m)	5	2	2	10
BFW	Mean bankfull width (m)	10	4	4	23
% Pool	Percent of reach area classified as pool	30	23	0	100
maxpool	Maximum pool depth for the reach (cm)	70	25	37	125
maxriff	Maximum riffle depth for the reach (cm)	34	15	6	67
maxrun	Maximum run depth for the reach (cm)	44	20	21	110
woodtot	Total wood within the bankfull area (no./ha)	391	363	24	1,710
woodfun	Wood having some perceived function (no./ha)	298	348	0	1,710
slope	Water surface slope (%)	1.9	1.2	0.3	4.5
elev	Elevation (m)	416	56	301	546
drain	Drainage area (km^2)	15	11	2	50

and alkalinity. Conductivity and pH were measured in the field with a digital pH–conductivity meter. Alkalinity was measured in the laboratory by titration (APHA 2005). Most of the alkalinity values used in the study came from 2011 data, but water samples from some stations were lost when the laboratory was flooded by tropical storm Irene in late August 2011, so alkalinity values measured in 2008 were used for those stations.

Habitat was assessed during low-flow conditions in September using standard procedures developed by the New Hampshire Fish and Game Department (John Magee, personal communication). The first step was to delineate the riffle, run, and pool habitat units within the study reach and measure the length, typical wetted width, and typical bankfull width for each unit. Typical widths were measured at the point that appeared to be most representative of the average width of the habitat unit. We used the length and width data to calculate average wetted width, average bankfull width, and total wetted area for the study reach and the percent pool habitat. We also recorded the maximum depths for each riffle, run, and pool. Each piece of wood within the bankfull area having a diameter of at least 10 cm was recorded along with the habitat type (riffle, run, or pool); wood type (log, rootwad, or wood jam); and the expected function of the wood (none, pool formation, sediment retention, fish cover, or some combination). Finally, we estimated slope using a clinometer, elevation using Google Earth, and drainage area using the U.S. Geological Survey's StreamStats Web site (USGS 2012).

We fit multiple generalized additive models (GAMs) with thin-plate regression splines to investigate the potential for linear and nonlinear relationships between the various water temperature, water chemistry, and physical habitat metrics and Brook Trout biomass (kg/ha). The GAMs were fit using a generalized cross-validation procedure using the gam function in the mgcv package in R (version 2.10.1; Wood 2004, 2006, 2008, 2010). Before running the models, we used histograms to assess the normality of our data and $\log_{10}$ transformed all data that were not normally distributed. It would be statistically inappropriate and time-consuming to investigate all the models that could be developed from all combinations of habitat metrics (Burnham and Anderson 2002), so we developed 24 potential models based on a priori assumptions informed by observations made in the field. We assumed that temperature and wood would be the two factors most strongly related to Brook Trout biomass, so all one- and two-predictor GAMs included a water temperature metric and most three- and four-predictor GAMs included one temperature metric and one wood metric. We limited the degrees of freedom used to smooth each independent variable to a maximum of three. Models were compared using Akaike's information criterion corrected for small sample sizes (AIC_c; Burnham and Anderson 2002).

RESULTS

Brook Trout biomass ranged from 0 to 123 kg/ha, with a mean of 22 kg/ha (Table 1). The only station where no Brook Trout were collected was the warmest one, where water temperatures exceeded 20°C for 586 h. Water temperature never exceeded 20°C at nine stations. Alkalinity and conductivity were low, with minimums of 2 mg/L $CaCO_3$ and 16 μS, respectively. Wood densities ranged widely, from a minimum of 24 to a maximum of 1,710 pieces/ha.

TABLE 2. The generalized additive models for Brook Trout biomass ranked by AIC_c, along with the R^2, log likelihood (logLik), and number of parameters (k). Included in k are the parameters in the GAM and the smoothing parameters used in the splines.

Model	AIC_c	R^2	logLik	k
dur20 + woodtot + maxriff	27.19	0.766	0.97	9.8
dur20 + woodtot + maxriff + wetW	31.36	0.762	1.13	10.8
dur20 + woodtot + cond	33.87	0.663	–6.48	7.7
dur20 + woodtot	33.88	0.639	–8.2	6.7
dur20 + woodfun	34.10	0.655	–6.95	7.5
dur20 + woodtot + % pool	34.15	0.703	–3.14	9.5
dur20 + maxriff + wetW	34.57	0.682	–4.77	8.8
dur20 + woodtot + maxpool	37.04	0.625	–8.24	7.6
dur20 + woodtot + pH	37.49	0.639	–7.19	8.3
dur22 + woodfun	39.77	0.587	–9.96	7.4
dur20 + maxriff	40.31	0.589	–9.7	7.7
dur20	40.96	0.498	–14.8	4.7
dur20 + pool	42.03	0.558	–11.09	7.4
dur22 + maxriff	42.16	0.535	–12.34	6.7
dur20 + cond	42.32	0.504	–14.01	5.7
dur22 + % pool	42.92	0.544	–11.71	7.3
dur22 + woodtot	43.00	0.518	–13.09	6.5
dur20 + pH	43.16	0.504	–13.81	6.1
dur20 + maxpool	43.38	0.488	–14.54	5.7
dur22 + maxriff + wetW	44.37	0.571	–9.67	8.8
dur22	46.50	0.401	–17.99	4.4
dur22 + cond	48.46	0.400	–17.38	5.5
dur22 + maxpool	48.60	0.393	–17.45	5.5
dur22 + pH	49.06	0.445	–15.12	7.1

The models that included temperature and wood metrics were the best predictors of Brook Trout biomass (Table 2). The duration of water temperatures over 20°C (dur20) was a better predictor than the duration of water temperatures over 22°C (dur22). Both wood metrics performed similarly when paired with dur20. Maximum riffle depth was included in the top-ranked model, and the increase in R^2 from the two-predictor model that included only dur20 and woodtot to the three-predictor model that also included maxriff was 0.13.

Brook trout biomass generally decreased with increasing water temperature and increased with increasing wood density, but these relationships were not linear (Figure 2). The top-ranked model predicted relatively high Brook Trout biomass for streams in which water temperatures exceeded 20°C for less than approximately 20 h but decreasing Brook Trout biomass with increasing dur20. Brook Trout biomass increased with increasing wood density only when woodtot exceeded approximately 100 pieces/ha, with the strongest relationship being observed when woodtot exceeded 200 pieces/ha. A straight line sufficiently described the relationship between maximum riffle depth and Brook Trout biomass.

DISCUSSION

The top-ranked model suggested that water temperature, wood density, and maximum riffle depth were all related to Brook Trout biomass in headwater streams of northeastern Vermont. Water temperature was the controlling factor in stream reaches where it exceeded 20°C for 200 h or more. Relatively low Brook Trout biomass was predicted for those reaches regardless of wood density or riffle depth (Figure 3). For stations where water temperatures were suitably cool, total wood density was an important factor in accounting for Brook Trout biomass, with a strong positive relationship between wood density and the biomass of Brook Trout. The relationship between maximum riffle depth and Brook Trout biomass was not as strong, but this factor was an important component of our best model, with Brook Trout biomass tending to increase with increases in maximum riffle depth.

Brook trout require cold water. The incipient lethal temperature, or the temperature at which at least 50% of the test subjects are expected to die, is 24.5°C (McCormick et al. 1972). Brook trout exhibit a heat-shock response at 22°C and above (Lund et al. 2003). Various studies have found preferred temperatures of 14–19°C (Jobling 1981). Of the two temperature metrics (duration over 20°C and 22°C), the amount of time that water temperatures exceeded 20°C was most closely related to Brook Trout biomass, suggesting that preferred temperatures are more deterministic of Brook Trout biomass in our study area than are stressful or lethal temperatures. Water temperatures exceeded 24°C at five study sites. We collected Brook Trout at the four sites where water temperatures exceeded 24°C for 2–17 h, where it is likely that cold spring seeps allowed trout to survive periods of lethal water temperatures (Baird and Krueger 2003). No Brook Trout were present at the warmest site, where temperatures exceeded 24°C for 184 h.

We demonstrated that wood was indeed an important feature of Brook Trout habitat in this region. Rather than there being a strictly linear relationship between wood abundance and fish biomass, wood's influence on the Brook Trout populations in these streams appeared to be tied to a threshold wood density. Wood was positively and significantly related to Brook Trout biomass once wood reached or surpassed a density of 100 pieces/ha. At low wood densities, the minor contributions to pool formation or habitat complexity were not sufficient to increase biomass above and beyond that in nonwood conditions. This may be due to influences on total fish abundance or to the presence or absence of a few larger fish that hold in and defend only the highly complex habitat resulting from the interaction of multiple pieces of wood rather than individual pieces. The potential importance of interaction between multiple wood pieces was also highlighted by the AIC_c analysis, which indicated that a simple measure of total wood count was a better predictor of

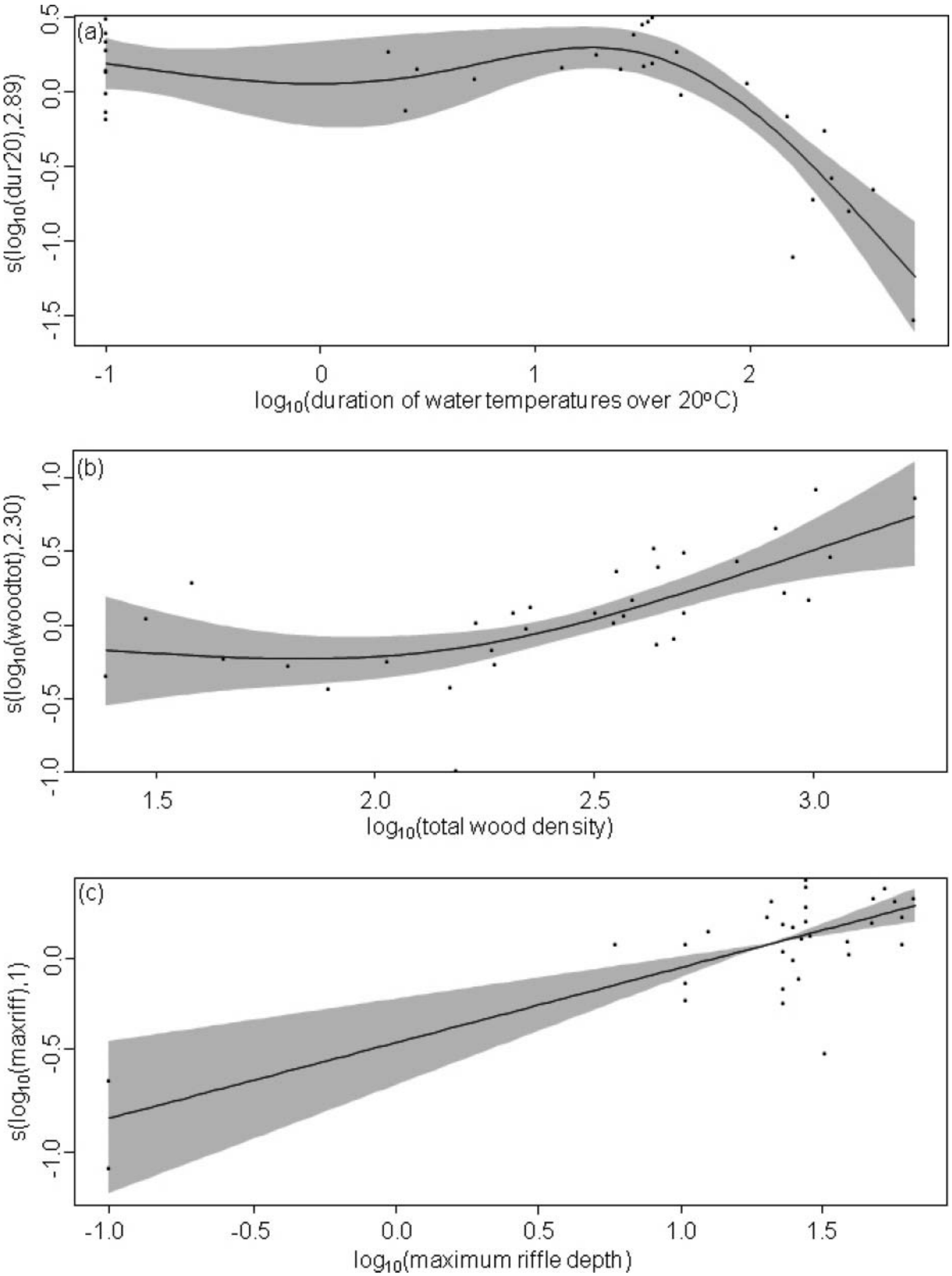

FIGURE 2. Partial residual plots for the three predictors included in the top-ranked model: **(a)** the duration of water temperatures exceeding 20°C (h), **(b)** total wood density (pieces/ha), and **(c)** maximum riffle depth (cm). The shaded areas represent two standard errors. The *y*-axis represents the effect of each metric on Brook Trout biomass, where *s* is the smoother term and the number in parentheses is the equivalent degrees of freedom (edf). An edf of 1.0 corresponds to a linear relationship, while larger edfs correspond to increasingly nonlinear relationships. The merging of confidence limits in panel (c), where the line passes through zero on the *x*-axis, is the result of the identifiability constraints applied to the smoothed terms (see Wood 2006:222).

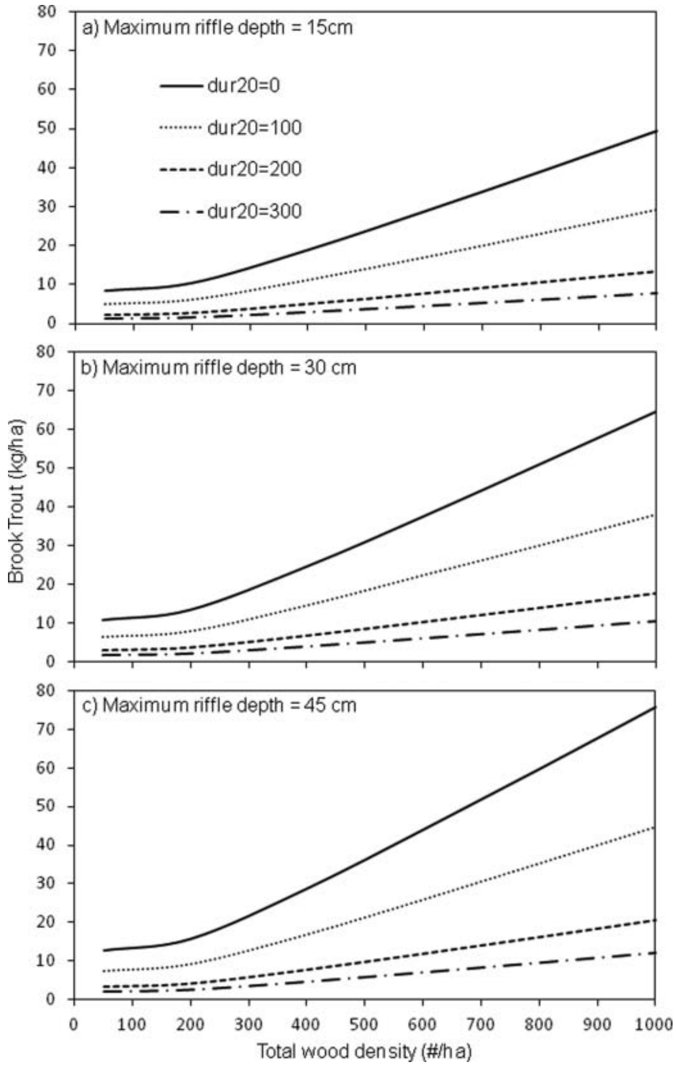

FIGURE 3. Brook Trout biomass predicted by the top-ranked model at various durations of water temperatures exceeding 20°C (dur20 [h]) and total wood densities at (**a**)–(**c**) three different maximum riffle depths.

total trout biomass than the number of wood pieces that clearly performed some function, such as pool formation or cover. So, despite perceived function during summer surveys, the relationship between wood and trout biomass was limited at low wood densities. When wood occurs at high densities, it is more likely to interact with other wood to create a higher degree of habitat complexity and accumulate into a wood jam, which may be more likely to influence pool formation or provide cover than an individual piece of wood.

This result was consistent with expectations regarding the role of wood in these glaciated streams. Wood was important but it was not the only feature of importance, and wood only truly mattered when there was a lot of it. Berg et al. (1998) found that wood was not the primary preferred habitat type in streams of the Sierra Nevada Mountains, but wood was utilized to a greater degree than its availability. Therefore, although a limited number of wood pieces may not necessarily affect total fish densities, a large number of wood pieces may indeed lead to measureable increases in fish biomass (or abundance). White et al. (2011) found that wood additions to streams in Colorado led to a long-term increase in fish production, but those logs were explicitly placed and anchored to promote pool formation. Only a small proportion of the logs that naturally recruit to a stream may create pools, or pool creation may require wood jams rather than individual wood pieces (especially in higher-gradient systems with more stable substrates). In these cases, it makes sense that a minimum threshold of wood abundance may be needed before a clear influence of wood on fish biomass can be quantified. The greater descriptive ability of the model including total wood count rather than just the number of functional wood pieces suggests that wood function during the nonsurvey periods (e.g., during high-flow events) may persist.

While much less important than water temperature and wood, riffle depth was also included as a key factor in our top model relating habitat characteristics to Brook Trout biomass. The riffle is the shallowest part of the stream, so a stream with deeper riffles should generally be deeper overall. Trout often select deepwater habitat (Berg et al. 1998), and several studies have demonstrated a relationship between the width : depth ratio and salmonid abundance (Chisholm and Hubert 1986; Lanka et al. 1987; Scarnecchia and Bergersen 1987; Kozel and Hubert 1989). While width : depth ratio was not explicitly included in our analysis, both width and depth measures were and the model with the second lowest AIC_c included both mean wetted width and maximum riffle depth. Depth may be a more important habitat component in larger streams, where wood is less abundant. In streams that lack wood, Brook Trout may seek other sources of cover, such as large boulders, deep water, or surface turbulence (Berg et al. 1998; Warren and Kraft 2003). In addition to providing the cover of surface turbulence, deep riffles may also provide preferred feeding locations for Brook Trout (Fausch 1984; Hughes and Dill 1990; Hayes and Jowett 1994; Baker and Coon 1997). During electrofishing surveys on the larger streams that generally lacked woody habitat, we routinely observed concentrations of Brook Trout in the deepest riffles, and the largest Brook Trout at these study sites were often found in these deep-riffle areas.

Our results contrast somewhat with those of Warren et al. (2010), who found pool area, cover, and stream pH to be the primary habitat factors accounting for the variability in total fish biomass in streams in northern New York and northern Vermont. As neither wood frequency nor temperature were included in their best model, however, these results are not as contradictory as they at first appear. As with any study evaluating biotic responses across a gradient, the range of values within each factor can influence its importance in accounting for the variability in the response metric. The pH values that we observed had a smaller range and were generally higher than the values observed in the Warren et al. (2010) study. Conversely, the Warren et al. (2010) study had a limited range in temperature, with almost all streams occurring in cool, well-forested environments. The lack of a strong relationship between trout abundance and pool area was somewhat surprising. Inconsistency with the Warren et al. (2010) result on this point may be due to the focus here on Brook Trout alone rather than Brook Trout and Slimy Sculpin *Cottus cognatus* together, though it is more likely that within this region temperature and the combined habitat functions of large wood have a stronger influence on trout than pool area alone. The contrast between these two studies highlights the importance of study design and regional context when considering factors related to fish abundance or biomass in streams. Collecting data across a large and strong habitat gradient is more likely to yield a significant result for a factor in terms of accounting for the variability in biomass or abundance. However, in most practical field studies a comparable gradient among factors is unlikely to be achieved. This is often due to regional conditions which restrict the values within a region (e.g., pH, which had a narrower range in our study area than it would across the entire northeastern USA). This is not necessarily detrimental to studies of fish ecology and fish management, but it does highlight the need to consider regional conditions when evaluating the relative importance of various habitat characteristics. Fisheries managers in other regions are likely to observe that Brook Trout abundance is most strongly related to the habitat features in their region that have the largest variability.

We drew two primary conclusions. First, trout biomass in northeastern Vermont's headwater streams was strongly associated with stream temperature, high wood density, and deepwater habitat. Management activities that promote cooler temperatures (e.g., planting riparian shade trees), increase wood abundance (e.g., chop-and-drop wood additions), or create deeper habitat (e.g., wing deflectors and V-weirs) would probably increase total Brook Trout biomass in these streams. The abiotic stream characteristics accounting for the greatest variability in trout biomass differed somewhat from the most important factors identified in an earlier study in this region (Warren et al. 2010) but are broadly consistent with the results of other studies (Berg et al. 1998; Poff and Huryn 1998; Rosenfeld 2003; Rosenfeld and Taylor 2009; Minns et al. 2011). This led us to our second conclusion: the habitat factors that limit fish abundance or biomass may be highly variable between regions, and conclusions about which factors are important may also be influenced by study design or, more specifically, the range of chemical and physical attributes included in the study.

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