

Burbot resource selection in small streams near the southern extent of the species range

Dixon CJ, Vokoun JC. Burbot resource selection in small streams near the southern extent of the species range.

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Abstract – Burbot *Lota lota* are of global conservation concern particularly near the southern extent of the species range. Populations in small streams lack quantitative descriptions of resource selection. Microhabitat and reach-scale habitat were surveyed at occupied and unoccupied locations. Data were analyzed with logistic regression to develop resource selection function models which predicted the probability of occurrence and abundance categories for microhabitat and reach-scale habitat, respectively. Information-theoretic model selection methods were used in an exploratory context, and four competing models were multi-model averaged to create a microhabitat resource selection function. The sum of Akaike's Information Criterion weights across the four competing models indicated that substrate type, substrate embeddedness, and depth were equally the most important microhabitat explanatory variables. At the reach scale, high correlation among explanatory variables precluded multivariate model development. Stream-reach gradient was the most supported univariate model. Three additional models competed as important; mean summer temperature, sinuosity, and dominant substrate type. The created resource selection functions can be used in ranking potential translocation sites, used in instream flow assessments, and provide habitat selection information that can provide context for habitat management decisions.

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Key words: burbot *Lota lota*; resource selection function; logistic regression; habitat suitability; habitat use

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Introduction

Many species of fish in stream ecosystems are threatened by degradation of habitat by human development and landscape alteration (Wang et al. 2000; Wheeler et al. 2005). As humans alter aquatic systems many fish species are likely to face population declines and range reductions (Neves & Angermeier 1990; Rahel et al. 1999; Mattson & Angermeier 2007). Declines of burbot *Lota lota* populations throughout much of their holarctic range have resulted in their inclusion on species of conservation concern lists (Kirchhofer & Hefti 1996; Paragamian & Bennett 2008). Further, interest in the conservation of biodiversity of fish has increased attention to burbot management among fisheries scientists (Arndt & Hutchinson 2000; Fisher et al. 2000). This study was

prompted by the desire better to understand habitat use of burbot occurring in small streams near the southern extent of the species range in North America, ostensibly threatened by limited range, suburban sprawl and the predicted loss of coldwater streams in a changing climate.

The conservation of aquatic habitat is a goal of biodiversity management because human effects on aquatic systems are often in conflict with species persistence (Abell et al. 2000; Labonne & Gaudin 2006). Aquatic conservation is informed by identifying the physical habitat variables most influencing fish abundance in streams (Ahmadi-Nedushan et al. 2006; *and references therein*); it is important to understand the relative influence of each habitat variable and the spatial scale over which each variable functions (Rabeni & Sowa 1996). Information about habitat

selection can be informative to instream flow analyses intended to guide regulated river management and ecosystem conservation (Tharme 2003). Further, translocation is a prominently used strategy in recovery programs for threatened fishes (Williams et al. 1988), and identifying the suite of habitat variables selected (and perhaps required) is an important step in predicting the eventual success of a translocation site (Harig & Fausch 2002).

The spatiotemporal scales of analyses are important components of research designed to identify habitat characteristics influencing fish presence and abundance and to develop effective habitat restoration and conservation strategies (Frissell et al. 1986; Schlosser 1991, 1995; Lewis et al. 1996; Rabeni & Sowa 1996; Mattingly & Galat 2002; Lowe et al. 2006). A hierarchical approach allows managers to identify processes that may affect species distribution and abundance and that limit processes at smaller scales.

Our goal was to identify habitat conditions associated with the presence of burbot in CT, USA. In CT, burbot have been consistently found only in small streams in one tributary watershed of the Housatonic River (Linsley 1844; Whitworth 1996). Other records of burbot in CT are inconsistent among locations and few in number, and the species is listed as state-endangered (CTDEP 2004). Translocation of burbot to new sites is a potential tool to increase the number of population occurrences (Dillen et al. 2008b) and lessen the threat of extirpation due to environmental catastrophes.

Specifically, we sought to identify through statistical model selection a suite of habitat characteristics that burbot select at the microhabitat and reach spatial scales to develop resource selection functions (RSF). An RSF is defined as any model that identifies parameters of the environment that predict the probability of use of a resource by an organism (Boyce et al. 2002). An RSF then, is a probabilistic form of habitat suitability criteria (Boyce et al. 2002; Ahmadi-Nedushan et al. 2006).

Methods

Study sites

In northwest CT USA the Housatonic River basin topography is characterized by rounded hills and mountains draped with glacial deposits, with steep-sided valleys cut into the hills (USEPA 2002). Study sites were selected and expanded from river segments where burbot had been previously documented by CT Department of Environmental Protection fisheries biologists. The sites were located within the Hollenbeck River and Blackberry River tributary watersheds (Fig. S1). Two of these sites, the Hollenbeck/Brown

and Lower Hollenbeck, were in the Hollenbeck watershed, that drained an area of 112 km². The Hollenbeck/Brown site was approximately 2 km long and included the Hollenbeck River mainstem and the junction with the lower portion of Brown Brook. The Hollenbeck River has ~5 m bankfull width channel and 0.3 m mean pool depth. Brown Brook was ~3 m wide and had 0.15 m mean pool depth. The Hollenbeck River streambed was characterized by sand in the lower section of the site shifting to predominantly cobble and boulder at upstream higher elevations, with well-defined pool-riffle sequences. The Brown Brook channel was characterized by cobble and boulder substrate with step-pool sequences. Land surrounding this site was primarily forested, with a single agricultural field at the lower end. The Lower Hollenbeck site was 3.7 km long and ~5.5 m wide located on the mainstem Hollenbeck River downstream of the Hollenbeck/Brown site. The channel was highly sinuous and characterized by sand substrate with pool-run sequences lacking defined riffles: average depth was approximately 0.3 m. Large woody debris was prevalent throughout the lower site. Land surrounding this site was primarily deciduous forest, with patches of conifer stands and occasional agricultural fields.

The Blackberry site was located in the Blackberry River watershed and drained an area of 120 km². Only one burbot has been recorded in the Blackberry watershed, discovered during a fish kill. The Blackberry site was 5.4 km long and bounded upstream by a small run-of-river dam (~1.8 m tall), a likely barrier to upstream fish movement. The channel was approximately 7.0 m wide with a mean pool depth of 0.4 m. The Blackberry River streambed was characterized by sand, gravel, and cobble in the lower section shifting to boulder and bedrock upstream near the dam. Pool-riffle sequences were well defined throughout the site. Land surrounding the site was predominately agricultural in the floodplain and forested on the mountain-sides.

Fish sampling

We electrofished the three study sites during July–September 2005. Burbot were collected in shallow areas (<0.6 m) with a model LR-24 pulsed-DC backpack electrofisher (Smith-Root Inc., Vancouver, WA, USA). Electrofishing voltage ranged between 200 and 350 volts based on measures of water temperature, conductivity, and specific conductivity of the water with a model 556 multimeter (YSI Inc., Yellow Springs, OH, USA). Sampling was conducted with one person wearing the backpack and two people on each side who waded the channel with dip nets to capture fish. In the infrequent deeper areas of stream,

a push-barge electrofishing raft (Smith-Root Inc.) powered by a 3600 watt gasoline generator was used. Electrofishing was methodical and thorough, probing all available habitat. Sampling proceeded upstream and continued until a burbot was captured. The location of capture was marked with a surveyor's flag. Although the positions of fish prior to capture were not known, burbot were not observed swimming ahead of the crew and were observed experiencing limited electrotaxis and then narcosis from concealed locations in the stream bottom because the water was clear during all sampling. We also waded into the sites, located rocks under which burbot were present and lifted them before the burbot swam away. Although our methods are not quantitative and are without an estimate of absolute capture efficiency, we are confident they revealed actual burbot locations during daytime. Water depths sampled ranged from 0.1 to 0.9 m with a mean of 0.3 m. Captured burbot were measured to the nearest mm total length (TL), and weighed to the nearest g. We wore wetted wool gloves to maintain better control of the fish and reduce handling time and stress.

Water temperature

Water temperature was measured with HOBO[®] Water Temp Pro temperature loggers (Onset Computer Corp., Pocasset, MA, USA). Temperatures were sampled hourly in 15 locations in each stream, with multiple loggers in each site, and at the upstream and downstream boundaries. Loggers recorded stream temperature (± 0.02 °C) 24 times a day for a year, but only summer data (June–August) were used.

Microhabitat

Microhabitat was described at the time and location of capture for each burbot. Depth, velocity, temperature, pH, dissolved oxygen, dominant substrate type, a visual estimate of embeddedness, and percent canopy cover were measured. Velocity was measured using a Flo-Mate model 2000 portable flowmeter (Hach/Marsh-McBirney Inc., Frederick, MD, USA). Dominant substrate type classes were determined using a modified Wentworth scale. Wentworth substrate size categories used were: fines (< 0.25 mm); sand (0.25–2.0 mm); gravel (2–16 mm); pebble (16–64 mm); cobble (64–256 mm); boulder (> 256 mm); and bedrock (*after* Mattingly & Galat 2002). Substrate embeddedness was visually estimated into categories of low, intermediate, and high using methods adapted from Platts et al. (1983). Percent canopy cover was measured with a spherical densiometer. Samplers faced each cardinal direction and counted cells with canopy coverage. The mean of the

four measurements was used to characterize the capture location.

Microhabitat measurements at capture locations constituted used habitat datasets to develop RSF models. Available habitat was collected at random locations within three channel units (pool, riffle, run) that were randomly-selected upstream or downstream from the location of each capture. Microhabitat location within a channel unit was determined by visualizing a 10×10 grid over the channel and then measuring habitat in a random cell within that grid. Random microhabitats were measured with the same procedures as capture locations.

Reach-scale

A reach was defined as 3–5 pool-riffle sequences and a length of at least 20 bankfull channel widths (Arend 1999). Reach-scale habitat characteristics were collected by surveying thalweg longitudinal profiles for each sample reach and by summarizing the habitat in channel units along the thalweg.

Thalweg longitudinal profiles were measured using a total station (model TCR307; Leica Geosystems AG, Heerbrugg, Switzerland) with methodology adapted from Panfil & Jacobson (2001). Cross-sections were surveyed above riffle crests and through the deepest sections of pool channel units. Mean channel width of a reach was calculated from the bankfull widths of these cross-sections. The number of discrete points surveyed along the stream thalweg was based on geomorphic complexity with the objective of capturing important changes in streambed elevation and channel unit boundaries along the thalweg; they averaged out to approximately 2 survey points per longitudinal meter of streambed. Channel unit boundaries (e.g., pool, riffle, and run) along the thalweg were visually identified, surveyed, and used to calculate the percent of pool habitat in each reach. Elevations of surveyed points at the upstream and downstream ends of each reach were used to determine reach gradient.

Stream habitat used to characterize channel units were dominant substrate type, substrate embeddedness, bank vegetation, a canopy-shade index, an instream-cover index, and a tributary index. Dominant substrate type was assessed visually as the substrate size that was covering the largest percentage of streambed in a channel unit, and observations were combined to represent dominant substrate in a reach. Substrate embeddedness was also visually estimated, and similarly combined to determine the embeddedness category with the largest percentage of occurrence and was used to represent a reach condition. Criteria for classifying canopy-shade index, instream-cover index, and tributary index were

categorical and modeled after Mattingly & Galat (2002), with four categories representing increasing levels of presence of each respective reach-scale habitat component and are reported in detail in Dixon (2007).

Mean residual pool depth, a discharge-independent measurement of pool depth defined as the difference between the lowest elevation in a pool and the elevation of the downstream riffle crest, required an objective determination of the riffle crest (or geomorphic equivalent) streambed elevation. The bed form differencing technique was used to measure elevation changes in the streambed that exceeded a calculated reach-specific tolerance value to determine the riffle crest elevations within each reach (O'Neil & Abrahams 1987). We followed the methods described by Arend (1999) for calculating bed form differencing. Mean reach residual pool depth was then calculated as the average of residual pool depths within a reach.

Mean reach temperature of the summer sampling period was calculated from the hourly temperature data. Reaches with a temperature logger in the reach were assigned the mean of that logger. Mean reach temperature of reaches without a logger were estimated using the mean of the two nearest loggers, one upstream and one downstream of the reach.

Data analysis

An information-theoretic approach was used to develop RSF that predict the presence of burbot using the presence versus availability dataset (Boyce et al. 2002). Information-theoretic approaches rank competing hypotheses (expressed as statistical models) and use simple calculations to estimate a formal strength of evidence for alternative hypotheses rather than statistical tests of null hypotheses and decisions based on P-values (Burnham & Anderson 1998; Anderson et al. 2001; Anderson & Burnham 2002). Using this approach, evidence for alternative hypotheses include the rank of each hypothesis (an estimate of the formal likelihood of each hypothesis), and a measure of precision that incorporates model selection uncertainty. Information-theoretic approaches use the set of alternative models to make formal inference (Anderson et al. 2000).

No quantitative data within the literature was available on the habitat use of burbot in small streams in North America (but see Dillen et al. (2008a) in France). We adapted the exploratory approach of Amadio et al. (2005). Selected microhabitat-scale and reach-scale habitat characteristics were hypothesized to affect occurrence based on the literature describing burbot ecology in lotic and lentic systems. A limited set of habitat characteristics that were correlated to the

occurrence of burbot, but not highly intercorrelated were identified. Dependence among predictor variables (including habitat characteristics) in observational studies is commonplace (Burnham & Anderson 1998). Therefore we retained habitat characteristics for subsequent analysis that were intercorrelated at $|r| < 0.50$ to reduce multicollinearity among models (Glanz & Slinker 1990; Graham 2003). All model subsets using the resulting set of habitat characteristics were then created and fitted with logistic regression using PROC LOGISTIC in SAS (SAS Institute Inc. 2003).

Support for candidate models was assessed using the small sample bias adjustment of Hurvich & Tsai (1989) to Akaike's Information Criterion (AIC_c ; Burnham & Anderson 1998; Amadio et al. 2005). The AIC_c weights (w_i) were used to rank models. The model with the greatest w_i was considered to best fit the data (Burnham & Anderson 1998). Competing models were identified as models with $w_i \geq 10\%$ of the highest ranking model. Model selection uncertainty was addressed among competing models by multi-model averaging and calculating model-averaged estimates of the coefficients and their standard errors (Burnham & Anderson 1998). The w_i of predictor variables (habitat characteristics) were summed across competing models included in the calculation of the multi-model averaged coefficients to estimate their relative importance (Burnham & Anderson 1998). The variable depth and its squared transformation were both included in models in which depth appeared to improve model fit.

Polytomous logistic regression was used to predict the probability of reach use based on a dataset categorized into four ordinal responses representing the number of burbot sampled within a reach (absent, low, moderate, high) at the reach scale and therefore, RSF models. Ordinal categories were determined by identifying natural breaks in the data. Polytomous logistic regression model diagnostics included the Score Test for Proportional Odds Assumption, Deviance and Pearson Goodness-of-fit statistics (Stokes et al. 2000). Separation of ordinal-category probabilities were calculated and are presented in the results following conventions used by Harig & Fausch (2002). Model development progression was similar at both spatial scales, except to accommodate the ordinal responses in the dependent variable (burbot presence) at the reach scale.

Results

Summer electrofishing captured 201 burbot, 141 at the Hollenbeck/Brown site, 57 at the Lower Hollenbeck site, and 3 burbot at the Blackberry site. The mean length of burbot was 191 mm and ranged from 84 to

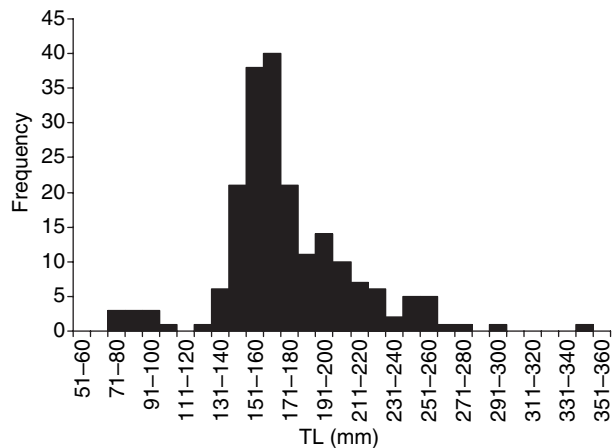


Fig. 1. Length–frequency histogram of the 201 burbot captured at the study sites.

356 mm TL (Fig. 1). The mean weight was 45 g and ranged from 4 to 240 g. Sixty percent of fish caught were from 160 to 200 mm. Large burbot (over 500 mm) have never been recorded in the Housatonic River watershed. Age estimated from otoliths of 32 fish revealed that fish were 1–5 years of age with a modal age of 2–3 years (Dixon 2007). Examining sacrificed fish revealed that fish estimated to be 2 or more years old were mature. Additional samples of burbot in November 2005 revealed male and female fish in this size range expressing gametes.

Microhabitat resource selection

Burbot sampled during the summer of 2005 in the Lower Hollenbeck and Hollenbeck/Brown sites were used to build an RSF. Data collected in the Blackberry River site were not used because few burbot were collected. Consequently, the use versus availability data set used to develop RSF had 396 microhabitat descriptions including an equal number of capture locations and random locations.

Five habitat characteristics that were correlated ($P < 0.05$) with burbot presence, and not highly correlated with each other, were used in RSF development. They were; substrate type, substrate embeddedness, channel unit type, velocity, and depth. All unique subsets of these five were combined to propose 31 logistic regression models. The model with the highest w_i value contained four of the five variables (Table 1) and three competing models had w_i values within 10% of the top-ranked model. These four models were multi-model averaged to create the microhabitat RSF (Table 2). The sum of w_i values across the four competing models indicated that substrate, substrate embeddedness, and depth were equally important microhabitat predictor variables, each had a summed w_i of 0.98. These three variables

Table 1. Microhabitat variables comprising competing logistic regression models predicting occurrence of burbot.

Model	K	$-2\log_e L$	AIC_c	w_i
Substrate, embeddedness, depth, channel unit	15	201.58	217.33	0.33
Substrate, embeddedness, depth, velocity	16	204.49	217.82	0.26
Substrate, embeddedness, depth, velocity, channel unit	13	201.03	218.00	0.24
Substrate, embeddedness, depth	12	206.74	218.88	0.15

Variable were; substrate type, substrate embeddedness, depth, channel unit type, and velocity. Models are ranked according to Akaike's Information Criterion corrected for small sample size (AIC_c), which was calculated from the number of estimated parameters (K), and the log likelihood ($-2\log_e L$). AIC weights (w_i) were used to select the 'best approximating' models from a set of candidate exploratory models. Competing models with w_i values that were 10% or greater than the maximum w_i are included in the table.

Table 2. Explanatory microhabitat predictor variables included in competing models, multi-model averaged coefficients (standard error), and sums of Akaike Information Criterion (AIC_c) weights summed across competing models (see Table 1).

Model variable	Averaged coefficient	Sum of AIC_c weights
Intercept	-1.52 (0.17)	
Substrate		0.98
Fines	N/A	
Sand	-0.19 (0.16)	
Gravel	-0.35 (0.24)	
Pebble	-0.22 (0.23)	
Cobble	0.28 (0.11)	
Boulder	0.73 (0.10)	
Substrate embeddedness		0.98
Low	0.27 (0.09)	
Intermediate	N/A	
High	-0.09 (0.15)	
Depth		0.98
Depth	3.36 (0.82)	
Depth ²	-3.03 (0.90)	
Channel unit		0.57
Pool	0.08 (0.05)	
Riffle	N/A	
Run	0.06 (0.05)	
Velocity	-0.44 (0.41)	0.50

N/A denotes category used as reference in coefficient determinations so no estimate is available.

appeared in all the competing models. Channel unit type (*i.e.*, pool, riffle, or run) had a summed w_i of 0.57 (Table 2), and occurred in the top and third ranked models. Velocity was the least influential variable (summed w_i of 0.50), and occurred in the second and third ranked models. Note that there is some inherent bias in the interpretation of the sum of AIC w_i because not all variables were represented in all four candidate models.

The direction of effect indicated by competing models and the multi-model averaged RSF suggested that burbot selected pools over riffles and runs, and

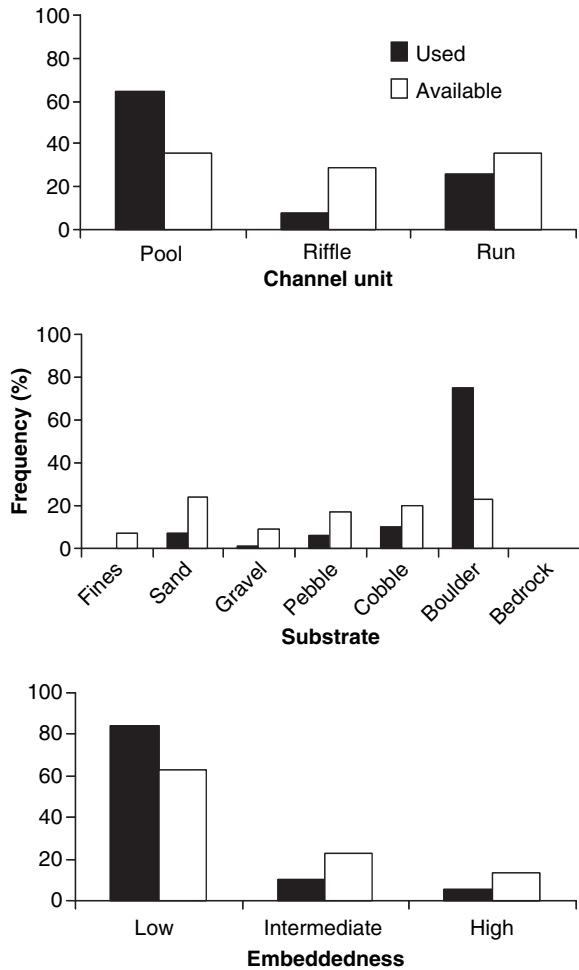


Fig. 2. Frequency of use and availability histograms of categorical habitat characteristics in the Lower Hollenbeck and Hollenbeck/Brown samples sites.

locations with the largest dominant substrates, lowest levels of embeddedness, greatest water depths, and lowest water velocities. Use and availability frequency histograms were developed to provide additional support for categorical habitat parameters (Fig. 2).

Reach-scale resource selection

The number of burbot captured ranged from 0–26 in the reaches sampled ($N = 24$). Categorization of reaches as absent, low, moderate, and high reflected burbot numbers of 0, 1–5, 8–15, and 22–26, respectively (Fig. 3). Six of the reach-scale variables were significantly correlated with burbot occurrence ($|r| > 0.50$; $P < 0.05$); gradient, mean temperature, sinuosity, dominant substrate, canopy shade index, and instream cover index. High multicollinearity among the variables was present and precluded multivariable model development (Table 3). Therefore, the six univariate models were considered a candidate model set and AIC_c values and w_i were calculated. A top-ranked model was identified along with three competing models with w_i values within 10% of that of the top-ranked model (Table 4).

The AIC_c values and respective w_i of the four candidate models indicated that the model containing gradient was the most supported for predicting burbot abundance within reaches. The fitted polytomous logistic regression model intercept and coefficient for gradient were used to develop probability functions given by the following;

Fig. 3. Frequency of burbot abundance in study site stream reaches. Categorization of reaches as absent, low, moderate, and high abundance based on capture numbers of 0, 1–5, 8–15, and 22–26 burbot during electrofishing sampling.

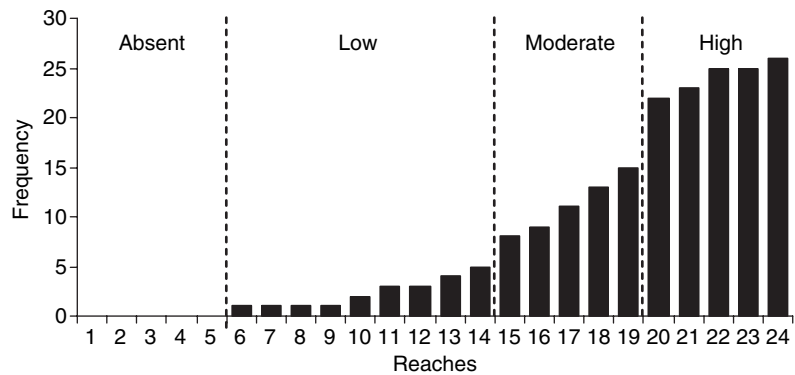


Table 3. Pearson correlation coefficients (P -values) among reach-scale habitat characteristics correlated with burbot abundance.

	Gradient	Mean temp.	Sinuosity	Dominant substrate	Canopy shade index	Instream cover index
Gradient	1.0000	-0.4332 (0.0344)	-0.4715 (0.0200)	0.8626 (0.0001)	0.6630 (0.0004)	0.3970 (0.0547)
Mean temp.		1.0000	0.2317 0.2760	-0.6781 (0.0003)	-0.2283 (0.2834)	-0.4141 (0.0443)
Sinuosity			1.0000	-0.4658 (0.0218)	-0.4245 (0.0387)	-0.3562 (0.0876)
Dominant substrate				1.0000	0.5932 (0.0022)	0.3470 (0.0967)
Canopy shade index					1.0000	0.3952 (0.0560)

Values from 24 stream reaches were used. Correlations significant at $\alpha = 0.05$ are in bold.

Table 4. Polytomous logistic regression models predicting occurrence of burbot from reach-scale explanatory variables.

Model	K	-2Log _e L	AIC _c	w _i
Gradient	4	55.76	60.43	0.46
Mean temperature	4	57.02	61.70	0.24
Sinuosity	4	58.21	62.88	0.13
Dominant substrate	6	54.76	63.26	0.11

Models are ranked according to Akaike's Information Criterion corrected for small sample size (AIC_c), which was calculated from the number of estimated parameters (K), the log likelihood (-2log_eL). AIC weights (w_i) were used to select the 'best approximating' models from a set of candidate exploratory models. Competing models with w_i values that were 10% or greater than the maximum w_i are included in the table.

$$P(\text{"absent"}) = \frac{\exp(0.7394 - 0.193 \times \text{gradient})}{1 + \exp(0.7394 - 0.193 \times \text{gradient})}$$

$$P(\text{"low + absent"}) = \frac{\exp(-1.3414 - 0.193 \times \text{gradient})}{1 + \exp(-1.3414 - 0.193 \times \text{gradient})}$$

$$P(\text{"moderate + low + absent"}) = \frac{\exp(-2.7727 - 0.193 \times \text{gradient})}{1 + \exp(-2.7727 - 0.193 \times \text{gradient})}$$

where *P* = probability of a reach having burbot abundances of 'absent', 'low and absent combined' or 'moderate, low, and absent combined'. Isolating the probabilities for low, moderate, and high categories was calculated by; *P*(low) = *P*(low + absent) - *P*(absent), *P*(moderate) = *P*(moderate + low + absent) - *P*(low + absent), and *P*(high) = 1 - *P*(moderate + low + absent), respectively. The separated probabilities for low, moderate, and high burbot abundance in stream reaches are plotted together against gradient (Fig. 4). Reaches with low, moderate, or high abundance of burbot were predicted to have steeper gradients than reaches where burbot were absent.

The second-ranked polytomous logistic regression model contained mean temperature and was given by the following;

$$P(\text{"absent"}) = \frac{\exp(51.5822 - 2.2945 \times \text{temperature})}{1 + \exp(51.5822 - 2.2945 \times \text{temperature})}$$

$$P(\text{"low + absent"}) = \frac{\exp(49.5075 - 2.2945 \times \text{temperature})}{1 + \exp(49.5075 - 2.2945 \times \text{temperature})}$$

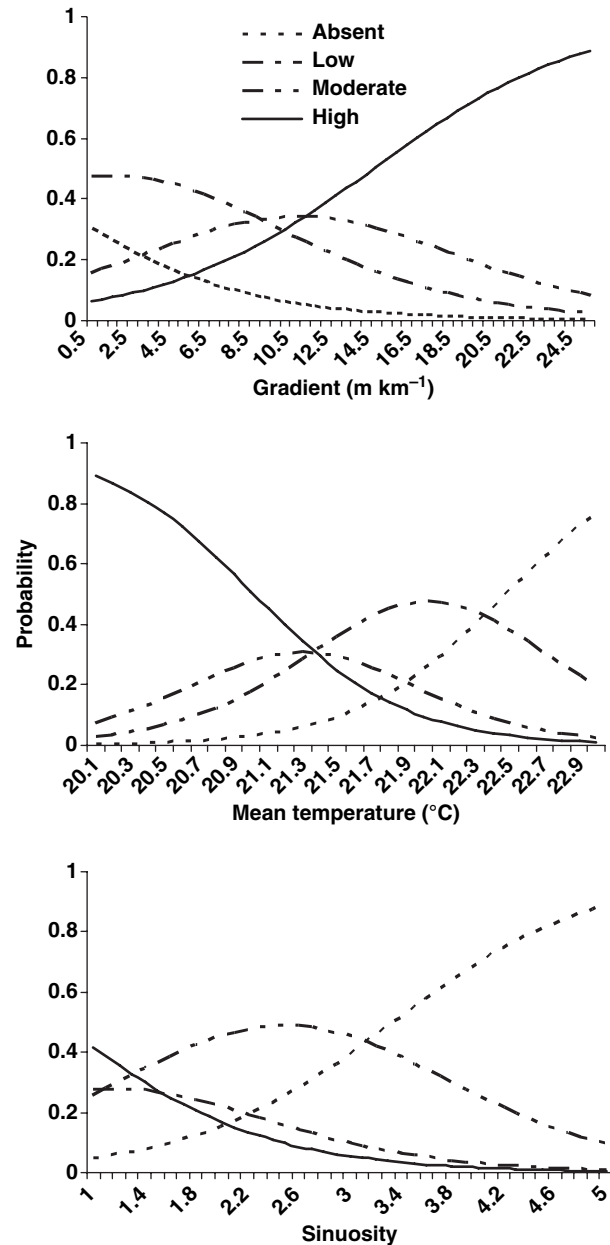


Fig. 4. Probability plots of single-variable polytomous logistic regression models that predict burbot abundance levels in stream reaches. Plots show the predicted probabilities of occurrence for abundance categories of absent (0 burbot), low (1–5 burbot), moderate (8–15 burbot) and high (22–26 burbot) in terms of levels of habitat predictor variables gradient, mean summer temperature, and stream channel sinuosity.

$$P(\text{"moderate + low + absent"}) = \frac{\exp(48.2238 - 2.2945 \times \text{temperature})}{1 + \exp(48.2238 - 2.2945 \times \text{temperature})}$$

Separated probabilities were calculated the same as for gradient. The probability plot indicated that the number of burbot within a reach was predicted to decrease as mean temperature increased (Fig. 4).

The model containing sinuosity was also used to develop probability functions and was given by the following;

$$P(\text{"absent"}) = \frac{\exp(4.2032 - 1.2564 \times \text{sinuosity})}{1 + \exp(4.2032 - 1.2564 \times \text{sinuosity})}$$

$$P(\text{"low + absent"}) = \frac{\exp(2.0599 - 1.2564 \times \text{sinuosity})}{1 + \exp(2.0599 - 1.2564 \times \text{sinuosity})}$$

$$P(\text{"moderate + low + absent"}) = \frac{\exp(0.9109 - 1.2564 \times \text{sinuosity})}{1 + \exp(0.9109 - 1.2564 \times \text{sinuosity})}$$

The probability plot indicated that the number of burbot within a reach was predicted to decrease as sinuosity increased (Fig. 4).

In the fourth-ranked model, dominant substrate was a categorical explanatory parameter; and a probability plot similar to gradient, mean temperature, and sinuosity could not be developed. Instead, frequency histograms of predicted abundance levels of burbot within a reach were constructed based on substrate category. The fitted polytomous logistic regression model intercepts for each category of dominant reach-level substrate were given by the following;

$$P(\text{"absent"}) = \frac{\exp(2.3972 - 1.4514 \times \text{sand})}{1 + \exp(2.3972 - 1.4514 \times \text{sand})}$$

$$P(\text{"low + absent"}) = \frac{\exp(0.2901 - 1.4514 \times \text{sand})}{1 + \exp(0.2901 - 1.4514 \times \text{sand})}$$

$$P(\text{"moderate + low + absent"}) = \frac{\exp(-1.2466 - 1.4514 \times \text{sand})}{1 + \exp(-1.2466 - 1.4514 \times \text{sand})}$$

Separating probabilities of low, moderate, and high abundances were conducted the same as for continuous variables. Burbot were predicted to be absent in reaches dominated by sand 62% of the time, and to have low abundances 31%, moderate 5%, and high 2% (Fig. 5).

The model intercepts for cobble were given by the following;

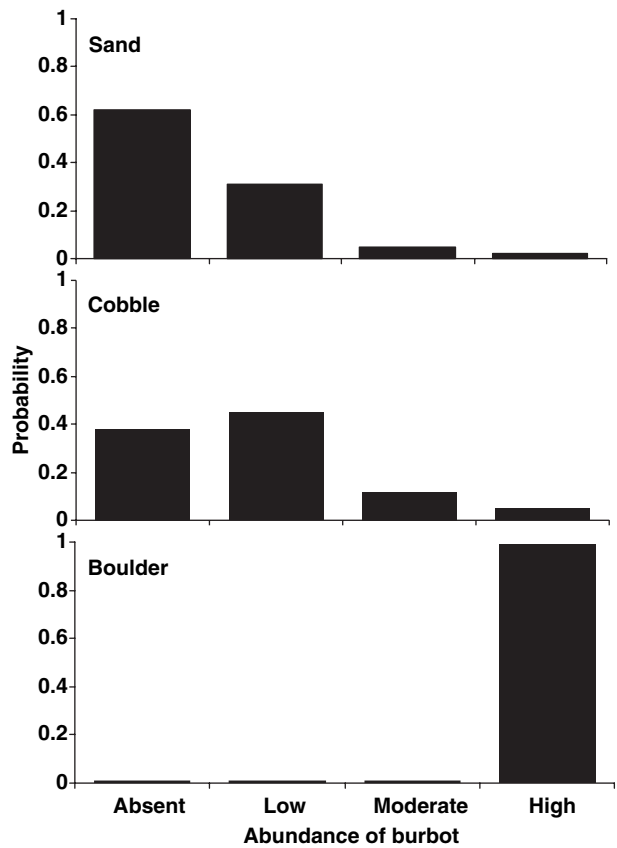


Fig. 5. Probabilities of burbot abundance categories among categories of the habitat predictor variable dominant substrate. Reaches sampled only contained dominant substrates of sand, cobble, and boulder.

$$P(\text{"absent"}) = \frac{\exp(2.3972 - 0.3824 \times \text{cobble})}{1 + \exp(2.3972 - 0.3824 \times \text{cobble})}$$

$$P(\text{"low + absent"}) = \frac{\exp(0.2901 - 0.3824 \times \text{cobble})}{1 + \exp(0.2901 - 0.3824 \times \text{cobble})}$$

$$P(\text{"moderate + low + absent"}) = \frac{\exp(-1.2466 - 0.3824 \times \text{cobble})}{1 + \exp(-1.2466 - 0.3824 \times \text{cobble})}$$

Burbot were predicted to be absent in reaches dominated by cobble 38% of the time, to have low abundances 45%, moderate 12%, and high 5% (Fig. 5).

The model intercepts for boulder were given by the following;

$$P(\text{"absent"}) = \frac{\exp(-2.3972 - 1.8338 \times \text{boulder})}{1 + \exp(-2.3972 - 1.8338 \times \text{boulder})},$$

$$P(\text{"low + absent"}) = \frac{\exp(-0.2901 - 1.8338 \times \text{boulder})}{1 + \exp(-0.2901 - 1.8338 \times \text{boulder})},$$

$$P(\text{"moderate + low + absent"}) = \frac{\exp(1.2466 - 1.8338 \times \text{boulder})}{1 + \exp(1.2466 - 1.8338 \times \text{boulder})}.$$

Burbot were predicted to be absent in reaches dominated by boulder <1% of the time, and have low abundances <1%, moderate <1%, and high 99% (Fig. 5). The abundance of burbot within a reach was predicted to increase as substrate size increases.

Discussion

Five microhabitat predictor variables were supported as influencing burbot occurrence, the most important being substrate type, substrate embeddedness, and depth. Robins & Deubler (1955) reported that the most important habitat feature for burbot was shelter of sufficient size to completely hide. In lakes, shelter among the interstices of large stones in the littoral zone is more important than temperature preferences of burbot during their first year of life (Hofmann & Fischer 2002). Cover might provide protection from predators and refuge from current velocities for burbot (McMahon et al. 1996; Fisher 2000b). Laboratory experiments have shown that the unavailability of refuges stressed burbot, even when predators were absent (Fischer 2000a). Burbot used boulder size substrate with low levels of embeddedness in greater proportion than availability in the Hollenbeck drainage sample sites that may have optimized opportunities to inhabit shelter of sufficient size. Although large woody debris was prevalent throughout samples sites, relatively few burbot used it at the time of capture.

The influence of depth on burbot presence was also well supported in the models. In general, burbot selected deeper locations, but the result was conditional on substrate size and embeddedness. Mean residual pool depth of available pools was one-third greater than the average pool depth at capture locations, which suggests that burbot may select large substrate for cover over depth at the microhabitat scale. Depth selection might not be realized beyond a

threshold depth. Also, our microhabitat analysis was based on daylight sampling when burbot typically are sedentary (Carl 1995). This may also partly explain why velocity was the least important of the variables included in candidate models, even though velocity and discharge affect burbot migration in rivers (Jones et al. 1974; Paragamian 2000). In the Ohře River in the Czech Republic, burbot occupied relatively shallow habitats with large substrate size and high velocities during daylight hours, shifting to deeper areas with lower velocities and small substrate size at dusk (Slavík et al. 2005). Also, our sampling captured predominantly adult burbot, age 0-sized fish were noticeably rare, and the resulting RSF and predictor variables must be interpreted accordingly. Various life stages require different types of physical habitats (Fischer 1999; Fisher 2000b). Future research should describe the habitat requirements of larval and juvenile burbot in streams because little information exists (Fisher 2000b). Several factors affected the probability of burbot occurrence at the reach-scale, with gradient being the most supported explanatory variable. Gradient has been a good predictor of fish distributions as observed in changes in assemblage memberships at different elevations in stream systems and littoral zones (Rahel & Hubert 1991; Fladung et al. 2003; Robinson & Rand 2005). Study reaches with a gradient of 8 m·km⁻¹ or greater contained a moderate or high abundance of burbot and accounted for 49% of all burbot captured. Gradient was correlated with several other reach-scale features, including mean temperature, sinuosity, and dominant substrate. In observational studies such as this one there is a high probability that some of the predictor variables will be correlated (Burnham & Anderson 1998). For example, as mean gradient decreases longitudinally downstream from the headwaters mean water temperature increases as the influence of riparian vegetation declines, reducing shading within the channel (Rutherford et al. 2004). Gradient may therefore be a surrogate for several other reach-scale features affecting burbot occurrence in these small streams. In the La Bar River watershed in France, burbot were similarly more abundant in narrow upstream reaches than in the lower reaches (Dillen et al. 2008a).

Mean water temperature was the second most supported reach-scale model in the candidate set. The probability plot suggested that habitat was maximized below a mean temperature of 21.5 °C. The trend illustrated by the model indicated that burbot occupy reaches with cooler average temperatures which were found at higher elevations within the watershed. Water temperature affects all biochemical processes (Hardewig et al. 2004) and was considered the most important environmental factor controlling the distribution of burbot in areas of suitable habitat in

Pennsylvania rivers (Robins & Deubler 1955). In contrast to the reach-scale, water temperature was not correlated with burbot presence at the microhabitat-scale. Water temperatures at capture locations ranged from 16.0–26.8 °C which subjected 83% of all burbot to temperatures above the reported optimal thermal preference of 15.6–18.2 °C (Scott & Crossman 1973). All reaches within the study sites exceeded mean daily temperatures of 20 °C in July and August 2005. Burbot have an evolutionarily-adapted strategy to survive warm water temperatures by going into a quiescent state during the summer months and restricting activities such as spawning to the winter season when water temperatures are lower (Hölker et al. 2004). This project was not intended to evaluate diel activity levels of burbot during summer months, but future investigations could prove useful in understanding survival mechanisms in these thermally variable watersheds.

Stream ecosystems may be viewed as hierarchal environments (Frissell et al. 1986) such that processes that structure habitat at larger spatial scales may directly influence the structure of habitat at smaller scales. For example, gradient on the reach scale directly affects dominant substrate type at the microhabitat scale through sediment transport mechanisms (Knighton 1998). These relationships can be altered by anthropogenic activities, as evidenced by two low-gradient reaches comprised of primarily sand substrate within the Lower Hollenbeck study site which contained a moderate and high abundance of burbot. These reaches were both areas where meander bends neared roadways and large boulders (rip-rap) had been placed within the stream to increase bank stability.

The information-theoretic approach is not often considered in exploratory data analyses, however, it proved to be a useful framework for this research even though little *a priori* knowledge was available on the resource selection of burbot in small streams. The approach allowed us to identify competing combinations of habitat features associated with burbot occurrence and address model uncertainty through multi-model averaging. Our limited all-subsets approach can potentially stabilize the negative characteristics of multicollinearity among explanatory variables (Graham 2003). Future researchers now have our RSFs to hypothesize upon when investigating lotic populations. Additionally, the RSFs can be paired with hydrodynamic models of riverine habitat to perform instream flow assessments (Guay et al. 2000). Specifically this study probabilistically quantified that at the microhabitat-scale burbot used channel units with low current velocities, increased depth, and large substrate particles that have low levels of embeddedness. At the reach-scale burbot used reaches associated

with higher gradients, relatively less sinuosity, cooler mean water temperatures, and large substrate.

At the onset of the project we hoped to discover many burbot in the Blackberry River, but only three fish were captured by thoroughly sampling 5.4 km encompassing the fish kill zone where burbot were first observed in the watershed. Although we could not use these limited data in RSF model development, it provides an example of how results can be used to inform conservation and management decisions. Given lower gradient and higher water temperature, our RSFs do not predict the Blackberry site be as highly populated as the higher-gradient, cooler reaches in the Hollenbeck watershed. These reach-scale observations modify the similarity of the sites when only microhabitat is considered. For example, the mean gradient of the reaches at the Blackberry site was $4.3 \text{ m}\cdot\text{km}^{-1}$. The probability plot for the gradient RSF predicts a 45 % chance of observing low abundance and only a 12% chance of observing high abundance. Mean temperature in the Blackberry site (21.8° C) was near the higher end of the range observed, and the RSF predicted again a 45% chance of low abundance and a 14% chance of high abundance. With this information, fisheries biologists may choose to turn attention elsewhere, such as higher gradient reaches further upstream in the Blackberry watershed which may be better candidates for translocation. The microhabitat and reach RSFs we developed can be used to evaluate potential translocation sites in other locales by collecting the reduced suite of habitat measurements to quantitatively evaluate sites.

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Supporting information

Additional Supporting Information may be found in the online version of this article.

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Fig. S1. Location of study sites in northwest CT that were selected based on locations where burbot were recently found. The Blackberry site was located on the Blackberry River in the town of North Canaan. The Lower Hollenbeck and the Hollenbeck/Brown sites were located in the Hollenbeck River watershed in Canaan.

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