



Land cover influences on juvenile Rainbow Trout diet composition and condition in Lake Michigan tributaries

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Funding information

Great Lakes Fishery Trust, Grant/Award Number: 1298; George L. Disborough TU Research Grant Fund

Abstract

Watershed development may alter tributaries in ways that influence the growth and development of juvenile fish. For Rainbow Trout *Oncorhynchus mykiss*, the extent of land cover influence on the diet composition of stream-residing juveniles is still an open but important question, particularly given their broad global distribution. Our study evaluated the effect of land cover on diet composition and condition metrics of juvenile Rainbow Trout in Lake Michigan tributaries. Juveniles were collected in the fall of 2014 and 2015 from 18 sampling locations across the Lake Michigan basin and included a wide variety of land cover types. Multivariate statistical procedures were used to quantitatively score sites along axes that maximized variation in land cover and diet composition. Subsequently, Spearman's rank correlations were used to test for significance of correlations between (a) land cover and diet composition, (b) land cover and fish condition, and (c) diet composition and fish condition. Our results indicated that land cover had an influence on the diet compositions of juvenile Rainbow Trout, but neither land cover nor diet composition had a significant influence on Rainbow Trout condition. These findings contrast with previously published work focusing on the growth responses of other fish species and provide insight into the plastic nature of Rainbow Trout. Further, we discuss potential ways in which fish may mitigate the effect of land cover changes as they are transmitted through stream food webs; however, the magnitude of the mitigation likely varies among fish species.

KEYWORDS

diet composition, fish condition, great lakes, land cover, Rainbow Trout, tributary

1 | INTRODUCTION

The expansion and sprawl of the human population in recent decades has largely altered the composition of previously forested landscapes. Urbanization and agricultural practices indirectly alter natural watershed functions and often have negative consequences for aquatic life. In urban and agricultural systems, benthic richness and diversity scores tend to be lower than in forested streams (Allan, 2004; Lenat & Crawford, 1994; Quinn, Cooper, Davies-Colley,

Rutherford, & Williamson, 1997; Waters, 1995). These land cover practices can result in simplified benthic assemblages as increased sedimentation, altered temperature regimes and nonnatural nutrient additions influence taxa according to a tolerance gradient (Hilsenhoff, 1988).

Impervious surfaces in urban settings reduce infiltration to both subsurface and groundwater sources, resulting in an accumulation of runoff through storm drains. Drains serve as conduits for human influences by acting as vectors for the transport of pollutants from

urban activities (e.g., vehicle lubricants and coolants, road salts) to streams (Changnon & Demissie, 1996; Klein, 1979). This nonnatural water return heightens stream flow rates, increasing the risk of bank erosion and sedimentation (Stepenuck, Crunkilton, & Wang, 2002). Likewise, areas dominated by agriculture are vulnerable to similar effects especially if riparian vegetation has been removed (Lemly, 1982).

Watershed development and deforestation may alter available water temperature regimes in a given stream habitat. Reductions in riparian vegetation which are often associated with land development expose streams to more direct sunlight, increasing water temperatures and heightening the metabolic activities of fish (Huryn, 1998; Tumbiolo & Downing, 1994). Increases in available water temperatures mean that metabolic demands and therefore consumption by fish will be higher. In situations where benthic assemblages have additionally been impacted by sedimentation, the pressure of increased fish consumption, along with reduced habitable substrates (via sedimentation), may result in a less diverse prey base. Urban (Kemp & Spotila, 1997) and agricultural runoff (Lemly, 1982) may contribute to the benthic dominance of Chironomidae spp. and Simuliidae spp., both of which are less energy dense than more sensitive species such as Ephemeroptera spp. or Trichoptera spp. (Kemp & Spotila, 1997; Klein, 1979). That is to say, as pollutants leach into streams and sedimentation rates increase, populations of sensitive, high-energy taxa (Ephemeroptera, Plecoptera, and Trichoptera) are often reduced (Sponseller, Benfield, & Valett, 2001), if not lost altogether. Streambed sedimentation, altered temperature regimes and nutrient fluxes contribute to shifts in macroinvertebrate community compositions which serve as the primary food source for many stream fish species.

Rainbow Trout *Oncorhynchus mykiss*, the focal species of this study, are generalist feeders, with diet compositions reflective of the benthos (Di Prinzie, Miserendino, & Casaux, 2013; Godby, Rutherford, & Mason, 2007). In Michigan streams, the diets of juvenile Rainbow Trout largely consist of the most abundant taxa in the benthos (Godby et al., 2007). Similarly, Fierro et al. (2016) noted that Rainbow Trout predominantly preyed upon the dominant taxa in streams of southern Chile, and their diet compositions were altered by riparian disturbances. This led us to hypothesize that diet compositions and weight-at-length fish conditions may be influenced by land cover development. Rainbow Trout are present in a diverse array of stream habitats and therefore provide an excellent resource for contrasting stream fish diets across land cover types.

Although land covers within and across watersheds vary greatly, and implications to stream habitats have been explored, there is much less information on the direct and indirect effects of land cover on fish. The goals of this study were to (a) determine how land cover within the catchment influenced diet compositions of juvenile Rainbow Trout and (b) evaluate the consequent effects of land cover and diet composition on the condition of juvenile Rainbow Trout. We hypothesized a positive relationship between catchment disturbance and the dietary importance of tolerant macroinvertebrate species that would lead to a negative effect of catchment disturbance on Rainbow Trout condition.

2 | METHODS

Juvenile Rainbow Trout (age 0+) were sampled from streams throughout the basin of Lake Michigan (Figure 1; Table 1) in the fall of 2014 and 2015, and were collected through backpack electrofishing. Sampling locations were initially selected to encompass a large spatial extent within the basin of Lake Michigan as part of a previous study; from an initial set of 46 sites, 18 were chosen for the focus of this study based on the number of juvenile Rainbow Trout collected, and to encompass a catchment disturbance gradient. For each sampling location, the per cent land cover was calculated for the network catchment spatial extent described by Brenden et al. (2006) using the 2006 National Land Cover Database (Fry et al., 2011). For each of 8 land use categories, we summed the percentages of similar land cover classifications (Table 1): (a) water (open water), (b) developed (developed—open space, developed—low intensity, developed—medium intensity, and developed—high intensity), (c) barren (barren land—rock/sand/clay), (d) forest (deciduous forest, evergreen forest, mixed forest), (e) shrubland (shrub/scrub), (f) herbaceous (grassland/herbaceous, sedge/herbaceous), (g) planted/cultivated (pasture/hay, cultivated crops), and (h) wetlands (woody wetlands, emergent herbaceous wetlands). See Anderson, Hardy, Roach, and Witmer (1976) for more detailed descriptions of land cover classifications. To meet the assumptions of multivariate normality, land cover percentages were arcsine square root transformed. Principal component analysis (PCA; R prcomp) was applied to (a) maximize the variability among sites with a reduced number of synthetic land cover variables, (b) visualize the distribution of sites according to land cover, and (c) assess which land cover variables drive variation within our sites.

Upon collection, the juvenile Rainbow Trout were placed on ice in the field, and to reduce the extent of length and weight shrinkage (Sayers, 1987), frozen in water upon returning to the lab. At the time of laboratory processing, total body length (mm) and mass (0.1 g) were measured for each fish, and the stomach (including pyloric caecum) and oesophagus were removed and preserved in 95% ethyl alcohol. Stomach contents of 10 fish were analysed from each site, with the exception of Eighteen Mile and Hibbard creeks from which only nine stomachs were analysed. Each identifiable prey item was analysed in a petri dish of reverse osmosis water using a dissecting microscope, classified to the lowest possible taxon, and then placed back into the original glass vial for storage. When the classification level of a given prey type was consistent among all samples, that level was used in our analyses. However, when taxonomic classification was possible to Family in some samples and only to Order in others, all identifications were adjusted to fit into the most encompassing category (i.e., Order).

Stomach contents were quantified by calculating the Index of Relative Importance (IRI), a composite measure designed by Pinkas, Oliphant, and Iverson (1971) to assess each taxon's contribution to the overall diet. This methodology is reliable in determining relative taxon importance (Hyslop, 1980) and has been a common metric used in similar studies (e.g., Fierro et al., 2016; Miller, Brodeur, Rau, & Omori, 2010). The IRI values for each prey item were calculated as

the product of the frequency of appearance (%F) and the abundance of occurrence (%N) scores, divided by 100. Frequency of appearance (%F) was the percentage of stomachs at each site containing a given taxon, and %N was the percentage of individual diet items at each site from a given taxon. Nonmetric multidimensional scaling (NMDS) was used to summarize and analyse the IRI matrix in R (Field, Clarke, & Warwick, 1982; Mueter & Norcross, 1999), utilizing the metaMDS function (Bray-Curtis distance calculation method; 2 dimensions) of the "vegan" package.

Lastly, to generate indices of fish condition, we estimated site-specific expected Rainbow Trout weights at a total length representative of the whole study area. These were used as site-specific indices of mean fish condition in the subsequent correlation analyses. Weight W of fish j from site i was assumed to be exponentially related to its total length L according to an allometric growth model with a multiplicative error structure (Equation 1; Quinn & Deriso, 1999). We used least squares linear regression to estimate growth parameters for each site (i.e., slope $\ln(a)$ and intercept b) according

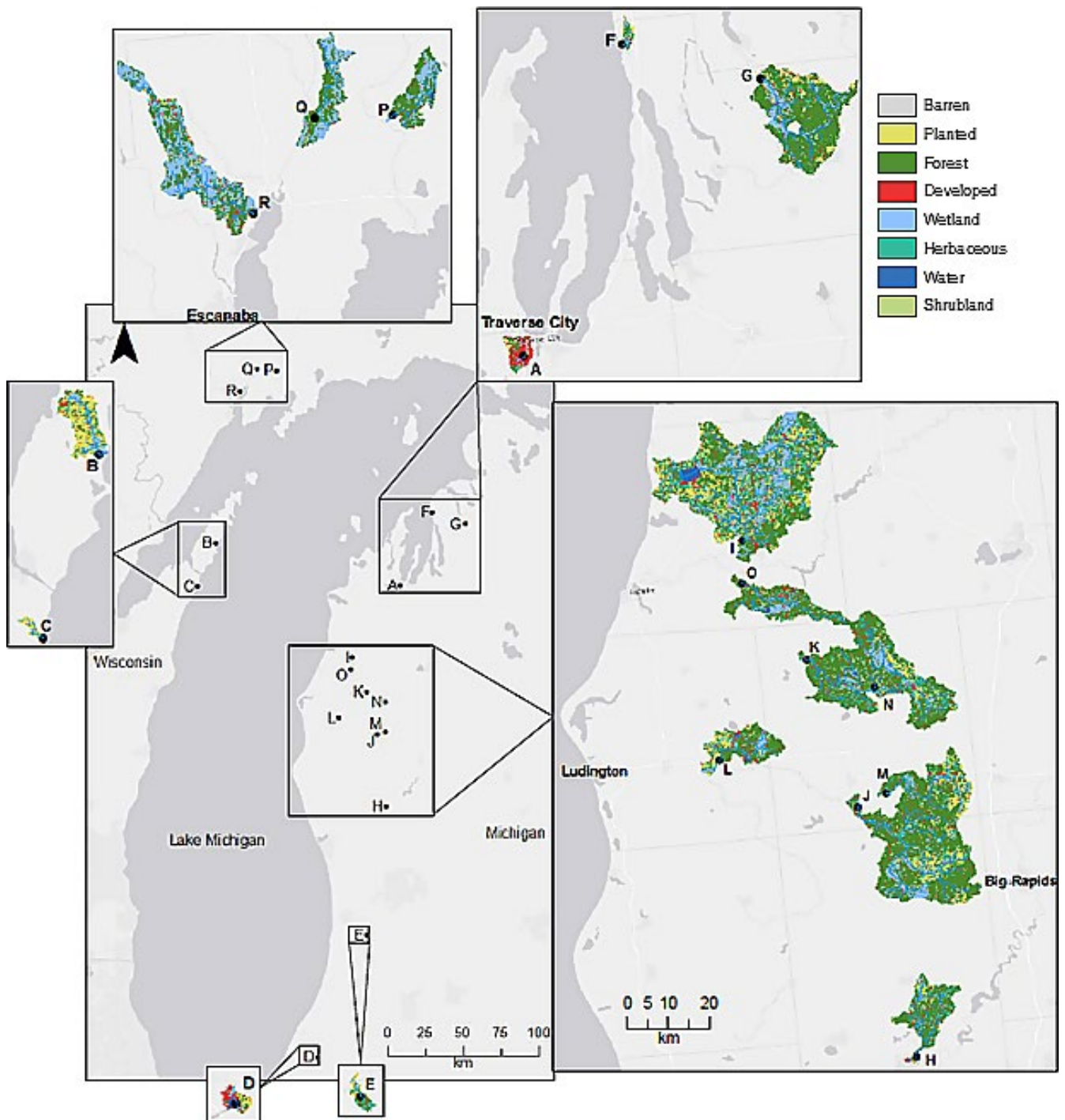


FIGURE 1 Catchment land covers of the 18 sites from which Rainbow Trout were collected for this study. Site IDs are given in Table 1

TABLE 1 This table serves to summarize site IDs, fish collection dates, sample sizes, mean total fish lengths (\pm SE) used to evaluate fish conditions and network catchment land cover percentages incorporated into the PCA

Site	ID	Date	Order	N	Fish samples		Land cover (%)								
					TL \pm SE	Water	Developed	Barren	Forest	Shrubland	Herbaceous	Planted	Wetlands		
Antrim Cr	F	9-17-2014	1	10	59.30 \pm 2.73	0.0	7.1	0.5	36.4	1.3	12.2	25.2	17.3		
Bear Cr	I	9-18-2014	2	10	76.70 \pm 4.03	1.6	6.1	0.1	40.6	4.0	14.8	15.5	17.2		
Bigelow Cr	H	9-24-2014	2	10	71.20 \pm 3.33	0.5	4.6	0.1	67.6	1.7	10.1	8.0	7.4		
Days R	R	8-26-2015	2	10	77.90 \pm 2.69	0.1	3.5	0.0	38.0	1.1	1.1	2.8	53.4		
Eighteen Mile Cr	P	8-26-2015	2	9	70.00 \pm 2.08	1.3	1.7	0.0	64.3	0.2	0.2	0.0	32.3		
Haymeadow Cr	Q	8-26-2015	2	10	73.40 \pm 2.77	1.6	1.3	0.1	48.0	0.1	0.1	0.0	48.8		
Hibbard Cr	B	9-2-2014	2	9	76.22 \pm 2.84	0.1	6.1	<0.1	17.0	0.4	0.5	56.0	19.7		
Jordan R	G	8-28-2014	3	10	65.10 \pm 3.74	<0.1	3.2	<0.1	70.7	1.4	4.9	7.8	12.0		
Kids Cr	A	8-30-2014	1	10	59.50 \pm 2.57	0.0	62.9	0.0	16.1	0.1	1.3	16.2	3.4		
Little Manistee R	K	10-10-2014	3	10	64.30 \pm 5.35	0.6	4.6	0.1	66.3	7.2	6.8	4.8	9.6		
Pere Marquette R ^a	J	10-9-2014	3	10	75.10 \pm 4.01	0.2	3.3	<0.1	66.8	3.8	4.5	8.8	12.5		
Pere Marquette R ^b	M	10-25-2014	3	10	62.70 \pm 5.11	0.5	5.3	0.0	58.3	3.5	7.1	15.8	9.7		
Pine Cr	O	11-4-2014	2	10	73.30 \pm 3.96	1.5	7.3	0.1	66.9	4.7	3.7	0.4	15.4		
Silver Cr	E	9-3-2014	1	10	67.10 \pm 3.25	0.1	4.1	0.2	55.9	0.1	11.8	16.7	11.1		
Townsend Cr	D	9-3-2014	1	10	71.90 \pm 2.33	0.0	16.1	0.0	28.5	0.0	2.2	41.9	11.3		
Twin Cr	N	11-4-2014	2	10	73.70 \pm 3.89	<0.1	4.2	0.0	58.3	10.4	6.4	7.2	13.4		
Weldon Cr	L	10-10-2014	2	10	84.40 \pm 2.30	2.5	5.7	0.1	58.0	2.7	6.3	10.2	14.6		
Woodard Cr	C	9-2-2014	1	10	72.80 \pm 2.42	<0.1	3.9	<0.1	6.8	2.2	0.4	69.4	17.3		

Note. ^aLittle South Branch of the Pere Marquette River; ^bMiddle Branch of the Pere Marquette River.

to Equation 2 (which is derived ln-transforming Equation 1 and results in an additive error structure on the ln-scale).

$$W_{ij} = a_i L_{ij}^{b_i} e^{\epsilon_{ij}} \quad (1)$$

$$\ln(W_{ij}) = \ln(a_i) + b_i \ln(L_{ij}) + \epsilon_{ij} \quad (2)$$

We used the site-specific growth parameters estimated from equation 2 to calculate $\bar{W}_{i,70.79}$'s which are the geometric mean expected Rainbow Trout weights at 70.79 mm for each site (Table 2).

Spearman's rank correlations were used to test for significant relationships ($\alpha = 0.05$) between (a) land cover and diet compositions, (b) land cover and fish conditions, and (c) diet compositions and fish conditions. Throughout the analyses, site land cover was ranked on the first principal component axis (rank 1 = most disturbed; rank 18 = most forested), diet composition ranked on the first NMDS axis (rank 1 = tolerant taxa; rank 18 = sensitive taxa), and fish condition ranked in terms of weight-at-length (g) predictions (rank 1 = predicted to be lightest; rank 18 = predicted to be heaviest).

3 | RESULTS

In total, 60.15% of the variation among land cover percentages was explained by the first 2 PCA axes (Figure 2). Principal component 1 explained 35.25% of the variation and was most strongly correlated to forest ($r = 0.525$), planted/cultivated ($r = -0.450$), and developed

($r = -0.381$) land cover. Principal component 2 explained 24.89% of the variation and was correlated to wetland ($r = -0.586$) and herbaceous ($r = 0.588$) land cover. The first principal component axis explained the most variation related to watershed development and was therefore selected for use in subsequent Spearman's rank correlation analyses.

Stomach contents were analysed from a total of 178 juvenile Rainbow Trout. Fish ranged from 28 mm to 99 mm in length, and weighed between 0.05 g and 10.40 g. Their diets were composed of prey from 18 orders, largely consisting of macroinvertebrate nymph and larval forms, interspersed with terrestrial insects (Figure 3). An average of 14.15 prey items were counted in each diet sample, and of the 18 orders observed, Ephemeroptera, Plecoptera, Trichoptera, and Diptera were consistently consumed across all sites. The values of the diet taxa with respect to the first NMDS axis were significantly correlated with their respective pollution-sensitivity values as reported by Hilsenhoff (1988; $F_{1,14} = 26.9$, $p < 0.001$, $r^2 = 0.634$; see Table 3). Given this relationship, the first NMDS axis was incorporated into the Spearman's rank analyses.

We observed a strong correlation between land cover and diet composition (Figure 4a; $p = 0.012$, $\rho = 0.585$, $n = 18$) such that the importance of sensitive taxa in the diet increased as sites became more forested. The relationship between fish condition and taxa sensitivity was weak (Figure 4b; $p = 0.114$, $\rho = 0.387$, $n = 18$) and clearly not related to land cover whose relationship to fish condition was even weaker (Figure 4c; $p = 0.536$, $\rho = 0.156$,

TABLE 2 Growth model parameters ($\ln(a)$ and b) and estimated weights at 70.79 mm ($\bar{W}_{70.79}$) for each site i based upon Equation 2

Site	$\bar{W}_{i,70.79}$ (g)	$\ln(a)$	b
Antrim Cr	4.3625	-13.0506	3.4096
Bear Cr	4.2612	-10.1761	2.7292
Bigelow Cr	3.7379	-10.6497	2.8097
Days R	3.4596	-14.2010	3.6252
Eighteen Mile Cr	3.7949	-11.9106	3.1092
Haymeadow Cr	3.6423	-11.4617	2.9942
Hibbard Cr	4.2135	-11.6550	3.0738
Jordan R	3.2704	-13.7074	3.4961
Kids Cr	3.2858	-11.5756	2.9968
Little Manistee R	4.1663	-13.3424	3.4673
Pere Marquette R ^a	3.7324	-12.1439	3.1601
Pere Marquette R ^b	4.1368	-17.3534	4.4072
Pine Cr	4.0136	-12.9703	3.3711
Silver Cr	4.1737	-13.3501	3.4695
Townsend Cr	3.9244	-10.9048	2.8810
Twin Cr	3.8645	-11.3268	2.9764
Weldon Cr	4.0420	-11.0838	2.9299
Woodard Cr	3.7741	-14.4744	3.7098

Note. ^aLittle South Branch of the Pere Marquette River; ^bMiddle Branch of the Pere Marquette River.

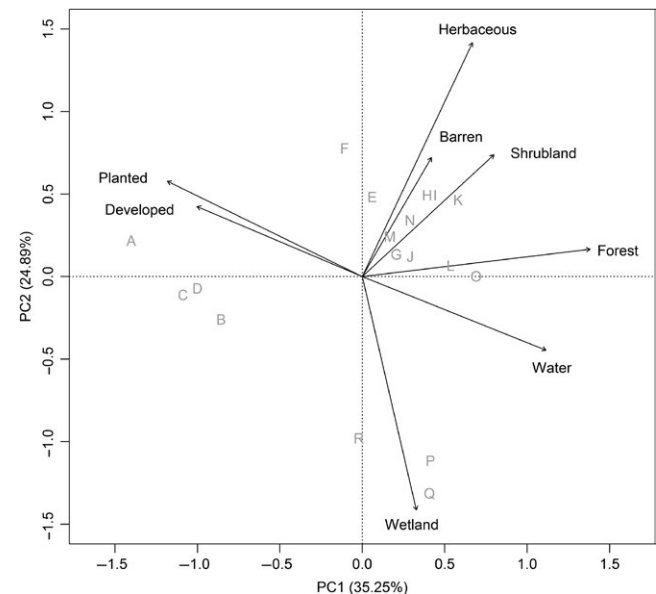


FIGURE 2 In this PCA analysis relating sampling locations to catchment land cover, PC1 explained 35.25% of the variance while PC2 explained an additional 24.89%. Positive values on the first PC axis were strongly correlated to forested land cover ($r = 0.525$), and negative values corresponded to planted/cultivated ($r = -0.450$) and developed ($r = -0.381$) land covers. Positive values on the second PC axis were correlated to herbaceous land cover ($r = 0.588$), and negative values corresponded to wetland land cover ($r = -0.586$). Letters A-Q refer to the site ID in Table 1

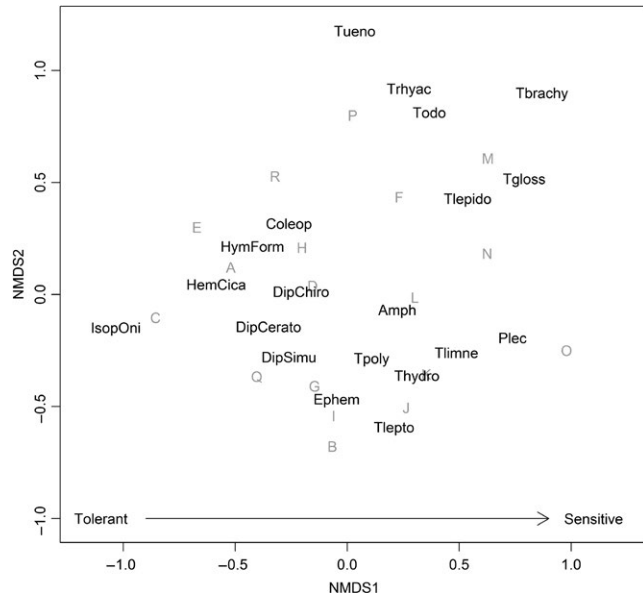


FIGURE 3 An NMDS analysis was used to arrange sites according to diet compositions, based on taxa IRI scores. Positive NMDS1 values were representative of sensitive benthic taxa (Amphipoda, Ephemeroptera, Plecoptera, Trichoptera), whereas negative NMDS1 values represented tolerant taxa (Coleoptera, Diptera) and terrestrial insects (Hymenoptera Formicidae, Hemiptera Cicadellidae, Isopoda Oniscidea). The second NMDS axis did not appear to correlate with taxa sensitivity scores. Letters A-Q refer to the site ID in Table 1

TABLE 3 Benthic Family Biotic Integrity (FBI) scores were adopted from Hilsenhoff (1988) to interpret results of the NMDS analysis

Taxonomic name	ID	Sensitivity
Amphipoda	Amph	4 ^b
Coleoptera	Coleop	5 ^c
Diptera Ceratopogonidae	DipCerato	6 ^c
Diptera Chironomidae	DipChiro	7 ^c
Diptera Simuliidae	DipSimu	6 ^c
Ephemeroptera	Ephem	3 ^b
Hemiptera Cicadellidae	HemCica	- ^d
Hymenoptera Formicidae	HymForm	- ^d
Isopoda Oniscidea	IsopOni	- ^d
Plecoptera	Plec	1 ^a
Trichoptera Brachycentridae	Tbrachy	1 ^a
Trichoptera Glossosomatidae	Tgloss	0 ^a
Trichoptera Hydropsychidae	Thydro	4 ^b
Trichoptera Lepidostomatidae	Tlepido	1 ^a
Trichoptera Leptoceridae	Tlepto	4 ^b
Trichoptera Limnephilidae	Tlimne	4 ^b
Trichoptera Polycentropodidae	Tpoly	6 ^c
Trichoptera Rhyacophilidae	Trhyac	0 ^a
Trichoptera Uenoidae	Tueno	3 ^b

Note. ^aSensitive; ^bModerately Sensitive; ^cTolerant; ^dTerrestrial.

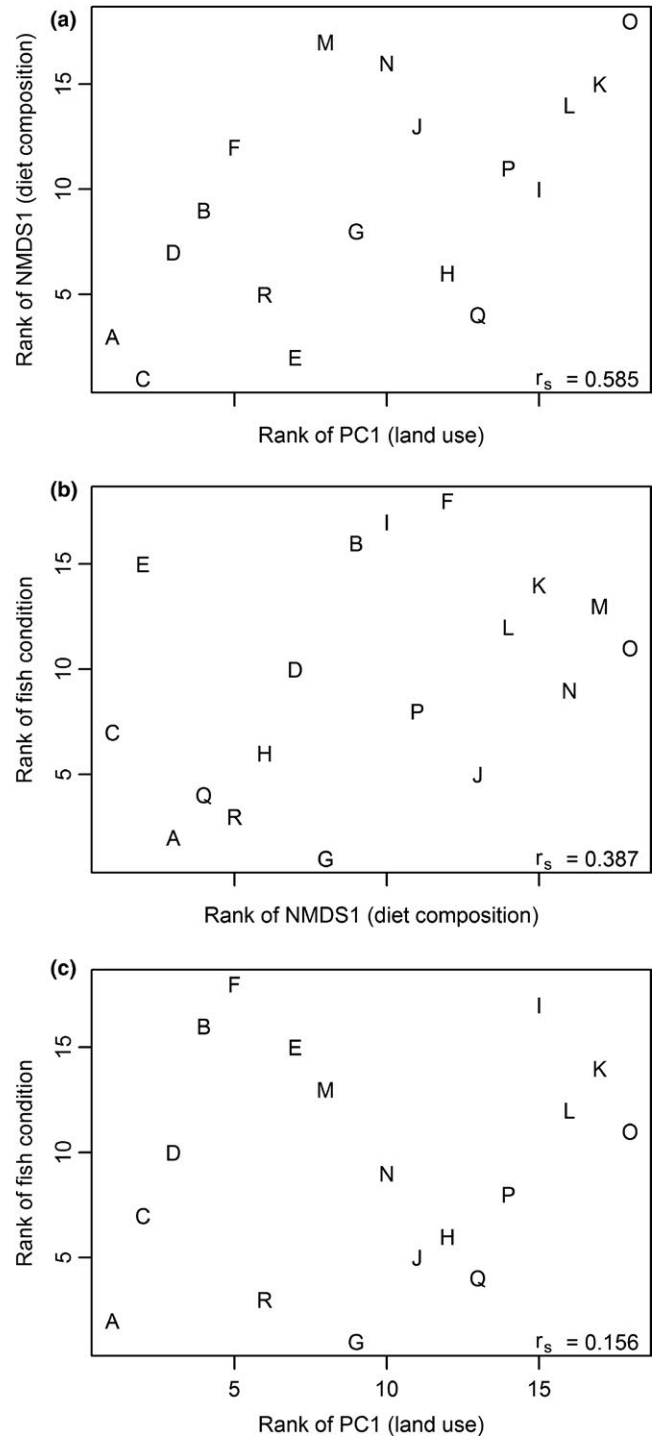


FIGURE 4 Spearman's rank correlation analyses revealed (a) a significant positive correlation between ranked land cover PC1 scores (rank 1 = most disturbed; rank 18 = most forested) and ranked diet composition NMDS1 values (rank 1 = tolerant taxa; rank 18 = sensitive taxa; $p = 0.012$). (b) No correlation between diet composition and fish condition (rank 1 = predicted to be lightest; rank 18 = predicted to be heaviest; $p = 0.114$). (c) No significant correlation between catchment land cover and fish condition ($p = 0.536$). Spearman's rho statistics are reported within each panel and should be evaluated based on $r_{s(0.05,18)} = 0.399$. Letters A-Q refer to the site ID in Table 1

$n = 18$). There were no significant confounding correlations between mean fish length and diet composition data, average prey mass (g) and land cover, nor between average prey mass (g) and fish condition.

4 | DISCUSSION

This study explored the effects of catchment land cover on the diet composition and body condition metrics of juvenile Rainbow Trout in Lake Michigan tributaries, as well as the effects of diet composition on condition. Although date of collection had a confounding relationship with diet composition data, there was no confounding correlation between date and land cover data. Therefore, our results suggest that land cover has a significant influence on the benthic taxa communities consumed by Rainbow Trout. The observed diet compositions were most highly correlated to forested, planted/cultivated, and developed land covers, lending support to relevant studies that have quantified the biological changes associated with watershed development (e.g., dominance of tolerant species (Lemly, 1982; Kemp & Spotila, 1997), loss of sensitive species (Sponseller et al., 2001)).

As was the case in previous studies (Di Prinzio et al., 2013; Fierro et al., 2016; Godby et al., 2007; McCarthy, Duda, Emlen, Hodgson, & Beauchamp, 2009; Whiting, Paukert, Healy, & Spurgeon, 2014), the diets of sampled Rainbow Trout were dominated by benthic taxa, whose presence and abundance in streams has been known to vary with relation to land cover. For example, Wang, Lyons, Kanehl, and Gatti (1997) concluded that forested land cover was positively correlated to Index of Biological Integrity (IBI) scores of benthic taxa in Wisconsin streams, while urban land covers have been shown to reduce benthic parameters of diversity and richness (Stepenuck et al., 2002; Weijters, Janse, Alkemade, & Verhoeven, 2009). Here, Rainbow Trout diet compositions mirrored these relationships; tolerant macroinvertebrate species increased in dietary importance as catchment development increased. In southern Chile, Fierro et al. (2016) found consumption of a higher diversity of taxa and higher IRI scores for pollution-sensitive taxa at native forest sites than at disturbed sites, a trend supporting our observations. Our results suggest that as riverine landscapes are altered, prey base and food chain interactions are affected.

Changes to benthic taxa compositions induced by land cover development were directly translated into the diets of juvenile Rainbow Trout. We observed shifts in the dietary importance of benthic taxa along a gradient of land covers such that Ephemeropterans, Plecopterans, and Trichopterans were most important to fish collected from forested sites, and on the contrary, Dipterans and terrestrial insects were most important to fish from urban and agricultural locations. Altered diet compositions may introduce bioenergetic differences to fish populations; terrestrial insects generally offer higher energies to the consumer than aquatic insects (Benjamin, Connolly, Romine, & Perry, 2013; Cummins & Wuycheck, 1971). In

our investigation, however, land cover mediated influences on diet composition did not equate to changes in fish condition. Despite what appeared to be a strong response in diet composition to land cover patterns, and a minor response relating diet composition to fish condition, there was clearly no relationship between fish condition and land cover patterns.

Rainbow Trout are known to be highly adaptable to changing environments and will adjust feeding patterns to sustain growth and condition (Di Prinzio et al., 2013). Some studies have found a positive relationship between consumption rates and growth rates of fish in streams having developed land covers (Cunjak, Curry, & Power, 1987; Dineen, Harrison, & Giller, 2007; Ensign, Strange, & Moore, 1990), and consumption rate has been thought to be more important for growth than consumption quality (Alexander & Gowing, 1976). When stream conditions become less favourable, however, high consumption rates may not allow for increased growth rates. In our study, there was no significant correlation between mass of prey consumed and fish condition indices. Similarly, Godby et al. (2007) found that age0+ Rainbow Trout consumed 84% greater biomass per day just to maintain similar growth rates in a high-temperature Michigan stream (as opposed to a thermally optimal tributary). This example helps illustrate the adaptability of Rainbow Trout to a range of environmental conditions and helps to explain how an alternative measure of diet, such as consumption rate, may not reliably correlate to indices of Rainbow Trout growth or condition.

In extreme situations of land cover development, fish assemblage diversity may be reduced due to simplified benthic assemblages, as well as a host of other changes (i.e., warmer water temperatures, decreased water quality, altered flow dynamics). For tolerant fish species, this may cause a decrease in interspecific resource competition. A development threshold exists at a proportion of degradation (agriculture and urbanization together) upwards of 85%, at which point resource acquisition and length-at-age significantly increased in populations of Central Mudminnow *Umbra limi* (Filgueira, Chapman, Suski, & Cooke, 2016). We did not encounter such a threshold for juvenile Rainbow Trout, but if one does exist, it may be outside the range of our study (i.e., greater than 79.13% total degradation). Both Rainbow Trout and Central Mudminnow are tolerant to lower dissolved oxygen levels and have higher critical water temperatures than other species in their respective families, and thus may exhibit similar body condition responses at high levels of land cover disturbance. The ability to adapt to diverse conditions allows Rainbow Trout to be successful in a variety of systems throughout the world. Therefore, by evaluating changes in diet and condition of successful and relatively abundant fish species like Rainbow Trout, insight could be gained by relating outcomes to other species that may be more at risk and less adaptable.

Since many fish species, including Rainbow Trout, have juvenile life stages that prey primarily on macroinvertebrates, reductions in benthic richness and altered benthic dominance occurring in degraded streams may ultimately limit the diversity of fish species that can be supported. Shifts in diet compositions related to watershed disturbances may affect ecological interactions at the community

level and increase dietary overlap among fishes. On average, for every 10% of the natural land cover that is lost or converted, 6% of a stream's native fish and benthic species are lost (Weijters et al., 2009). Additionally, introduced Rainbow Trout populations have been shown to displace native Brook Trout *Salvelinus fontinalis* and other salmonid species, resulting in increased niche overlap in suboptimal, partially covered (i.e., relatively unshaded, midstream reaches) stream habitats (Thibault & Dodson, 2013). Juvenile Rainbow Trout that occupied the preferred, fully covered habitats (i.e., shaded riparian corridors) close in proximity to the riverbank had higher growth rates than the displaced native species (Thibault & Dodson, 2013). Although we did not quantify fish assemblages directly, this example illustrates the tolerance of Rainbow Trout to degraded stream conditions and highlights the acceleration of niche competition that may occur in disturbed regions.

It is important to note here that Rainbow Trout have been present in the Lake Michigan Basin since the late 1800s and are considered a naturalized species. Comparisons within this manuscript are between Rainbow Trout that reside in different watersheds of the Lake Michigan Basin, and our results should be relevant to both native and nonnative Rainbow Trout populations in other systems.

To summarize, catchment land cover had a significant influence on the diet compositions of juvenile Rainbow Trout, whereas measures of fish condition did not differ between our sampling locations. This contrasts with previous studies which have discussed the role of land cover development in influencing fish growth (i.e., high consumption rates, reduced competition). Land cover may indirectly influence predator-prey interactions by reducing habitable substrate availability, altering water temperature regimes and affecting flow rates and water qualities, but land cover development did not significantly affect the conditions of juvenile Rainbow Trout within the range of our study. We suggest that tolerances of lower dissolved oxygen levels, lower water quality and warmer temperatures may allow Rainbow Trout to survive more degraded stream conditions than other cold-water fish species, allowing Rainbow Trout to benefit from reduced interspecific competition. Rainbow Trout populations have also been known to self-thin in response to food limitations, allowing body conditions to be maintained (Dunham & Vinyard, 1997). Our findings may guide future projects seeking to examine the interrelationships between landscape and freshwater ecologies, especially as they pertain to watershed development and its effects on bioenergetic relationships.

ACKNOWLEDGEMENTS

We thank researchers from Michigan State University and the National Fish Habitat Partnership for providing land cover percentage data, the Kalamazoo Valley Chapter of Trout Unlimited for providing support under the George L. Disborough TU Research Grant Fund and three anonymous reviewers for their editorial suggestions. Sampling for this project was carried out under a State of Michigan sampling permit and followed IACUC standards under permit #15-04.

AUTHOR CONTRIBUTIONS

N.W. and K.P. devised the original project idea and secured grant funding. K.B., N.W. and K.P. conducted preliminary literature research. K.B. carried out the diet analysis and was aided by C.P. and K.P. in the data analysis. K.B. took the lead in writing the manuscript. All authors provided critical feedback to help shape the final version of the manuscript.

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How to cite this article: Brumm KJ, Jonas JL, Prichard CG, Watson NM, Pangle KL. Land cover influences on juvenile Rainbow Trout diet composition and condition in Lake Michigan tributaries. *Ecol Freshw Fish*. 2019;28:11–19. <https://doi.org/10.1111/eff.12422>