Assessment of Economic Effects of Increased Production at the Grayling Trout Hatchery

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Introduction

There are many effects that conduct under the NPDES permit issued to Harrietta Hills Trout Farm could have on the local economy and on the people that benefit from unimpaired quality of the Au Sable River. For example, increased phosphorus and possible increases in whirling disease threaten to decrease the amount of fish in the river. The degradations to water quality are also expected to increase algae.

The public interest: From an economic perspective, the public has an interest in natural resources because they provide people with well-being and hence provide economic values and support business activities. Some of these economic values are reflected in market transactions. These are called market values. Other values for natural resources are referred to as non-market values because they are for environmental goods or services not directly traded in markets. There is also a public and private distinction to be made.

For example, consider growing fish in a river for later sale. The value of the fish that are sold would be a privately captured market value whereas the value of public recreational uses of the river would be a nonmarket good (river use is not directly sold in a market and does not have a readily observed price). Economists and the public are familiar with the idea of values for market goods. The field of environmental and natural resource economics has developed well-established techniques for valuing non-market values for natural resources.

Types of economic values and impacts: This summary presents two distinct economic concepts that relate to the issue of impairments to the Au Sable: (1) economic impacts and (2) economic values. Economic impacts measure changes in regional economic activity such as economic output (e.g., sales), incomes, and jobs (Watson et al., 2007). Broadly speaking, economic values accrue to people and businesses and reflect their well-being net of their costs, whereas economic impacts are the total effects on the economy. Notably, the two types of economic measures are not always directly comparable (i.e., care is required if both types of measures are to be used in a benefit-cost analysis that is conducted following economic standards). However, both types are directly relevant to the permit at issue since they are standard approaches for measuring changes in public well-being (i.e., people's welfare) and measuring economic importance.

1. Property values:

Based on a Public Sector Consultants report (PSC, 2013), there are a large number of properties along the river (11%) and these properties hold a disproportionately large share of the total value of property in Crawford County (26%). Consequently, the properties pay a large relative share of property tax (11% of parcels pay 23% of property taxes).

It is well established in the real estate and economics literature that proximity to amenities, especially water, increases property values. Although no specific study is available to link water quality and fishing quality to property values surrounding the Au Sable River, such relationships are well known in the literature. For example, the literature on factors affecting property values routinely demonstrates the increased property values associated with proximity to lakes and rivers (Olmstead 2010; Muller 2009). The relationship between property values and water quality has also been widely documented (Leggett & Bockstael 2000; Michael et al, 2000; Epp and Al-Ani, 1979; Poor et al. 2007).

As a premier trout stream, the literature suggests that proximity and access to the river would influence property values, and hence any changes in the quality of the fishery would affect property values. Anecdotally, a search of rental properties along the river reveals that several dozen advertise their proximity to the Au Sable for its fishing, floating, and aesthetic offerings.

In sum, the published literature shows a range of impacts that water quality can have on property values, but it consistently shows that lower water quality adversely affects property values. Considering the value and economic significance of riparian property in Crawford County, taking percentage declines in property value from the existing literature that are on the low end of the published amounts and applying these percentage declines to affected properties would generate significant total reductions in property values due to lower water quality. Correspondingly, reductions in property value will reduce property tax receipts.

2. **Recreation**:

The increased pollution associated with the lowering of water quality is expected to have several effects, including increased phosphorus, increased dissolved solids, increased organic matter, increases in algae, and potential increases in whirling disease, among others. Any of these could have deleterious effects on water-based recreation. I focus in this section on the impacts of increased P on fishing followed by a discussion of the impacts of degraded water quality on water sports (canoeing, kayaking, and floating).

2.1 Recreational Fishing

The Au Sable River is a premier trout fishing destination and numerous businesses support the fishing-related activities. A decrease in water quality is expected to result in fewer trips, and hence a loss in economic value to the recreational anglers and a corresponding loss in economic impacts to the region. Table 1 summarizes my estimated losses for recreational fishing. The text that follows provides details of the derivations.

Table 1. Estimated high and low range of losses of recreational fishing days, lost value to anglers, and lost economic impacts associated with increased phosphorous in the Au Sable River.

	Fishing	
	Low*	High**
Days	17,425	45,291
Effect of pollution (% trip decline)	69%	69%
Lost days	11,981	31,142
Value per lost day	$20.70	$20.70
Lost value to recreation users	$248,022	$644,660
Spending per day	$82.75	$82.75
Lost Spending (direct)	$991,452	$2,576,988
Multiplier	1.78	1.78
Lost Economic Impact	$1,764,537	$4,586,397
Annual full-time jobs lost	14.6	37.9

* extrapolated from creel studies
** derived from NSFHWAR MI (2011) data combined with Klatt (2014)

Effect of Phosphorus on Fish:

The first step in connecting recreational fishing to phosphorus (P) is to relate fish abundance to P levels. Key sport fish in the East Branch and in the Au Sable River are Brook Trout and Brown Trout. Trout are known from the literature and from nutrient criteria for Michigan to be sensitive to high P levels (Stevenson et al, 2006). A recent peer-reviewed publication utilizes available data from the Michigan DNR's fish sampling stream surveys to develop statistical models of fish biomass in Michigan rivers. The amounts of fish are related to summer baseflow P loading. Models for brook and for brown trout confirm these species are particularly sensitive to small increases in P. Figure 1 shows graphs of the response of trout biomass to levels of P. As Esselman et al (2015) note, the decrease in brook trout biomass when μg/l TP increases from 13 to 20 was sharp and statistically significant ($P < 0.05$). Similarly, brown trout had a stress response to increased TP concentrations, with biomass showing a declining trend as TP concentrations increased.

Note from figure 1 the pronounced predicted decrease in both species' biomass as TP increases from 13 to 25 mg/l.

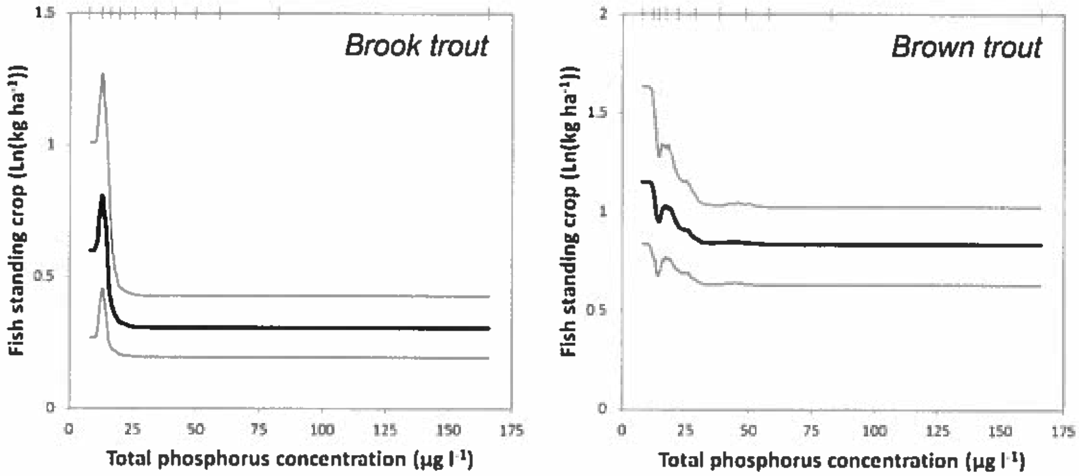

Figure 1. Plots showing the predicted response (black line) of target fisheries to total phosphorus concentrations with 95% confidence interval (gray lines). *[Excerpt from author's pre-publication copy of Figure 4, Esselman et al, 2015].*

Linking Fishing Trips and Values to Fish Biomass:

The next step in connecting recreational fishing to phosphorus (P) is to relate fish biomass to the locations where recreational anglers choose to go fishing. This is done using an economic demand model. Such models are well-established methods for estimating the economic demand and values of users, and can relate both of these to the features of a site such as fish biomass. A recent peer-reviewed publication presents such a model for river fishing in Michigan (Melstrom et al, 2015). The model shows that biomass of brook and brown trout (as estimated by the Esselman et al biomass models) are significant predictors of where anglers go fishing (i.e., angler demand for fishing sites). Thus, reductions in fish biomass at a site will reduce trips to the site and will reduce the economic value anglers receive from fishing.

To proceed with the estimation of losses, we need estimates of the number of fishing trips in the baseline without any increase in P. Two separate estimates are derived to give an idea of the range of results. The first is derived from information in Table 27 of Zorn et al (2001), which reports average results from past creel studies of the Au Sable River from Grayling to Wakeley Bridge. For fishing, they report an average of 3290 hours per river mile. This can be expanded to days for the river segment by multiplying by the 14.3 miles of river in this segment and dividing by an estimate of hours fished per day. Studies of angling on other trout rivers report values of 1.7 hours per day in Wisconsin and 2.7 hours per trip in Pennsylvania. I also made calculations for hours per trips using Michigan DNR Creel data for the Au Sable just downstream of Mio (DNR 2015). Since that segment of the river is larger and includes a significant boat fishery, I used the shore fishing data, which across the four zones sampled averaged 2.68 hours per trip. Thus, to convert the hours to trips I used 2.7 hours per day. This translates into an estimated 17,425 days fished per year.

For comparison, I provide another approach to estimating the baseline number of trips. The U.S. Census provides bi-decadal surveys that estimate fishing in each state (NSFHWAR MI 2011). The data reveals an estimated 23.37 million fishing days in Michigan. Using data from Klatt (2104), 25% of fishing in Michigan is at rivers, and using data from Melstrom et al, 0.78% of river fishing in Michigan is to the affected stretch of the Au Sable. Combining these yields an estimated 45,291 days fished per year.

The Melstrom et al model is used to map changes in fish biomass into estimates of the lost number of fishing trips. Using the percentage changes in biomass derived from Figure 1 for a change in TP from 13 mg/l to 25 mg/l TP results in a predicted decline in trips to the upper portions of the Au Sable River and East Branch of 69%.

The Melstrom et al model is also used to derive the economic value to anglers of these lost trips. The estimate is that lost trips were worth $20.70 in net economic value to the anglers. Since this value is smaller than the values estimated in many other river fishing studies of economic value, the value can be considered conservative relative to the use of other studies.

Combining the lost trips with the value per day yields a total lost value to anglers of $248,022 to $644,660 depending on which estimate of baseline trips is used. Either way the losses are significant and are likely conservative since single day trip values are used in place of multiple day trip values.

Lost Economic Impacts:

In addition to the losses in economic values to the recreational anglers, the reduction in biomass has an associated loss of economic impacts due to the lost trips. To derive this, spending data for trout fishing in rivers comes from a survey conducted by Knoche (2014), which gives spending on trout fishing trips to rivers of $70 on single day trips and $278 on multiple day trips. These are converted to a day equivalent of $82.75 using information from Klatt (2014) on the statewide share of single and multiple day trips in Michigan. Note that this spending figure is for the portion of trip expenditures that occurs within 35 miles of the fishing site so it is a contribution to the local economy and does not include money spend outside the region.

The estimates of lost fishing days are combined with the spending per day to develop a range of lost spending. The literature provides a multiplier on fishing trip expenditures of 1.78 (Southwick 2007). Combining the lost spending with the multiplier yields a range of estimated economic impacts on the economy of about $1.7 to $4.6 million per year, depending on the baseline estimate of trips.

Note too that these are for impacts from tourists. Ninety-four percent of the anglers fishing this reach are from outside of Crawford County, with 74% being from other counties in Michigan, and 20% from other states and Canada (author's calculations from data in Gigliotti and Peyton, 1993). Moreover, most river fishing trips come from outside the local area of a fishing site; even for day trips 95% are from greater than 35 miles away from the fishing locations (author's calculations from data in Melstrom et al, 2015). The economic model in Melstrom et al (2015) does not include multiple day trips and does not include trips by non-residents. Thus, for visitors that are not Michigan residents, I assumed their trip lengths and spending per day is the same as for residents. This almost certainly underestimates spending and associated economic impacts given the greater distances these people would need to travel and the usual observation that people that travel farther distances tend to spend more time on-site and spend more; data suggests that 20% of the fishing trips to this part of the river are made by non-residents (author's calculations from data on page 494, Gigliotti and Peyton, 1993). Thus failing to account for these added on-resident expenditures leads to smaller estimated economic impacts.

In summary, recreational fishing is expected to be affected by degradation in water quality with increased P and thereby decreased brook and brown trout biomass. Two estimates of baseline trips for the Au Sable were used to derive estimates of losses in economic value *to recreational anglers* of about $250,000 to $645,000 per year and *lost impacts to the regional economy* of about $1.77 to $4.6 million per year.

2.2 Water Sports: Canoeing, Kayaking, Floating

The Au Sable River is a desired destination for water sports and numerous businesses support these activities. A decrease in water quality is expected to result in fewer trips and hence a loss in economic value to the recreational users and a corresponding loss in economic impacts to the region. Table 2 summarizes my estimated losses for water sports. The text that follows proves details of the derivations.

Table 2. Estimated losses of recreational watersports days, lost value to recreational users, and lost economic impacts associated with decreased water quality in the Au Sable River.

	Watersports
Days	31,460
Effect of pollution (% trip decline)	50%
Lost days	16,359
Value per lost day	$25.81
Lost value to recreation users	$422,173
Spending per day	$37.87
Lost Spending (direct)	$619,481
Multiplier	1.42
Lost Economic Impact	$879,664
Annual full-time jobs lost	12.1

This section provides the details of the derivations in Table 2 for watersports.

Lost Value for the Users:

The literature reports values per trip for canoeing of $20 to $50 dollars per day in 2015 dollars (Boxall et al 1996; Englin et al, 1996). Another study yields values per trip of $25.81 in 2015 dollars for boating activities that include canoeing, kayaking, floating and tubing (Parsons et al, 2004). The latter study is most appropriate for our application since it better matches the range of activities on the Au Sable and it also relates trips to levels of water quality. The study used three water quality levels: high, medium and low, where high water quality was characterized by high levels of dissolved oxygen and low levels of suspended solids. In their study, a change in water quality reduces the value of a trip by about 50%. They do not report demand elasticities (i.e., how trips respond to quality changes), but in my experience they tend to be proportional to value changes. Thus, the trip change that corresponds with this change in value is a 50% reduction in trips. Table 1 uses the Parsons et al (2004) value per day and trip response. This is the best matching estimate from the literature on how water-sports would change in response to a change in water quality similar to that expected in the Au Sable.

The baseline trips in Table 1 are derived from information in Table 27 of Zorn et al (2001), which reports average results from past creel studies of the Au Sable River from Grayling to Wakeley Bridge. For pleasure boating (canoeing, kayaking, and floating), they report an average of 8800 hours per mile. This can be expanded to days for the river segment by multiplying by the 14.3 miles of river in this segment and assuming 4 hours per day. The result is an estimated 31,460 days.

Combining the estimated baseline days for water sports with the 50% reduction in trips yields 16,359 lost trips. The resulting lost benefits to recreational users are about $422,000. This is my best estimate of the economic costs incurred by those engaging in water sports due to a reduction of water quality on this segment of the Au Sable River from a high level to a medium level of water quality.

Lost Economic Impacts:

In addition to the losses in economic values to the recreational users, the reduction in water quality has an associated loss of economic impacts due to the lost trips. To derive this, estimates of spending per day are computed from available literature. Using data from Stynes for canoeing in Michigan, I derive a spending per day of $37.87. This is computed by converting Stynes' estimate for spending per party per trip into a spending per day and applying his reduction for trips that are not for the primary purpose of canoeing and excluding the portion of spending that is not in the area of the site. This result is in the range of estimates from other states, if not lower. In a multi-state study, Southwick and Bergstrom (2007) report paddle-sport spending of $60 per person per day trip, and Pollock et al (2007) report expenditures of $25 for day visitors and $186 for overnight visitors.

To get the relevant multiplier to convert spending changes into total changes in economic impact, I also rely on Stynes, whose results imply a multiplier of 1.42, which is consistent with the multiplier for canoeing of 1.5 that can be derived from Southwick (2012).

Note too that for the watersport recreational uses of the river, we can infer that, like fishing, the vast majority of visitors are non-locals. In a study on the Manistee River, MI, Nelson and Valentine (2002) found about 93% of those camping and 86% of others visiting the river were from outside their 3-county study area. Similarly, data from a national study of river recreation shows that for 75% of trips the primary purpose for visiting was using the river and that 85% of visits were from 35 miles away or more (Cole 2014).

In summary, water sports of canoeing, kayaking and floating are expected to be affected by degradation in water quality. The best matching study from the literature was applied to trip information for the Au Sable to derive estimates of losses in economic value to watersport recreation users of about $422,000 per year and lost impacts to the regional economy of about $880,000 per year. Alternative ways of linking algae or other water quality declines to this recreational activity might yield different results for predicted lost trips, but the values at risk are well aligned with what is found in the literature on recreational values and impacts.

2.3. Other pathways of effects on recreation

Above, evidence was presented on likely effects decreased water quality would have on recreational fishing and on water sports. There are other pathways of possible effects that have not yet been quantified. For example, the increased pollution could lead to increased whirling disease in trout, which is known to adversely affect trout populations. It was established above that decreased trout biomass can have significant affects on trips, angler wellbeing, and the local economy. While this potential also exists via whirling disease, estimates of economic effects would require linking the increased risk of disease to risks of biomass declines. Though not quantified, the risk remains.

3. Other economic effects

There are a variety of other ways that reduced water quality in the Au Sable River can harm the public interest and affect well-being. Better documentation of these is an area of ongoing investigation. An example of as yet undocumented harms would be trail uses and camping along the Au Sable. Not all visitors engage in the recreation activates examined above. Some of these visitors would be adversely affected by reductions in water quality and increases in algae.

Another area of possible harm that this report has not attempted to quantify are the non-use values Michigan citizens might have for natural resource quality of the Au Sable. For example, members of the public that will likely never make use of the resource might still have a willingness to pay to avoid any degradation in a renowned pristine river. Such nonuse values are valid for natural resource damage assessment cases (e.g., in oil spill damage recoveries) and are recognized as appropriate for inclusion in Federal benefit-cost analyses (BCA) that follow Office of Management and Budget economic guidelines for BCA.

4. **Anti-degradation**:

The Antidegradation Demonstration of the permittee and the associated Responsiveness Summary claim that a lowering of water quality is necessary to support important social and economic development in the area. The documents mention types of benefits which I paraphrase and regroup as follows:

A. Economic contributions from fish production: Preserve current employment and economic activity and allow increases (possibly 2 full time and two part time positions), allow for increases in related businesses, and help supply demands of Michigan food industry for Michigan-branded product.

B. Hatchery tourism: Maintaining the summer tourism and interpretation center, increased rate of tourism since permittee began managing the facility, preserving the associated local expenditures of tourism visits.

C. Youth exposure to fishing: Introducing children to fishing which might ultimately increase license sales and contribute to the fishing industry.

D. Abandonment and preservation: Prevent the facility from being abandoned and preserve the improvements that were made.

I will discuss these items in turn.

A. Economic contributions from fish production:

The economic contributions likely to stem from production expansion are uncertain and likely to be small for many reasons.

First, as noted in the antidegradation documentation, the expansion will add few jobs to the regional economy and the bulk of the economic gains from the use of the public resource will accrue to a handful of private individuals.

Second, the size of the likely amount of economic activity related to the expanded facility will depend in part on its profitability, which depends in turn on the prices it can receive for trout. It appears from the company's website and sales of fish caught on site that the prices currently received for their trout are significantly above the national prices. This likely reflects the niche markets in which the products are being sold, but such prices are more difficult to sustain with larger production volumes because the national prices for trout filets are low. For example, the National Agricultural Statistics Service of USDA maintains a well-regraded and reliable database on regional and national agricultural production and prices. The average national average prices for trout were $1.08 in 2005 and $1.63 in the 2013 (NASS 2015). However, the NASS database also reports a lone price of $3.39 specific to Michigan for 2013. It is possible that Michigan prices in NASS reflect niche markets (otherwise we would expect them to converge on the national price levels) and because the

2013 NASS data indicate only 13 Michigan producers reporting sales of trout for food fish (only 171,000 pounds were reported sold by Michigan producers out of 58 million pounds nationally). One possibility is that the trends in consumer preferences for local foods could be exploited to maintain prices above the national average (as alluded to in the Responsiveness Summary), but the possibility of capturing a price premium for being locally grown must be weighed against risks to this branding and pricing strategy that result from consumer awareness of the harms from expanded operations. Thus, it is unlikely higher prices can be sustained that are significantly above the national average at dramatically larger production volumes, especially in light of the small role Michigan suppliers play in this food chain. Lower retail prices for the increased production will dampen profitability and reduce any impacts on the broader regional economy.

Third, a recent peer-reviewed study has shown a limited market for fresh trout grown in the Midwest. Specifically, the published study shows limited local retailer willingness to pay any price premium for Midwestern (fresh on ice) fish, further suggesting the market may not support a price well above the national average. The study found 57% of retailers would not pay a price premium for fresh trout and the resulting overall mean price premium for was $0.29 for Midwestern-grown fresh trout. The study concludes there "is no room" to capture price premiums from retailers for fresh trout from Midwestern producers (Gvillo et al. 2013).

Thus, expanded production is likely to be beneficial for a few people and several connected businesses, but the above factors suggest the overall economic impacts for the broader community are likely limited.

B. Hatchery tourism:

The tourism impact of hatchery is likely limited. Why?

Regarding the above mentioned benefits of preserving the benefits of tourism visits, I begin by setting aside questions about the size of these benefits and consider the following question: Is an increase in production (a lowering in water quality) necessary to support these benefits? The antidegradation argument suggests that the only way to maintain any such benefits is to increase production (lower water quality). To the extent there are some tourism benefits to the local economy (and some benefits from introducing youth to angling), these benefits exist equally at the current production levels and at the proposed higher productions levels. Providing these benefits does not require expanded production and the accompanying pollution.

Second, public representatives have determined these tourism benefits are not worth it. News reports suggest the county was losing money operating the facility to produce these benefits, thereby suggesting that from the perspective of Crawford County administrators, the contributions the facility makes to Crawford County are not worth the costs of operating the facility. Regardless, if these benefits were deemed to be significant enough to warrant sustaining them, then there should be a willingness to pay to provide them from some source, and they can be provided without added pollution.

Third, the economic impact of the hatchery "tourism" is likely small. All else being equal, economic impacts from tourism will be larger for activities that attract non-local visitors who bring "outside" dollars into the community. To fully assess this would require data on the origins of the clientele of the fish farm, and data for the non-local visitors on their spending patterns, length of stay in the community, and primary purpose for their visits. However, given experiences with other types for recreation, I expect that for hatchery a nontrivial portion of visits are from local residents, and experts agree that local residents should be excluded from properly conducted economic impact analyses of tourism as their visits do not bringing new money into the region. Moreover, the activities at the hatchery, e.g., fish feeding or catching fish at the hatchery, are unlikely to be the primary purpose for a large number of visitors from outside of the Grayling area. For example, the downtown market plan notes that many visitors to Grayling "usually continue on to other attractions in Traverse City, Mackinac Island, or the Upper Peninsula" (p48, Vokes et al, 2004). Similarly, most of the visits to the hatchery likely constitute what tourism economists sometimes consider "stopover" or "side-trip" visits, that is, visits that are "along the way" or are part of a trip with another primary purpose. As such, only a small portion of the spending for these trips counts as a net economic impact to the area. (Alternatively, fishing and canoeing/floating are almost all non-local visitors and mainly for the primary purpose of that activity, so most of the spending factors into net economic impacts.)

C. Youth exposure to fishing:

The argument in the documents was that the hatchery introduces children to fishing, which might ultimately increase license sales and contribute to the fishing industry. As above, this may well be a benefit of hatchery visitation, but this benefit can be provided without expanding production and degrading water quality.

Note too that one could make a comparable argument associated with impairments to the fishery. That is, due to the degradation of water quality which affects fishing success and results in fewer trips, there will likely be (1) reduced purchases of fishing gear and reduced license sales from some current anglers, and (2) reduced exposure of youth to angling thereby reducing future license sales and fishing expenditures. In the above documented potential economic impacts due to decreased fishing, such impacts were not included (only the trip-spending in the vicinity of fishing sites was used to determine impacts).

Thus, while this type of future beneficial effect of exposing youth to fishing is possible as an outcome of hatchery visitation, I expect it is easily outweighed by the effect decreased water quality has on drop-off of current anglers (1 above) or future anglers (2 above).

D. Abandonment and preservation:

The point that was made here was that increased production would prevent the facility from being abandoned and preserve the improvements that were made. As with some of the other anti-degradation arguments, there would be other ways to accomplish this. Regarding the preservation of improvements, while understandable, economists typically calculate benefits and costs with respect to current and future actions. Effort and money spent to make these improvements are not irrelevant, but they are considered sunk costs (costs that were already incurred). From the standpoint of making more efficient current and future decisions, sunk costs are typically excluded.

5. Conclusions

The available evidence and related economics literature suggests that with increased production by the permittee there is the potential for significant losses to recreational anglers, to those engaged in recreational water sports, and to riparian and nearby property owners. In addition, associated reductions in trips would significantly affect the local economy. Alternatively, the likely economic impacts of the fish farm are modest relative to the likely costs. Many of the benefits laid out in the antidegradation documents can be sustained without altering the production amounts or increasing pollution. As such, the benefits of increased production accrue to a few people and businesses, whereas a comparatively large and dispersed number of others will bear the costs of reduced water quality.

I reserve the right to revise this report.

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Annex 1.

Stevenson et al, 2006

Annex 2.

Esselman et al. 2015

Annex 3.

Melstrom et al. 2015

Total Phosphorus Thresholds (Response Factors) Summary for Michigan [Stevenson et al. (1/19/2006)]

Database	Parameter	TP (ug/l) Threshold	
SAIN-MI	Diatom similarity to reference decreases	10	Low
SAIN-MI	Invert # Tolerant Taxa Increases	10	Low
SAIN-MI	% Sensitive Diatom Indicator drops	15	Low
SAIN-MI	Chlorophyll a increases	15	Low
MRI Data	Trout and cold water fish diversity decreases	15	Low
SAIN-MI	Non-native algal (individuals and taxa) increase	15	Low
SAIN-MI	Invertebrate similarity to reference decreases	15	Low
SAIN-MI	Cladophera cover increases	20	Low
MRI Data	Many fish metrics decrease	20	Low
MRI Data	Sculpin taxa decrease	20	Low
SAIN-MI	Cladophera cover jumps (increases)	30	Medium
SAIN-MI	Sensitive algal taxa drop	30	Medium
SAIN-MI	Invert # Sensitive Taxa decrease	30	Medium
MRI Data	Intolerant fish taxa decrease	30	Medium
MRI Data	Darter taxa decrease	30	Medium
SAIN-MI	Diatoms escape grazing	40	Medium
MRI Data	All and native fish taxa decrease	40	Medium
MRI Data	Moderately tolerant fish taxa decrease	40	Medium
MRI Data	Fish IBI I and II decrease	40	Medium
ILWIMI	Dissolve oxygen decreases	40	Medium
STORET	Water column chlorophyll a increases	45	Medium
STORET	Invertebrate EPT metrics and P51 decrease	>50	High
MRI Data	Cool/Warm Water fish taxa decrease	60	High
MRI Data	Increasing loss of many fish	60	High
MRI Data	Minimum restoration target for fish	80	High

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Water Resources Research

RESEARCH ARTICLE
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Valuing recreational fishing quality at rivers and streams

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Key Points:

- Demand was modeled for recreational fishing to rivers and streams
- Fishing site qualities were measured by biomass of five game fish species
- Fishing sites were defined by hydrological boundaries and stream type

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Abstract This paper describes an economic model that links the demand for recreational stream fishing to fish biomass. Useful measures of fishing quality are often difficult to obtain. In the past, economists have linked the demand for fishing sites to species presence-absence indicators or average self-reported catch rates. The demand model presented here takes advantage of a unique data set of statewide biomass estimates for several popular game fish species in Michigan, including trout, bass and walleye. These data are combined with fishing trip information from a 2008–2010 survey of Michigan anglers in order to estimate a demand model. Fishing sites are defined by hydrologic unit boundaries and information on fish assemblages so that each site corresponds to the area of a small subwatershed, about 100–200 square miles in size. The random utility model choice set includes nearly all fishable streams in the state. The results indicate a significant relationship between the site choice behavior of anglers and the biomass of certain species. Anglers are more likely to visit streams in watersheds high in fish abundance, particularly for brook trout and walleye. The paper includes estimates of the economic value of several quality change and site loss scenarios.

1. Introduction

Fishing at rivers and streams is a major recreational activity in the United States, with nearly 12 million participants in 2011 [*U.S. Fish and Wildlife Service (USFWS)*, 2012]. Rivers also support swimming, paddling and boating activities, provide ecosystem services such as spawning habitat for marine fishes, and are a source of substantial nonuse value [*Sanders et al.*, 1990; *Loomis*, 2003; *Debnath et al.*, 2014]. However, rivers and streams are susceptible to landscape and climate change, and the value of these resources is frequently impaired by human activity [*Allan*, 2004; *Suplee et al.*, 2012; *Ficklin et al.*, 2013]. A comparison of water quality indicators in the United States over the past decade indicates a significant decline in stream condition, predominantly in the Midwest and Plains regions [*U.S. Environmental Protection Agency (USEPA)*, 2013]. Stream anglers in particular will be sensitive to these changes, which directly affect valuable stream characteristics such as the biomass of game fish species.

The economic effects of watershed changes on stream anglers and other users can be measured with nonmarket valuation techniques. The random utility maximization (RUM) model is now a common means of estimating values for the recreational use of natural resources. In a recreational angling context, the RUM model explains the choice of fishing trip to a site among a set of many possible alternatives. By describing choice as a function of site characteristics, a RUM model is capable of predicting the monetary benefits or damages that will arise from changes in the environmental quality of sites [*Haab and McConnell*, 2003]. Below, we describe a RUM model of recreational fishing that can be used to value detailed changes in fish abundance and stream quality.

Identifying the influence of fishing quality on site choice can be challenging. Data on appropriate measures (e.g., fish abundance, catch and harvest) are often not available or are difficult to obtain for most sites. Several prior studies of stream fishing have addressed this problem by using proxies for fishing quality [*Jones and Lupi*, 2000] and presence-absence indicators [*Hunt et al.*, 2007]. Many others have elected to use anglers' self-reported catch rates, averaged by site (Table 1). These methods are less than ideal: proxies provide few insights into fishing quality, presence-absence indicators only capture discrete changes and some types of catch rate measures are prone to measurement error and estimation bias in the demand model

Table 1. Stream Angling RUM Model Studies

Authors and Year	Study Area	Site Definition	Selected Site Quality Variables
Hunt et al. [2007]	Ontario lakes and rivers	Known access points	Species-specific presence-absence indicator, walleye and trout catch rates (from observed trips)
Ji et al. [2014]	Iowa rivers	River segments	Fish presence index, water quality index, land use measures
Jakus et al. [1998]	Tennessee reservoirs	Reservoirs	Total catch rate (from observed trips) fish advisory indicator
Jones and Lupi [2000]	Michigan lakes and rivers	Counties	Species-specific catch rates at Great Lakes (from creel data), stream type indicators, landscape characteristics
Lin et al. [1996]	Willamette River basin	Four river segments	Fishing quality index, congestion
MacNair and Cox [2000]	Montana lakes and rivers	River segments and lakes	Total species biomass, restricted species, site size
Morey et al. [1993]	North Atlantic salmon rivers	Maine rivers and Canadian provinces	Total catch rate (from observed trips)
Morey and Waldman [1998]	Montana rivers	River segments	Total catch rate (from observed trips)
Morey et al. [2002]	Clark Fork River basin	River segments	Total catch rate (from observed trips), site size
Murdock [2006]	Wisconsin lakes and rivers	Rivers grouped by quadrangles and lakes	Species-specific catch rates (from observed trips), boating facilities, landscape characteristics
Parsons and Hauber [1998]	Maine lakes and rivers	River segments and lakes	Salmon presence-absence indicator, water toxicity
Peters et al. [1995]	Alberta lakes and rivers	River segments and lakes	Total and trout-specific catch rates (from observed trips), water quality index, site size
Phaneuf [2002]	North Carolina lakes and rivers	Subbasin watersheds	Phosphorous, dissolved oxygen, ammonia, acidity indexes
Train [1998]	Montana rivers	River segments	Total species biomass, restrictedspecies, site size
Von Haefen [2003]	Susquehanna River basin	Sub-subbasin watersheds	Trophic state index, dissolved oxygen index

[*Morey and Waldman*, 1998; *Train and McFadden*, 2000]. Furthermore, many of the catch rate measures employed in the literature are not designed to distinguish between fish species, although there is evidence that the impact of fishing quality on site choice is species-specific [*Peters et al.*, 1995; *Murdock*, 2006].

Another challenge in modeling the demand for stream fishing is determining what constitutes a fishing site. There is not yet a consensus in the literature on the site definition for stream fishing (Table 1), although it is generally recognized that large individual sites tend to be heterogeneous in site quality, suggesting that using small sites will result in a better model [*Lupi and Feather*, 1998]. Indeed, there does appear to be a trend toward more refined site definitions. For example, *Morey et al.* [1993] used rivers, *Parsons and Hauber* [1998] used river segments and *Hunt et al.* [2007] used river access points as sites. Several papers have also used hydrological boundaries to assist in defining sites [*Phaneuf*, 2002; *Von Haefen*, 2003].

This paper presents a site choice model of stream fishing using species-specific biomasses as measures of fishing quality. The biomass data come from biological stream surveys, i.e., a form of fisheries-independent data, which are generally preferred to self-reported angler catch rates, a form of fisheries-dependent data which can vary based on angler skill and gear [*Maunder and Punt*, 2004]. Fishery-independent biomass estimates are well suited to capturing relative differences in abundance across freshwater streams [*Hayes et al.*, 2007]. To date, biomass measures are rarely employed in models of stream fishing (*Train* [1998] is an exception), even though catch rates directly relate to biomass [*Clark*, 1990]. Our data are also unique in that they include several different species-specific measures of biomass rather than a single composite measure.

Valuation of recreational fishing is a key component in the science of river restoration. By including species-specific biomass, the site choice model can be used to value detailed and diverse changes in fishing quality—e.g., abundance increases for some species but decreases for others, as might be expected under a climate change scenario, under management changes that alter hydrology, or as a consequence of ecosystem restoration [*Meyer et al.*, 1999; *Bond and Lake*, 2003; *Palmer and Bernhardt*, 2006]. Communicating the role that restored ecosystem services have on individual and social benefits can have a significant impact on ecosystem management decisions, especially when there is conflict over which services a river system or watershed should support [*Wohl et al.*, 2005]. Valuation is especially useful if benefits can be measurably related to riparian landscape and habitat conditions that drive fishing quality, which is a major motivation for the fish biomass data used in the angler model below.

Table 2. Fishing Trip Characteristics

Characteristic	Mean
Restricted license[a]	0.397
Fished in spring[b]	0.292
Fished in summer	0.321
Fished in fall	0.341
Targeted trout[c]	0.395
Targeted bass	0.314
Targeted panfishes	0.272
Targeted walleye	0.176
Targeted other fishes	0.267
Did not target particular species	0.179

[a] Anglers have about a dozen different fishing license options in Michigan but there are two basic types: restricted licenses and all-species licenses. Restricted licenses permit fishing for all species except trout, salmon, lake sturgeon, lake herring, amphibians, reptiles and crustaceans. Typical sales consist of about 60% restricted and 40% all-species licenses.

[b] Spring: March–May. Summer: June–August. Fall: September–November. Approximately 4% of sample trips were taken in an unspecified month.

[c] A trip could have targeted more than one species group.

Our model makes several further contributions to the literature. Hydrological boundaries are used to construct the choice set in which fishing sites are classified at the subwatershed level. Additionally, many of the largest subwatersheds are broken down into two sites using information on site characteristics that relate to fish assemblages. This advances the trend in the literature to further refine fishing site definitions. To account for the role of latent fishing site characteristics, the variant of the model presented here includes site fixed effects (sometimes referred to as alternative specific constants). The model is applied to stream fishing in Michigan and the results are used to estimate the economic benefits of several hypothetical improvements in fishing quality.

2. Methods

2.1. Fishing Trip Data

We use data from the Michigan Recreational Angler Survey (MRAS), a mail survey that has been administered monthly to a random sample of Michigan fishing license holders since July 2008. The survey questionnaire inquires about the two most recent fishing trips and the household characteristics of anglers. The response rate is approximately 47%. Details of the MRAS survey instrument can be found in *Simoes* [2009]. The questionnaire includes the usual questions about demographics and economic status, including household income. Data from the MRAS available for our analysis include the responses from 2008 through the 2010 survey period. We focus on the subsample of day trips that respondents reported were for the purpose of fishing a river or stream and were within 200 miles of an angler's home. We dropped trips taken in December–February because these would have visited a distinct subgroup of sites, e.g., frozen impoundments. These refinements yielded a total of 2064 trips taken by 1591 anglers (some anglers reported only their most recent trip or a second trip that did not fall into the defined subsample). Relevant descriptive statistics of this sample are consistent with our expectations (Table 2), in that the most popular months for fishing are in the summer and fall. Approximately 40% of the stream trips are taken by anglers with a restricted license (which means they are not allowed to fish for trout). About 60% of the licenses sold in the state are restricted, so the data for stream fishing trips reflect the increased emphasis stream anglers place on trout.

We use hydrologic units to define the set of possible fishing destinations. A hydrologic unit defines an area of land with a common drainage outlet point (e.g., a river mouth). The U.S. Geological Survey and U.S. Department of Agriculture has divided the United States into nested hydrologic units that are classified within a six-level hierarchy, where each unit is identified by a "HUC" code consisting of two to twelve digits based on the position of a unit within the system [*U.S. Geological Survey (USGS) and U.S. Department of Agriculture, Natural Resources Conservation Service (USDA-NRCS)*, 2012]. At the top level of classification are 2-digit HUCs representing the major national river drainage regions, such as the Great Lakes. Each region then consists of several subregions (HUC4) that nest perfectly within them, with additional 6, 8, 10, and 12-digit nested units defined at progressively finer spatial resolutions. We initially distinguished fishing destinations at the level of the 10-digit HUC, which produced a tentative choice set of 258 watershed units (Figure 1). Fishable river reaches were defined within these units so that reach-level summaries of fisheries biomass and other covariates (described below) could be summarized without accounting for unfished headwater streams. A fishable reach was defined as a stream segment in the 1:100,000-scale National Hydrography Dataset (NHD) [*US Environmental Protection Agency (USEPA) and US Geological Survey (USGS)*, 2005] with an upstream catchment area greater than or equal to 50 km^2. Ninety seven percent of reported river fishing sites in the MRAS that could be matched to a specific reach fall within this cutoff.

A further refinement of the site definition was made to reduce heterogeneity of stream types within a watershed. Distinctive fish assemblages are associated with warm water and cold water habitats in Michigan on the basis of the fisheries they support [*Wehrly et al.*, 2006; *Zorn et al.*, 2011]. The NHD stream reaches

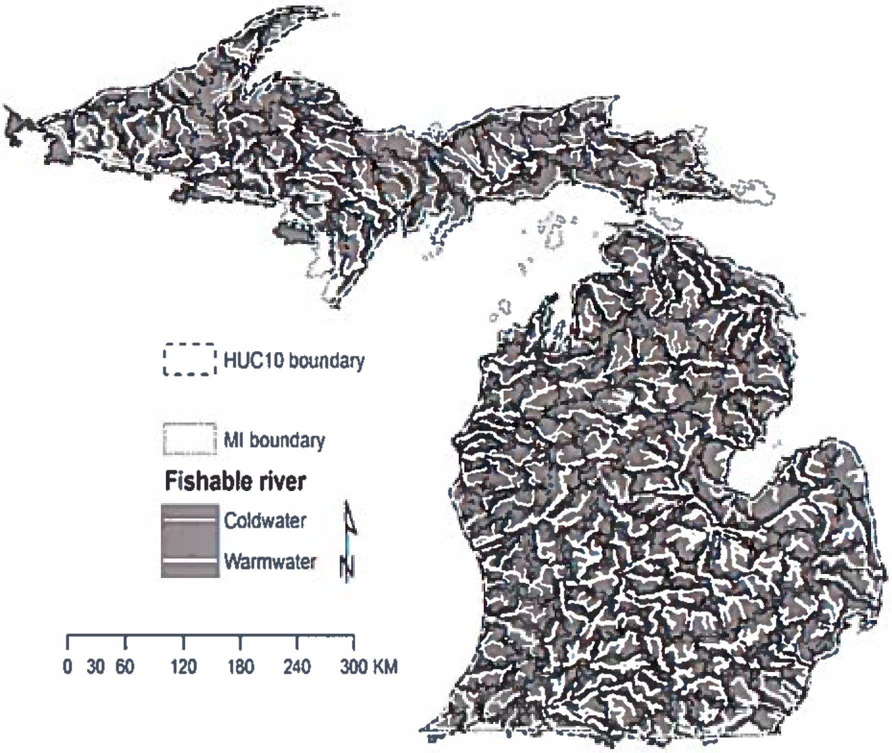

Figure 1. Fishable rivers and streams in Michigan with hydrological boundaries.

within each watershed were classified as cold water or warm water using a July mean temperature of 19.5° C as a cutoff [*Zorn et al.*, 2009]. A small watershed might only contain warm water streams and would therefore consist of a single, warm water fishable alternative, while a large watershed might contain both warm water (e.g., downstream) and cold water (e.g., upstream) reaches and would consist of two alternatives in each stream class. This refinement resulted in 408 fishable alternatives—the sites in the RUM model. Trip destinations were matched to sites based on the stream name, county and/or nearest city reported by the angler.

Although our river fishing model has a very large choice set with a broad range of fishing options, it does not include fishing at other waters such as the Great Lakes and inland lakes. This decision was made to maintain a tractable model but also because we know that for certain anglers (e.g., brook trout anglers) there are no feasible alternative water body types in Michigan. Moreover, prior research with models covering a statewide scale has demonstrated that for many changes in quality of site access there is a relatively small degree of substitution between fishing in different water body types in Michigan [*Jones and Lupi*, 2000; *Kotchen et al.*, 2006]. Thus, the insights from our model are likely to be accurate as long as they are interpreted in the context of the relevant population (in this case, only stream anglers) [*Jones and Lupi*, 2000; *Parsons et al.*, 2000].

Travel costs were calculated from travel distances, angler characteristics and gasoline prices. Travel distances from the centroid of an angler's home zip code to the centroid of each fishable alternative were estimated using the PC*Miler program [*ALK*]. The midpoint of an angler's income category from one of six possible categories on the questionnaire or, for anglers who omitted a response, the census-reported zip code median income was used as a measure of income. We then used one third of an angler's income divided by 2000 to proxy for the opportunity cost of travel time [*Parsons*, 2003]. Per-mile driving costs were computed from Michigan monthly retail gasoline prices (per gallon) [see *US Energy Information Administration (EIA)*, 2012] divided by the average per-gallon fuel economy for light vehicles in the year of the trip, plus per-mile maintenance and depreciation costs gathered from AAA reports. For undated trips we used the 2007–2010 average gasoline price and fuel economy. This yielded an average per-mile cost of fuel,

Table 3. Fish Biomass Estimates Across Fishable Alternatives[a]

Species	Min	Median	Mean	Max	% Occupied[b]
Brook trout	0.00	0.00	0.48	6.78	39
Brown trout	0.00	0.05	2.38	32.42	54
Smallmouth bass	0.00	0.00	0.62	9.60	49
Panfishes	0.00	1.98	3.67	292.66	83
Walleye	0.00	0.00	0.09	1.59	46

[a] These refer to the untargeted biomass estimated from *Esselman et al.* [2014].

[b] This is the percentage of sites that are predicted to have a positive amount of biomass for each species.

maintenance and depreciation of $0.40. Finally, travel costs were calculated as round-trip distance in miles times per mile fuel, maintenance and depreciation costs plus the opportunity cost of travel assuming an average driving speed of 45 miles per hour.

2.2. Fish Biomass Data

The fish biomass estimates for each HUC come from a series of models developed by *Esselman et al.* [2014]. To summarize, fish biomass for commonly targeted sport fisheries was modeled using biomass measures compiled in the Michigan Rivers Inventory (MRI) [*Seelbach and Wiley*, 1997]. The MRI data set contains biomass (kg ha^{-1}) by species measurements for 675 sites in Michigan cold and warm water rivers. Modeled fish species include brook trout, brown trout, walleye, smallmouth bass, and a combined group of panfishes that are targeted more generally with hook and line (including black crappie, white crappie, bluegill, green sunfish, hybrid sunfish, pumpkin seed sunfish, redear sunfish and rockbass). For each species or species group, a boosted regression tree model was trained and optimized on the MRI data. Predictors in the models were drawn from databases developed in the Great Lakes Aquatic Gap Analysis Program [*US Geological Survey Great Lakes Science Center (GLSC)*, 2006] and the Classification and Impairment Assessment of Upper Midwest Rivers project [*Brenden et al.*, 2006; *University of Michigan (UM)*, 2006]. The regression tree models predicted fish biomass to all confluence-to-confluence river reaches in fishable rivers predicted to be occupied by each species based on *Steen et al.* [2008]. Fish biomass was then summarized to the angler choice set as the length-weighted mean value of all warm or cold water reaches in each fishable alternative (Table 3). The predictions indicate that fish biomass for a particular species or species group is characterized by little-or-no abundance at most of our sites and high abundance at some sites. Among the species, brook trout are least likely to be found at our sites, which is not surprising given their habitat requirements. On the other hand, some kind of panfish can be expected at most sites, which is consistent with the variety of fish included in this species group.

The biomass measures enter the RUM model as individual (angler)-specific variables. The MRAS database includes information on the particular species targeted, if any, by anglers during a fishing trip. Five indicators classify anglers as targeting some combination of trout, bass, panfishes, walleye or other species, while a sixth indicator accounts for anglers who did not target a particular species on a trip (Table 4). Interacting these indicators with the species biomass predictions from Esselman et al. creates targeted biomass variables. This adjustment allows us to focus on the desirability of biomass for site choice taking fish preferences as given [*Scrogin et al.*, 2004]. The resulting biomass variables are used as individual-specific explanatory variables in the recreational fishing site choice model.

2.3. Site Choice Model

We use a RUM model to test and measure the importance of the site characteristics travel cost and fish biomass on stream choice. In general, recreational demand RUM models explain observed trip patterns in terms of the characteristics a trip-taker would experience at different alternatives. Each angler i has the choice to visit N_i sites, while each site $j \in 1,\ldots,N_i$ is associated with a utility level of U_{ij}. The indirect utility level measures the benefits an angler enjoys on a trip occasion to alternative j and is expressible as:

$$U_{ij}=U(y_i-p_{ij}, b_{ij}, q_j, \varepsilon_{ij}) \tag{1}$$

where y_i is the angler's income, p_{ij} is the travel cost, b_{ij} is the targeted species biomass, q_j is a vector of site-specific quality measures and ε_{ij} is the part of utility determined by factors unobserved by the researcher.

Table 4. Stream Fishing RUM Model Results[a]

Parameter	Coefficient	Clustered Standard Error
Targeted Fish Biomass		
Brook trout	0.400	0.180
Brown trout	0.132	0.057
Smallmouth bass	0.098	0.031
Panfishes	0.109	0.023
Walleye	0.364	0.084
Price Measure		
Travel cost	−0.031	0.003
Landscape		
NWSR[b]	0.563	0.236
Forest[b]	−1.540	0.491
Agriculture[b]	−2.325	0.745
Urban[b]	−3.165	1.279
Length[b]	0.181	0.073
Group Class		
Cold water[b]	−0.495	0.194
Dissimilarity, θ	0.582	0.065
Trips		2064
Rows of data		273,378

[a] All reported estimates are significant at the 5% level. The results for the site fixed effects are withheld for brevity.

[b] Identified via a regression of the site fixed effects on these variables ($N=232$; $R^2=0.552$), which included 12 basin-level fixed effects withheld for brevity.

Assuming utility is linear and additively separable in the observed and unobserved components, we can rewrite equation (1) as

$$U_{ij}=V_{ij}+\varepsilon_{ij} \text{ where } V_{ij}=\alpha(y_i-p_{ij})+\beta b_{ij}+\gamma q_j. \quad (2)$$

Trips are taken to the alternative that yields the highest utility among all possible choices, implying that site j is chosen when $U_{ij}>U_{ik}$, although the researcher only observes the portion V_{ij} and cannot predict with certainty the preferred fishing alternative for any given trip. However, by specifying a distribution for ε_{ij} the probability that the site visited is best can be formed:

$$\begin{aligned} prob_i(choose\ j) &= prob(U_{ij}>U_{ik})\ \forall\ j \neq k \\ &= prob(V_{ij}+\varepsilon_{ij}>V_{ik}+\varepsilon_{ik})\ \forall\ j \neq k \\ &= prob(V_{ij}-V_{ik}>\varepsilon_{ik}-\varepsilon_{ij})\ \forall\ j \neq k \end{aligned} \quad (3)$$

Note that in the probability only differences in utility matter so that with equation (2) angler-specific characteristics such as income are differenced away and have no role in the model. Following one common approach in the recreation demand literature, we assume ε_{ij} is distributed generalized extreme value. This yields the nested logit site choice model, which allows alternatives to be placed in groups to account for unobserved similarities between grouped alternatives. Within a group the alternatives are assumed to share common but unobserved characteristics that drive correlation between choices. We adopt a two-level model, where the upper level consists of the choice of group and the lower level consists of the choice of alternatives within the preferred group. We distinguish the alternatives by their cold water and warm water classification so the nested model consists of two groups. The probability of visiting a particular site j is therefore

$$prob_i(choose\ j)=e^{V_{ij}/\theta}\times\left[\sum_{k=1}^{N_g}e^{V_{ik}/\theta}\right]^{\theta-1}\Bigg/\sum_{g=1}^{G}\left[\sum_{k=1}^{N_g}e^{V_{ik}/\theta}\right]^{\theta} \quad (4)$$

where N_g is the number of sites in group g (in our particular case g = cold water, warm water) and θ is a "dissimilarity" parameter that captures the degree of correlation between alternatives within a group.

There are several types of variables used in the RUM model. Of primary interest are the targeted biomass variables, *brook trout, brown trout, smallmouth bass, panfishes* and *walleye*, measuring the fishing quality at each site. Although one could argue that biomass does not directly enter into an angler's utility function, using it as a measure of fishing quality has several advantages over catch rates: First, catch data gathered from surveys where the anglers are sampled rather than the sites tend to produce expected catch rates with measurement error, particularly for the least visited sites, and therefore biased demand model parameters [*Morey and Waldman*, 1998; *Train and McFadden*, 2000]. Second, catch is a function of biomass and fishing effort, which is endogenous [*Clark*, 1990; *Harley et al.*, 2001], so using biomass can be viewed as a sort of reduced-form approach to measuring site quality independent of effort. Third, fisheries managers in Michigan tend to stock streams based on added fish per unit area, which is akin to our biomass formulation [*Dexter and O'Neal*, 2004]. Of course, anglers might care about other factors such as fish sizes, but size-specific measures are generally unavailable for both biomass and catch rates.

Next, we include the variable *travel cost* to account for the individual-specific price of taking a fishing trip. The coefficient on this variable reflects the change in utility from a small increase in the cost of visiting a site.

The final set of variables controls for the influence of site-specific features on site choice, including landscape characteristics and built amenities. In the version of the model reported here we use site fixed effects

– that is, a full set of alternative specific constants – to avoid problems with omitted variables bias in the biomass and travel cost parameter estimates [*Moeltner and von Haefen*, 2011; *Weber et al.*, 2012]. We considered alternative specifications that combined observable landscape variables with more aggregated fixed effects but the results suggested that controlling for site-specific omitted characteristics was critical. To identify the importance of observed site-specific factors on site choice the estimated fixed effects were regressed on several landscape variables [*Murdock*, 2006], including: *NWSR*, a proxy for the remote and scenic setting around stream segments protected under the National Wild and Scenic Rivers Act of 1968 [*Sanders et al.*, 1990]; *forest*, *agriculture*, and *urban*, the percentages of the riparian landscape in different land uses (the omitted category is composed of scrub/shrub, grass and bare land); *length*, the natural logarithm of the aggregate stream lengths in the site (in km); and, finally, *cold water*, an indicator to capture the share of trips taken to cold water sites relative to warm water sites that remains unexplained by the other variables.

The RUM model is parameterized on the Michigan stream angler and biomass data. We use equation (4) to create a likelihood function across the possible choice alternatives for all trips and estimate the parameters by maximum likelihood. To control for monthly changes in MRAS surveying intensity, each trip is weighted by the inverse of the probability that it was collected from a survey in a particular month. Trips are also clustered by angler to account for individuals who have multiple trips in the sample. Due to the use of site fixed effects, the 176 of 408 fishable alternatives that did not receive any visits in the sample could not be included in the final RUM model choice set. We estimated variations of the model without site fixed effects that did and did not include unvisited sites and found few significant changes between the variants, suggesting that this decision has little bearing on the results.

2.4. Value Measurement

Changes in the characteristics and quality of the choice alternatives can be valued using the estimates of the RUM model. Monetary values are computed as anglers' willingness to pay (WTP) to forgo a quality change on a choice occasion [*Haab and McConnell*, 2003]. Following a quality change, WTP is the amount that leaves the angler no better or worse off than before the quality change. Let V_j and V_j^* refer to measurable utility before and after a quality change, respectively. In the context of the RUM model estimated as a nested logit it can be shown that

$$WTP_i=\frac{-1}{\rho}\left[ln\sum_{g=1}^{G}\left[\sum_{j=1}^{N_g}e^{V_{gj}/\theta}\right]^{\theta}-ln\sum_{g=1}^{G}\left[\sum_{j=1}^{N_g}e^{V_{gj}^{*}/\theta}\right]^{\theta}\right] \tag{5}$$

per choice occasion. Equation (5) can also be used to estimate the monetary damage of site loss, where the affected alternative is removed from the summation of V_j^* in the right hand side of the equation.

Following estimation of the RUM model, WTP is computed using the estimated parameters and the observed quality measures for V_j and quality measures for V_j^*. In our applications, we report WTP for several quality change scenarios. The first set of scenarios measure the benefits arising from a 50% increase in biomass for each species at all sites. The second set of scenarios evaluates the benefits arising from a 1 kg per ha increase in biomass at all sites. Each of these WTP estimates is a type of per-trip gain, and should be interpreted as the expected monetary benefit across day trips to every fishing site in the model.

We also examine the monetary damages from closing some of the fishable alternatives. These damages are calculated as loss-to-trip ratios by evaluating equation (5) and dividing by the average probability that a trip was taken to the affected (closed) site [*Parsons et al.*, 2009]. Loss-to-trip ratios are interpreted as the monetary damage to those fishing trips taken specifically to the lost site. Whether expressed as values across all trips in the choice set as in equation (5) or as loss-to-trip ratios, the measures are highly nonlinear in the estimated parameters. Thus, confidence intervals were computed by bootstapping the estimation of the model parameters 200 times.

3. Results and Discussion

3.1. RUM Model Estimates

Table 4 presents the estimated parameters of the RUM model. The travel cost parameter has the expected negative sign and is statistically significant at the 0.01 level, indicating that the probability of a trip to a site is decreasing in the trip price. Overall, the RUM model predicts a strong targeted biomass effect. The biomass parameters are positive and significant at traditional confidence levels for all five species. These estimates show that Michigan stream anglers respond to differences in fish abundance between sites and, specifically, that the probability of visiting a site increases with targeted biomass.

The estimates demonstrate that anglers do not react equivalently to changes in fish biomass across species. The hypothesis that the effect of targeted biomass on site choice is the same for all species is rejected at a high confidence level. Of the biomass parameters, the point estimates are greatest for brook trout and walleye, implying that anglers' site preferences are particularly sensitive to the biomass of these two species.

The fixed effects add significantly to the model based on the Akaike information criterion goodness-of-fit measure. For brevity the 232 estimates for these parameters are not reported but, in general, the fixed effects suggest that unmeasured site attributes enjoyed by all anglers tend to be important components of utility. The role of observed site attributes on site choice can be gauged through an auxiliary regression of the estimated fixed effects on site-specific variables [*Murdock*, 2006]. The results of this procedure in the present case are reported in Table 4 (that auxiliary regression also included 12 basin fixed effects which are omitted for brevity). The landscape variable estimates indicate that anglers tend to fish at sites with the National Wild and Scenic Rivers designation but avoid sites with a high proportion of urban or agricultural development in the riparian area, other things being equal.

The results further suggest that there are unobserved characteristics that are correlated within the nested groups. The dissimilarity parameter, which was constrained to be equal across groups, is significantly different from 1, suggesting that alternatives within the cold water or warm water group exhibit more similarities with alternatives in their own group than with alternatives in the other group. Though not reported here, we also considered a specification with different dissimilarity parameters by nests; we found this had a negligible effect on the estimated effects, although it did suggest that cold water alternatives were less correlated with one another than warm water alternatives.

3.2. Benefit Estimates

Welfare estimates are calculated for a 50% and for a one kilogram per hectare increase in biomass at all sites for each species (Table 5). Although these scenarios are for illustration of the model, in practice managers do adopt stocking strategies based on the added weight of a particular species per unit area [*Dexter and O'Neal*, 2004]. As discussed above, in these scenarios WTP is expressed in terms of a trip taken to any river or stream in Michigan.

WTP varies between the two welfare scenarios largely due to differences in the estimated parameters on the targeted biomass levels and differences in the mean targeted biomasses (see last column, Table 5). For example, the value of changing walleye biomass is less than that for panfishes for an equivalent percentage increase in in situ biomass, though walleye is more valuable per unit biomass. A 50% increase in walleye is worth about \$1.1/trip while a 50% increase in panfishes is worth about \$3.7/trip, but this equi-proportional increase in targeted biomass leads to a much greater total increase in panfishes (about 0.897 kg ha^{-1}) than in walleye (about 0.028 kg ha^{-1}). The WTP for walleye is greater for an equal increase in biomass: a 1 kg ha^{-1} increase is worth about \$4.0/trip for walleye versus \$1.5/trip for panfishes.

Overall, these estimates imply that increasing brook trout and walleye abundance would return the most value to Michigan's stream fisheries. These two game fish species also happen to have the least in situ biomass of the species considered in the model (Table 3 and last column of Table 5).

Comparing the WTP estimates from our quality change scenarios with those reported in the literature is difficult because our measures of fishing quality are distinct from prior studies. The ranking of values we identify is similar to *Murdock*'s [2006] results for a RUM model of Wisconsin fishing; both indicate that anglers are willing to pay significantly for increases in walleye and trout abundance. *Melstrom and Lupi* [2013] find that on average Great Lakes anglers are willing to pay \$4–6 per trip to avoid a 50% decline in walleye catch rates, which is more than our own willingness to pay estimate of about \$1 to obtain a 50% increase in walleye biomass in rivers (that could be expected to have a proportional impact on walleye catch); however, this difference may be attributable to the larger share of anglers who target walleye in the Great Lakes.

The average loss-to-trip ratio ranges from about \$19–23 depending on the closed site. For example, we find that, on average, trips to the warm water portion (i.e., the main stem) of the Muskegon River below Hardy

Table 5. Average per Trip WTP ($) for Increase in Targeted Biomass[a]

Species	50% Increase	1 kg ha^{-1} Increase	RUM Model Mean Targeted Biomass (kg ha^{-1})
Brook trout	2.372 (0.773–6.971)	7.104 (2.655–14.670)	0.249
Brown trout	3.370 (1.605–7.931)	2.346 (1.275–4.523)	1.198
Smallmouth bass	1.707 (0.836–2.571)	1.567 (0.836–2.216)	0.531
Panfishes	3.692 (2.531–4.836)	1.549 (1.073–1.984)	1.793
Walleye	1.149 (0.704–1.771)	4.032 (2.649–5.792)	0.055

[a] WTP 95% confidence intervals in parentheses below estimates computed by bootstrapping the model 200 times.

Dam, the most popular fishing alternative in the sample (receiving about 6% of sample trips), are worth $23 (95% confidence interval: $21–$24). For trips to the southern watershed of the Au Sable River, a more typical sportfishing site (receiving less than 1% of sample trips), we estimate an average value of $19 ($17–$21). Jointly closing groups of alternatives or entire river systems will produce higher damages on a per-trip basis: we find that access to the Au Sable River system subbasin has a mean estimated value of $26 ($23–$28). Furthermore, we estimate that access to the northwestern Lake Huron basin, which includes the Au Sable River subbasin, has a mean value of $45 ($40–$51).

The damages of lost access that we estimate, about $20 per trip, are somewhat smaller than those reported in the literature due in part to the comparatively fine scale of our site definitions. Not surprisingly, our damage estimates grow closer to these other estimates after conditioning on the scale of lost access. For example, *Train* [1998] estimates that the Madison River in Montana is worth around $40 per trip and *Von Haefen* [2003] estimates that the lower Susquehanna River is worth about $30 per trip, after adjusting for inflation. Both of these sites are on the scale of a subbasin, which makes the Train and the von Haefen estimates very similar to our own for access to subbasins in Michigan.

4. Conclusion

This paper developed a site choice model capable of valuing recreational fishing quality at Michigan rivers and streams. The objective was to identify angler preferences for various fish—trout, bass, panfishes and walleye—using species-specific biomass as an exogenous measure of fish abundance. Prior research has largely relied on presence-absence indicators or average catch rates to characterize fishing quality and was not designed to value a variety of individual fish species or biomass. Our model took advantage of species-specific biomass measures in order to derive anglers' willingness-to-pay for improvements in the quality of fishing for individual species. Our estimates indicate that anglers, conditional on the species or species groups they are targeting, tend to visit sites that are high in fish biomass. In particular, we found that brook trout followed by walleye had the most valuable biomasses for stream fishes in Michigan.

The set of fishable alternatives used in the model was characterized by watershed boundaries. These boundaries resulted in watershed areas that were generally 100–200 square miles (260–520 km^2) in size with the site containing a short river reach and its fishable tributaries. This site definition is useful because, first, it allows the researcher to value changes in the quality at a variety of watershed levels and, second, it was based on both stream temperatures and USGS hydrologic units (10-digit HUC), so the classification could be applied to any US state or region.

There are some caveats to this analysis that could be addressed by future research. The model only included single-day trips, and thus may not capture values and substitution in the same manner as a model that incorporates the behavior of anglers who take multiple-day trips. Furthermore, while angler heterogeneity was partially embedded into the model via targeted-species preferences, further insight may be gained by exploring the influence of other observable and unobservable angler characteristics on site choice. In terms of the species-specific biomass measures, our sites include tributaries considered fishable, but smallmouth bass were predicted by *Esselman et al.* [2014] to be limited to larger rivers, which might be taken into account in future site definitions focused on bass angling. Finally, angler welfare may be influenced by both the rate and size of catch, which biomass cannot distinguish between. The willingness of anglers to tradeoff catch rate for catch size needs further study.

Managing aquatic ecosystem services requires knowledge about the benefits that users gain from the resource. This paper provided benefit estimates that can be easily used in cost-benefit analysis. Although the model was applied to stream anglers taking single-day trips in Michigan, we expect that the reported WTP estimates are suitable for benefits transfer to streams around the Midwest and the Great Lakes region.

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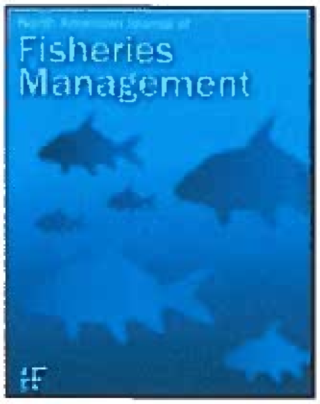

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Landscape Prediction and Mapping of Game Fish Biomass, an Ecosystem Service of Michigan Rivers

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ARTICLE

Landscape Prediction and Mapping of Game Fish Biomass, an Ecosystem Service of Michigan Rivers

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Abstract

The increased integration of ecosystem service concepts into natural resource management places renewed emphasis on prediction and mapping of fish biomass as a major provisioning service of rivers. The goals of this study were to predict and map patterns of fish biomass as a proxy for the availability of catchable fish for anglers in rivers and to identify the strongest landscape constraints on fish productivity. We examined hypotheses about fish responses to total phosphorus (TP), as TP is a growth-limiting nutrient known to cause increases (subsidy response) and/or decreases (stress response) in fish biomass depending on its concentration and the species being considered. Boosted regression trees were used to define nonlinear functions that predicted the standing crops of Brook Trout *Salvelinus fontinalis*, Brown Trout *Salmo trutta*, Smallmouth Bass *Micropterus dolomieu*, panfishes (seven centrarchid species), and Walleye *Sander vitreus* by using landscape and modeled local-scale predictors. Fitted models were highly significant and explained 22–56% of the variation in validation data sets. Nonlinear and threshold responses were apparent for numerous predictors, including TP concentration, which had significant effects on all except the Walleye fishery. Brook Trout and Smallmouth Bass exhibited both subsidy and stress responses, panfish biomass exhibited a subsidy response only, and Brown Trout exhibited a stress response. Maps of reach-specific standing crop predictions showed patterns of predicted fish biomass that corresponded to spatial patterns in catchment area, water temperature, land cover, and nutrient availability. Maps illustrated predictions of higher trout biomass in coldwater streams draining glacial till in northern Michigan, higher Smallmouth Bass and panfish biomasses in warmwater systems of southern Michigan, and high Walleye biomass in large main-stem rivers throughout the state. Our results allow fisheries managers to examine the biomass potential of streams, describe geographic patterns of fisheries, explore possible nutrient management targets, and identify habitats that are candidates for species management.

The increasing integration of ecosystem service concepts into environmental management places a new emphasis on research addressing the ecological drivers of fish productivity. Ecosystem services are defined as components of nature that are directly enjoyed or consumed by humans or that are used to yield human well-being (Boyd and Banzhaf 2007). Biomass of target fish populations is a crucial "provisioning service" of ecosystems that has a high economic and cultural value to

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society (Millennium Ecosystem Assessment 2005). In Michigan alone, total expenditures by recreational anglers are estimated at more than $2.4 billion annually (Southwick Associates 2007). Although the economic service values of Michigan's Great Lakes fisheries have been linked to fish catch rates (Melstrom and Lupi 2013) and fish productivity (Kotchen et al. 2006), the connection between ecosystem service values and fish productivity in rivers is poorly understood. An understanding of this connection is complicated because the species targeted by river and stream anglers are spread across heterogeneous landscapes with different capacities to provide fish to anglers and, by extension, differing capacities to accrue economic benefits to society. An understanding of which landscape conditions have the greatest potential to provide fish to anglers is a precursor to economic valuation and could facilitate strategies for maximizing this provisioning service of rivers. Maps of productive fish provisioning areas could be particularly useful to decision makers.

An important research question underlies the ability to map spatial variability in game fish availability to anglers: what factors constrain fish productivity at the landscape scale? If the constraints on measures of fish productivity (e.g., biomass) can be mapped continuously across the landscape, then it should also be feasible to model and continuously map the productivity of habitats. Previous work in rivers has identified a suite of local factors that are thought to constrain fish production. For instance, fishes in Michigan are strongly influenced by water temperature (Wiley et al. 1997; Wehrly et al. 2003; Zorn and Wiley 2006), which affects their metabolism and growth (Diana 2004) and has been correlated with fish presence and standing crops (Steen et al. 2008; Zorn et al. 2009). Other habitat characteristics that have been commonly associated with fish abundance or biomass are species dependent but include river depth, substrate, fish cover availability, and bank and riparian conditions (Jones et al. 1974; Hokanson 1977; Stuber et al. 1982a, 1982b; Johnson et al. 1988; Page and Burr 1991; Zorn and Wiley 2004).

Fish biomass has also been linked to concentrations of limiting nutrients, which are thought to act indirectly via a bottom-up trophic cascade to influence game fishes at higher trophic levels. For instance, Askey et al. (2007) found fivefold and 25-fold increases in biomass of Brown Trout *Salmo trutta* and Rainbow Trout *Oncorhynchus mykiss*, respectively, downstream from a municipal effluent source near Calgary, Alberta, and these increases were also accompanied by increases in invertebrate, macrophyte, and phytoplankton biomass. An 11-fold to 73-fold increase in piscivore biomass was found below sewage effluents in a river near Montreal, Quebec, with Smallmouth Bass *Micropterus dolomieu* being among the greatest beneficiaries in terms of increased daily production (deBruyn et al. 2003). In experimental settings, bottom-up trophic cascades in response to phosphorus enrichment have been demonstrated to increase production at all trophic levels (Slavik et al. 2004), and salmonids have been shown to attain greater lengths and biomasses in response to nutrient additions (Johnston et al. 1990; Peterson et al. 1993; Slaney et al. 2003). Thus, in addition to temperature and other local habitat factors, nutrients are an important mediator of rivers' ability to provide fish to anglers.

The local habitat constraints on fishes are in turn constrained by landscape factors occurring at coarser spatial scales (Frissell et al. 1986). For instance, channel depth, velocity, substrate, and food availability are all strongly linked to upstream catchment area or longitudinal position within the river continuum (Vannote et al. 1980; Wiley et al. 1990; Rahel and Hubert 1991; Poff 1997; Slaney et al. 2003). Landscape factors have been used previously to predict the productivity of river fishes, thereby creating the potential to map fish biomass continually as an index of fish availability to anglers. Zorn et al. (2004) used multiple linear regression to model standing crops of 63 Michigan fish species, and their models generally explained between 10% and 50% of the variance for game species. Steen et al. (2008) used classification tree models to predict and map abundance categories (low, medium, and high) of 93 fish species in Michigan rivers and obtained good classification accuracy (average of 76% correct classification across species). Species–habitat models using as many as 25 habitat variables explained between 35% and 91% of the variation in abundances of 11 fish species in the Genesee River basin, New York (McKenna et al. 2006), and other workers have also successfully modeled fish abundances by using landscape and local factors (e.g., Gido et al. 2006; Stanfield et al. 2006). Synthesis of prior work suggests that nonparametric machine learning modeling approaches perform favorably in comparison with linear models (McKenna et al. 2006) and that the inclusion of modeled local conditions (e.g., hydrology, nutrients, and temperature) with landscape variables can lead to greater predictive power (Zorn et al. 2004).

The primary goals of the current study were to (1) use models to predict game fish standing crops continuously across the entire state of Michigan by using landscape and modeled local habitat variables and (2) identify the strongest landscape constraints on the standing crops of economically important game fishes. Standing crops were thus treated as an indicator of a river's capacity to produce fish for anglers as an important provisioning service of waterways that yields benefits in the form of recreational and subsistence harvest (Boyd and Banzhaf 2007). We modeled standing crop (i.e., biomass density) rather than numerical density because standing crop is less affected by interannual variation in year-class strength (Zorn et al. 2004) and is a recommended indicator for ecosystem services (e.g., how much of the service is present; de Groot et al. 2010). Although biomass may be an imperfect measure of the availability of catchable fish to anglers, measures of catchable fish were not available for modeling. Furthermore, high biomass values in the Michigan Rivers Inventory data set were generally driven by the presence of large fish in a given sample (T. Zorn, Michigan Department of Natural Resources, personal communication), and a companion paper (Melstrom et al. 2015) demonstrated that fish biomass predictions across the landscape as generated by the current study were significantly correlated with angler choices about where to fish.

We were secondarily interested in testing hypotheses about game fish responses to total phosphorus (TP) concentrations. We focused on TP because (1) streams in Michigan tend to be phosphorus limited (Hart and Robinson 1990); (2) TP concentrations in water are significantly correlated with total fish standing crop (Hoyer and Canfield 1991; Randall et al. 1995); and (3) TP has been shown to drive positive (subsidy) responses in trout and bass fisheries (reviewed above). Thus, TP has the potential to increase the provision of fish to anglers. However, phosphorus is also a pervasive pollutant that can act as a stressor on stream ecosystems at higher concentrations (Miltner and Rankin 1998). Phosphorus-enriched streams support greater biomasses of benthic algae, macrophytes, and phytoplankton, which can lead to alterations in near-substrate flow velocities, dissolved oxygen, and pH dynamics (Welch et al. 1992; Dodds and Biggs 2002). These changes can be detrimental to sensitive species (Miltner and Rankin 1998), such as Brook Trout and Smallmouth Bass, leading us to hypothesize that these two species would respond positively to TP at low concentrations (a subsidy response) and negatively at higher concentrations (a stress response). More tolerant species, such as many sunfishes and Brown Trout, were expected to show only a subsidy response. Because Walleyes *Sander vitreus* make long in-channel migrations for spawning and are often sampled during their migration, we hypothesized that Walleyes would exhibit no response to nutrient levels at their place of capture. Below, we describe our approach to modeling and testing our nutrient effect hypotheses, present our model results, and describe our predictions of fish biomass as an indicator of Michigan rivers' potential to provide fish to anglers.

METHODS

Study site.—Michigan is divided geographically into the Upper Peninsula (UP) and Lower Peninsula (LP) at the point where Lake Michigan meets Lake Huron (Figure 1). The state is drained by approximately 85,000 km of streams that discharge into Lakes Erie, Huron, Michigan, and Superior. There are few high-gradient streams in the state, which has a low elevational range (174–603 m above sea level) and many wetlands. The surficial geology in much of the LP is dominated by glacial till and outwash deposits, the presence of which lead to high infiltration rates, high groundwater discharge, stable hydrology, cold water temperatures, and generally low nutrient concentrations (Olcott 1992; Wiley et al. 1997; Zorn et al. 2009). Cold water temperatures in the UP also result from the colder air temperatures at these northern latitudes and from the higher amounts of forest cover. The southeastern portion of the LP (i.e., from Saginaw Bay to the southern border of the state) deviates from the general pattern of till and outwash geology and is characterized by fine-textured lake plain deposits or postglacial alluvium. Streams in this area have lower infiltration rates, cool and warm surface waters, more flashy flow regimes, and higher natural nutrient concentrations. Distinctive fish communities are associated with coldwater and warmwater streams (Wiley et al. 1997; Zorn et al. 2002; Wehrly et al. 2003). Streams in the southern LP and main-stem rivers of the UP have summer temperatures that exceed 19°C, a threshold above which warmwater communities are found in Michigan (Wehrly et al. 2003).

Data sources.—The fish data used in this study came from the Michigan Rivers Inventory database (Seelbach and Wiley 1997). Between 1982 and 1995, fish populations were sampled at 675 sites in the LP by using rotenone, electrofishing depletion, or mark–recapture techniques (methods are described in more detail by Seelbach and Wiley 1997 and Zorn et al. 1998). Rotenone samples were collected mostly in third- to fifth-order warmwater streams, and the weights of species captured and area sampled were recorded. Multiple-pass depletion sampling with electrofishing was conducted mostly in small (first- or second-order) streams by using two to five passes with block nets set at the upper and lower extents of most reaches. The biomass of each sample was estimated by using the following equation: $N_i = (N_t/C_t) \times C$, where N_i is the estimated weight of species i; N_t is the total weight captured of species i; C is the estimated weight of all species combined (after Zippin 1958); and C_t is the combined weight of all species captured. Mark–recapture population estimates were made primarily for salmonids by using the Bailey modification (Cooper and Ryckman 1981). Our response variable was the estimated total biomass density (kg/ha; standing crop) of different target species at a sampling site. Because some targeted sampling occurred, the number of sites available for model training varied among species from 335 to 397 sites spread across the LP (Figure 1). Targeted collection samples were only used in models of the species targeted.

The following fisheries were modeled: Brook Trout *Salvelinus fontinalis*, Brown Trout, Smallmouth Bass, Walleye, and panfishes as a group (Bluegill *Lepomis macrochirus*, Green Sunfish *L. cyanellus*, Pumpkinseed *L. gibbosus*, Redear Sunfish *L. microlophus*, White Crappie *Pomoxis annularis*, Black Crappie *Pomoxis nigromaculatus*, and Rock Bass *Ambloplites rupestris*). Standing crop values were $\log_e(x + 1)$ transformed to improve normality and reduce the leverage of high observations.

Landscape environmental predictor variables (Table 1) were obtained from the Great Lakes Aquatic Gap Analysis Program (GLSC 2006) and the Classification and Impairment Assessment of Upper Midwest Rivers (Brenden et al. 2006). These databases contain GIS-linked databases with catchment, riparian, and channel data attributed to interconfluence stream reaches. The river line geometry was taken from the 1:100,000-scale National Hydrography Dataset (USEPA and USGS 2005) with modifications to provide a more accurate

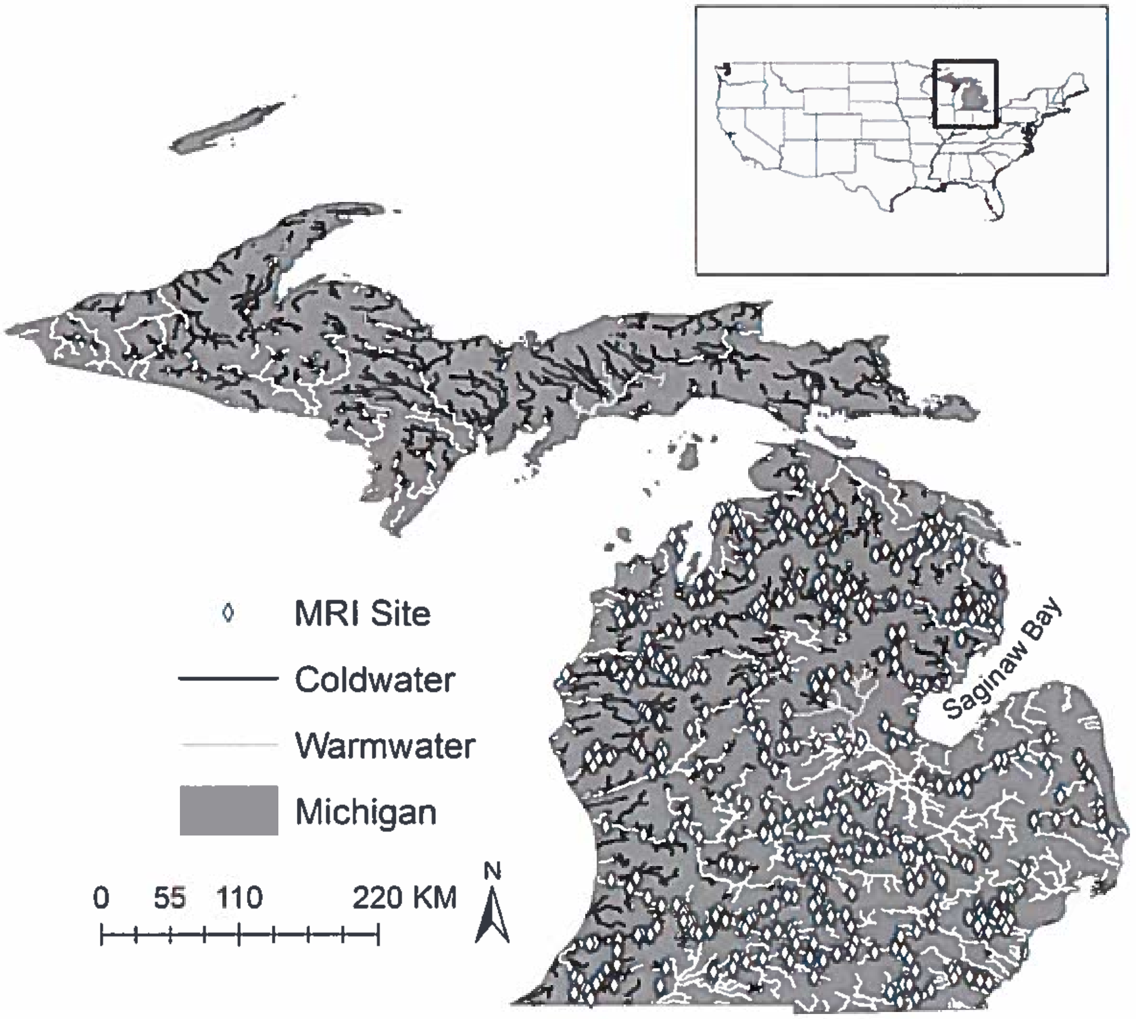

FIGURE 1. Locations of Michigan Rivers Inventory (MRI) sampling points for game fish standing crops. Not all points were sampled for all species. For the sake of clarity, only rivers with catchment areas greater than 50 km^2 are shown.

representation of Michigan rivers (Brenden et al. 2006). The databases contain approximately 320 variables for 31,817 stream reaches, including information about soil permeability, 1998 land cover, stream position, bedrock and surficial geology, climate, modeled hydrology, and modeled July mean stream temperatures (Brenden et al. 2006). Modeled summer TP concentrations (P. Esselman and R. J. Stevenson, unpublished data) were used to represent local nutrient conditions. The TP model explained more than 50% of the variation in a test data set of base flow TP concentrations and was used because it is superior to other TP estimates available for Michigan (Kleiman 1995). Reaches that had no upstream dams were attributed with an arbitrarily high value of 100,000 m for the "distance to upstream dams" variable to avoid missing values.

Fish standing crop models.—A boosted regression tree (BRT) model (Friedman 2001; Elith et al. 2008) was trained for each fishery considered. Boosted regression trees are good for the modeling problem at hand because they have generally high predictive performance and offer a clear way to describe potentially nonlinear statistical relationships between independent variables and a response. The latter characteristic of these models was necessary to test our hypotheses about subsidy and stress responses to TP concentration. We trained a model for each of the fish species by using the gbm.step algorithm of Elith et al. (2008) for the gbm package in R (R Development Core Team 2013). The algorithm progressively reduces predictive deviance until a stopping point is reached; the stopping point used was the point at which the average cross-validation deviation ceased to improve. Cross validation was performed after the addition of each set of 50 trees by dividing the data into 10 equal-sized subsets ("folds"), iteratively training the model with nine folds combined, and then calculating the deviation of predictions versus the held-out "test set" until all

TABLE 1. Predictors used to model game fish standing crops in Michigan, including summary statistics for measured values of predictors across all sampling sites (Min = minimum; Q25 = 25th percentile; Q75 = 75th percentile; Max = maximum).

Predictor variable	Min	Q25	Median	Mean	Q75	Max
Upstream catchment area (km^2)	1.3	37.7	189.5	712.3	636.1	14,103.5
Channel gradient (° × 1,000)	0.0	0.7	1.2	2.5	2.6	27.5
Water temperature (°C), predicted July mean	12.3	17.5	20.3	19.9	22.2	26.2
90% exceedance flow yield ($m^3 \cdot s^{-1} \cdot km^{-2} \times 1,000$)	0.1	1.2	2.7	3.4	4.9	13.5
50% annual exceedance flow (m^3/s)	0.0	0.2	1.0	5.5	4.6	110.8
50% exceedance flow in April (m^3/s)	0.0	0.7	3.2	12.4	11.6	215.6
10% annual exceedance flow (m^3/s)	0.0	0.9	5.4	18.7	15.8	290.3
Predicted base flow total phosphorus (μg/L)	8.4	14.9	28.9	37.8	51.5	165.7
Medium-grain surficial geology in the upstream riparian buffer (%)	0.0	0.0	0.0	15.0	25.6	100.0
Coarse and outwash geology in the upstream catchment (%)	0.0	37.5	81.4	67.5	99.0	100.0
Forest land cover in the local riparian zone (%)	1.7	54.7	70.8	65.8	82.7	99.1
Nonforested wetlands in the local riparian zone (%)	0.0	3.2	6.7	8.8	12.1	46.7
Upland forest cover in the local riparian zone (%)	0.0	14.1	24.0	28.2	39.1	85.3
Presence or absence of a dam downstream (0 or 1)	0.0	1.0	1.0	0.8	1.0	1.0
Distance to the nearest upstream dam (m/1,000)	0.1	7.7	25.7	52.1	100.0	100.0
Presence or absence of a dam upstream (0 or 1)	0.0	0.0	1.0	0.7	1.0	1.0

folds were used as test sets. The learning rate of each model was adjusted so that the cross-validation predictive deviance was minimized at between 1,500 and 3,500 trees.

A nonparametric permutation test was used to assess overall model significance. To implement this test, 1,000 data sets were created by randomizing the measured values of response variables. One-thousand models were run by using these data sets, and the cross-validation deviance of each model was recorded. The distribution of null deviance values was then compared to the model. The significance value (*P*) was calculated as the probability that the nonrandomized cross-validation deviance measured in the actual fishery was less than or equal to the mean of deviance values of all permutations assuming a standard normal distribution. After significance testing, the cross-validation results were used to examine (1) the precision of each fishery model based on the coefficient of determination (R^2); and (2) each model's accuracy based on the root mean square error (RMSE). The R^2 value was adjusted for the number of variables in each model relative to the number of observations (Theil 1961). The slope of the best-fit line between observed and predicted standing crop values was interpreted as a measure of model bias; residuals from the cross-validation calculations were plotted and examined for nonrandom structure and correlations with predictors to determine unmodeled input–output behavior.

A unique set of predictor variables was used to model each fishery based on a literature review of local habitat constraints on the species of interest (Supplementary Table S.1 available in the online version of this article). These constraining variables were then matched to our data set. In some cases, the habitat constraints could be represented directly from our data set by using modeled variables (e.g., temperature, phosphorus, and hydrology) or GIS-derived variables (e.g., sinuosity and channel gradient). In cases where local habitat constraints could not be represented directly, we attempted to identify suitable landscape proxies for the variable. Landscape proxies were established either as those with significant support from the analysis by Zorn and Wiley (2004) or as those with high correlation strengths to the corresponding local habitat variable in the Michigan Rivers Inventory (Table S.1).

Each predictor's relative importance for a model was expressed as the percentage of the total squared error improvement that could be attributed to that variable (Friedman 2001). We tested for the statistical significance of a TP effect by using a nonparametric permutation test in which 1,000 models were run with randomly reordered TP values while holding all other variables constant. Significance (*P*) was calculated as the probability that the relative importance of TP was greater than or equal to the mean relative importance value of all permutations assuming a standard normal distribution.

We interpreted partial dependence plots for each model to assess our hypotheses about the influence of TP concentration and the general effects of other variables. Partial dependence plots show the mean response of fish standing crops to a predictor after accounting for the average effects of all other predictors in the model (see Friedman and Meulman 2003). The *y*-axis of a partial dependence plot retains the original units of the response variable; thus, we were able to obtain insight into the magnitude of response that could be attributed to TP after controlling for the mean effects of other variables in the model. We used a bootstrap procedure whereby 1,000 models were run with a random selection of 75% of the data points to establish the 95% confidence interval (CI) around each mean predicted partial dependence curve.

Standing crops were predicted to stream reaches and were mapped on a continuous scale. Although we did not train our models with samples collected in the UP, our LP samples encompassed a range of habitats similar to those found in the UP, so we felt justified in predicting fishery responses to landscape conditions there. We examined the precision of our reach-specific standing crop predictions by mapping the SD around the mean prediction from the bootstrap procedure described above.

RESULTS

Model Performance

All models were highly significant ($P < 0.0001$) when compared with a null distribution of predictive deviance values from the permutation test on randomized response variables. The BRT models explained between 50% and 87% of the variation in training data and between 22% and 56% of the variation in cross-validation data for the fisheries considered; on average, the models had relatively low RMSE values (Table 2). The strongest model was for panfishes, followed by Brook Trout and Smallmouth Bass, Brown Trout, and Walleye. Scatter plots of observed versus predicted standing crops showed that the pattern of zero-value observations had a strong influence on the slope of the best-fit line (Figure 2), thus leading to slightly negative intercepts and to characteristic patterns of residual distributions (Figure 3). Brook Trout and panfish models tended to overpredict the zero and low values of standing crop while underpredicting the higher standing crop observations (Figure 2), although slopes were close to 1.0 (Table 2). For the Brown Trout and Walleye models, the zero values were overpredicted, whereas many of the positive standing crop observations were underestimated. The Smallmouth Bass model did a better job at predicting zero-value observations than the Brook Trout and panfish models, and the best-fit line was well centered through the cloud of positive standing crop observations. Significant correlations between residuals and model predictors were not observed (at the $P <$ 0.05 level), suggesting that little to no additional variation in standing crop could be accounted for by our predictor set.

The overprediction of zero values resulted in residual plots with a characteristic pattern of negative residuals for zero-value observations, leading to a decreasing linear pattern of negative residuals in the lower left quadrant of each plot (Figure 3). This pattern indicates that our models tended to overpredict standing crops at sites where game fishes were not detected during sampling. Such a pattern may have resulted from including sites outside of the occupied range of each species, which would lead to overprediction of biomass values in potentially productive habitats that were unoccupied. Overprediction of biomass at sites with observed zero values may have also resulted from prediction to habitat conditions that are degraded by unmeasured variables. In our study, the primary anthropogenically influenced variable considered was TP, but some factors that are known to degrade fisheries potential (e.g., substrate embeddedness from fine sediments) could not be modeled. Thus, it is possible that observed zero-biomass values resulted from prediction outside of range boundaries, unmeasured stressors, or inefficient sampling. We believe that inefficient sampling was least likely to have been a factor, as intense sampling methods were used. To ameliorate inaccuracies associated with prediction outside of range limits, prior to mapping we masked our model predictions to only those river habitats that were predicted to be within the occupied range of each fishery as reported by Steen et al. (2008).

Relative Importance of Predictors

The predicted relative importance of variables was consistent with our understanding of controls on fish productivity in rivers. For instance, water temperature was the strongest predictor for all but the Walleye model, accounting for between 26% and 59% of the mean square error reduction in models of Brook Trout, Brown Trout, panfishes, and Smallmouth Bass (Table 3). Other variables with relatively high effect sizes included upstream catchment area, river flow, and TP concentration (Table 3). Total phosphorus concentrations had statistically significant effects for all models except the Walleye model (Table 2). The modeled relative importance of TP

TABLE 2. Model performance and results of significance tests (N = number of sampling sites used; % occupied = percentage of sampled sites with positive abundance; RMSE = root mean square error; training R^2 = adjusted R^2 for observed versus predicted values for training data; cross-val. R^2 = adjusted cross-validation R^2; % TP import = relative importance of total phosphorus [TP] in each model, expressed as a percentage; TP significance = statistical significance [P-values] of TP importance in the model as judged from a permutation test; NS = not significant).

Model	N	% occupied	RMSE	Training R^2	Cross-val. R^2	Slope	% TP import	TP significance
Brook Trout	335	61	0.82	0.69	0.43	1.20	18.70	<0.0001
Brown Trout	388	46	1.37	0.58	0.30	1.33	9.20	<0.05
Panfishes	397	17	0.89	0.76	0.55	1.16	9.00	<0.05
Smallmouth Bass	367	51	0.75	0.87	0.43	1.18	14.90	<0.001
Walleye	392	54	0.43	0.49	0.20	1.66	3.80	NS

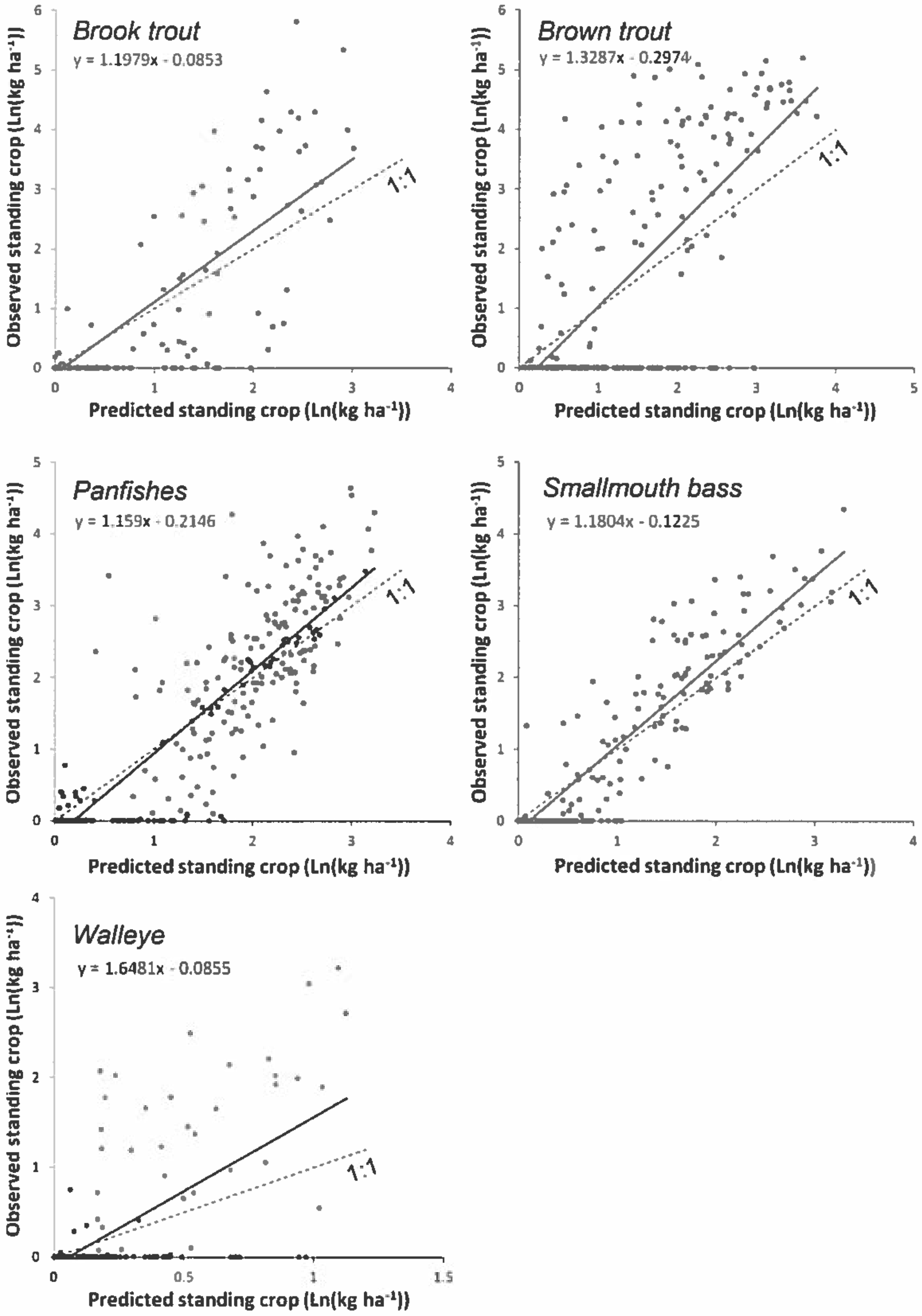

FIGURE 2. Observed versus predicted standing crops of Michigan game fishes for all sample data.

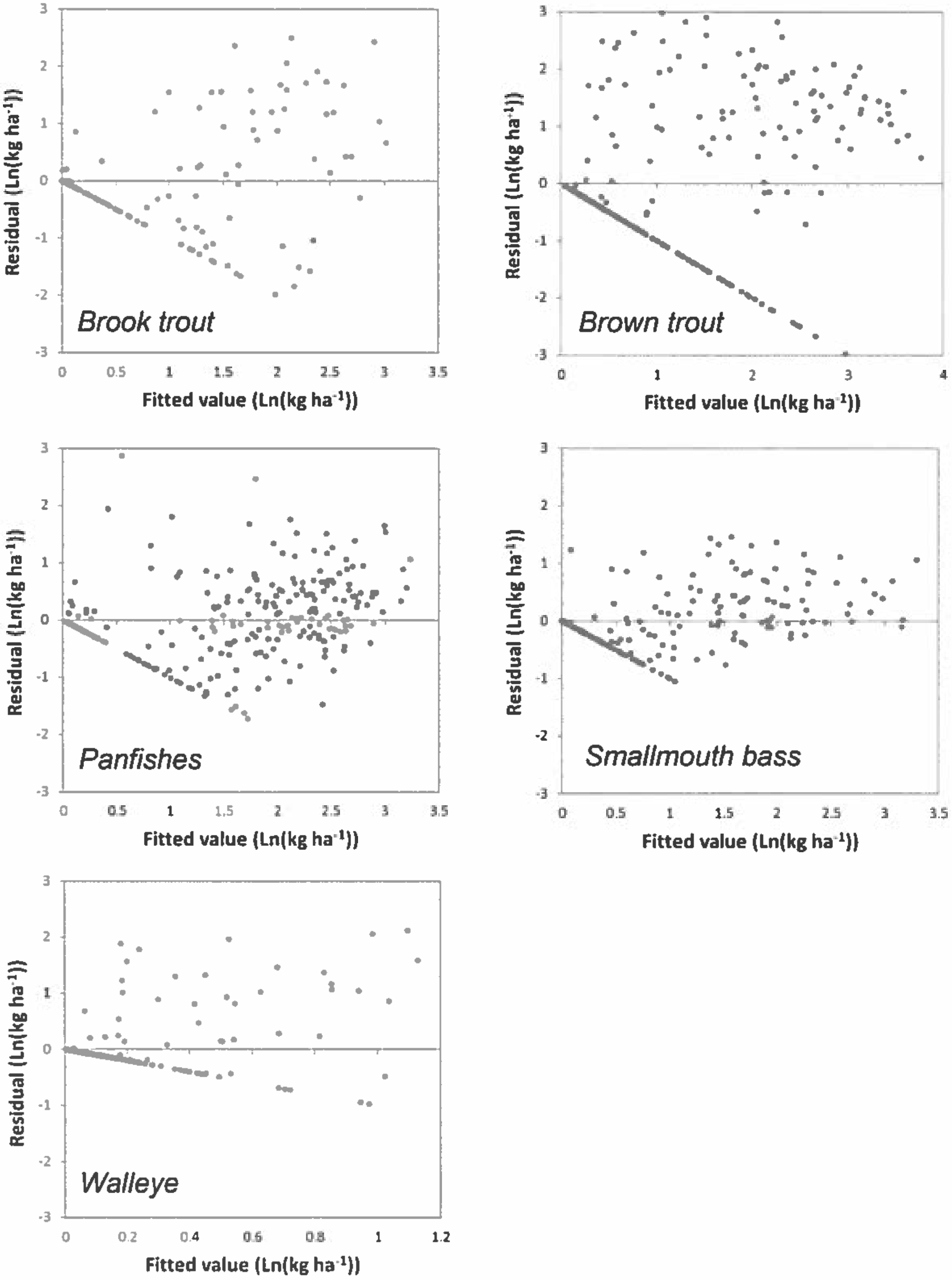

FIGURE 3. Residuals versus fitted values for predicted standing crops of game fishes in Michigan.

TABLE 3. Relative importance values of each predictor included in each species model expressed as a percentage of the total squared error improvement over all models. See Table S.1 for details about predictor selection for each model. A dash indicates that the predictor was not utilized for the model.

	Model				
Predictor variable	Brook Trout	Brown Trout	Panfishes	Smallmouth Bass	Walleye
Water temperature (°C), predicted July mean	58.7	29.6	55	26.1	10.4
Upstream catchment area (km^2)	8.7	7.6	4.7	23.8	30.4
Predicted base flow total phosphorus (μg/L)	18.7	9.2	9.0	14.9	3.8
90% exceedance flow yield (m^3·s^{-1}·km^{-2})	6.4	21.4	3.8	10.9	—
Channel gradient (°)	—	13.5	4.1	—	10.0
Forest land cover in the local riparian zone (%)	7.5	8.7	5.4	—	—
Medium-grain surficial geology in the upstream riparian buffer (%)	—	—	3.6	13.2	—
Nonforested wetlands in the local riparian zone (%)	—	—	6.1	—	7.3
50% exceedance flow in April (m^3/s)	—	—	—	—	29
Upland forest cover in the local riparian zone (%)	—	—	—	11.1	—
10% annual exceedance flow (m^3/s)	—	10.0	—	—	—
50% annual exceedance flow (m^3/s)	—	—	8.3	—	—
Distance to the nearest upstream dam (m)	—	—	—	—	4.7
Coarse and outwash geology in the upstream catchment (%)	—	—	—	—	3.3
Presence or absence of a dam downstream (0 or 1)	—	—	—	—	1.0
Presence or absence of a dam upstream (0 or 1)	—	—	—	—	1.0

ranged from 9% to 19% for all fishes except Walleyes (relative importance of TP = 3.8%). Relative importance values of TP were significantly greater than the null distribution for Brook Trout ($P < 0.0001$), Smallmouth Bass ($P < 0.001$), panfishes ($P < 0.05$), and Brown Trout ($P < 0.05$) according to the results of the permutation test on TP only.

Modeled Fish Responses to Predictors

Partial dependence plots illustrated the modeled influence of TP concentration (Figure 4) and the other predictors (Figure S.1) on the mean responses of fish standing crops and allowed us to examine our subsidy and stress hypotheses. Fish responses to TP agreed with our hypotheses for Brook Trout and Smallmouth Bass (predicted subsidy and stress responses), panfishes (subsidy responses only), and Walleyes (no response). In addition, the TP concentrations at which subsidy and stress responses occurred varied depending on the fishery. As hypothesized, the mean response of Brook Trout and Smallmouth Bass biomass increased to a peak at low TP concentrations and then declined to relatively low levels as TP increased. However, the subsidy effect was not statistically significant for Brook Trout because mean biomass at a TP concentration of 13 μg/L did not exceed the 95% CI for mean biomass at 8 μg TP/L (Figure 4). The decrease in Brook Trout biomass at TP values of 13 to 20 μg/L was statistically significant ($P < 0.05$). Smallmouth Bass biomass increased significantly between TP concentrations of 13 and 34 μg/L ($P < 0.05$) and decreased significantly at TP levels from 34 to 50 μg/L ($P < 0.05$), indicating that Smallmouth Bass are potentially less sensitive to the stressful effects of TP than are Brook Trout. The partial dependence plot for Smallmouth Bass (Figure 4) suggested that biomass increased at TP concentrations greater than 50 μg/L, but due to the wide 95% CI, the pattern was not significant relative to the minimum value.

Consistent with our hypothesis, panfish standing crops increased with increasing TP concentrations between 12 and 38 μg/L and thereafter remained at high levels (i.e., there was no obvious stress response across the range of TP concentrations studied). Contrary to expectations, Brown Trout exhibited a stress response to increased TP concentrations, as maximal biomass occurred at minimum TP concentrations and showed a declining trend as the TP level increased. Consistent with expectations, Walleye showed little response to TP, and 95% CIs were wide.

Partial responses to other variables revealed sometimes strongly nonlinear patterns of fish standing crops in relation to landscape constraints. For instance, fishery responses to temperature were strongly nonlinear: the two trout species presented distinct associations with streams having colder July mean temperatures (<18°C), while panfishes and Smallmouth Bass were associated with warmer waters (>22°C; Figure S.1). Brook Trout tended to occur in streams with small upstream drainage areas and benefited from local riparian forest cover that was greater than 90%. Brown Trout were predicted to benefit strongly from conditions with high discharge per unit area and higher channel gradients. Panfish biomass

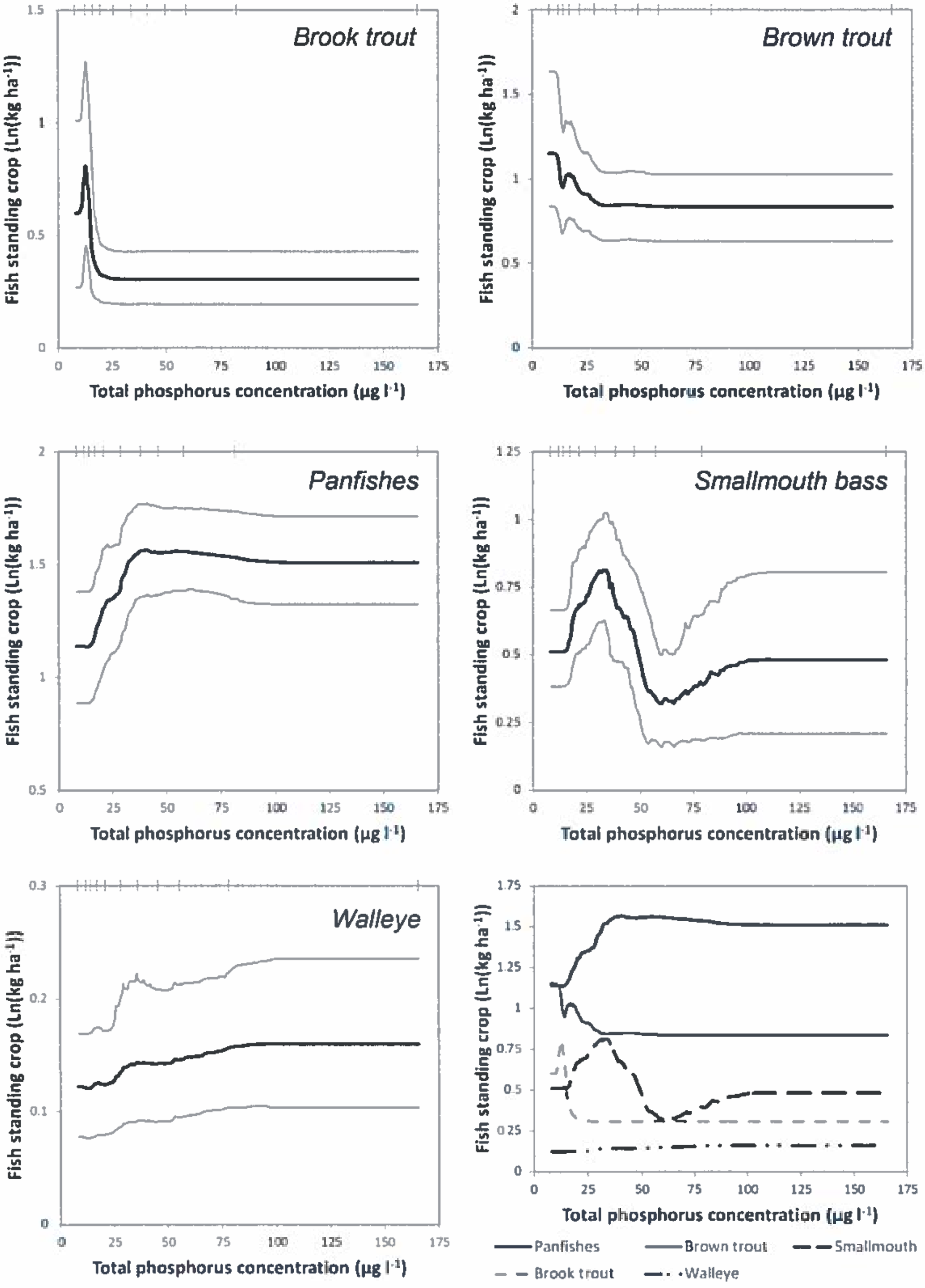

FIGURE 4. Partial dependence plots showing the predicted median response (black line) of target fisheries to predicted total phosphorus concentrations; the upper and lower boundaries of the 95% confidence interval (gray lines) are also shown. Small vertical lines at the top of each plot show the frequency distribution of sites (in deciles). The bottom right plot depicts the median responses for all fisheries on the same response scale.

was greatest in habitats with low median annual discharge magnitudes, higher proportions of nonforested wetland, and less forest cover within the local riparian buffer. Smallmouth Bass were constrained to warmwater streams with drainage areas greater than about 3,500 km^2 and higher proportions of medium-textured surface geology in the upstream riparian corridor. Medium-textured geology in the upstream landscape may translate to greater availability of cobble substrates in local habitats, which has been positively associated with Smallmouth Bass biomass (Zorn et al. 2004). Walleye biomass was predicted to be greatest in streams with large upstream catchments (>4,000 km^2) and high April flow volumes.

Maps of Results

Brown Trout were predicted to have the highest maximum biomass, followed by panfishes, Smallmouth Bass, Brook Trout, and Walleyes. However, predicted biomasses of panfishes and Brook Trout measured across their entire range in Michigan had higher means and medians than the biomasses of the other fisheries, including Brown Trout (Table 4). Brook Trout biomass was predicted to be greatest in the coldwater streams and rivers of the northern LP and streams draining north to Lake Superior in the UP (Figure 5). Streams with higher standing crop predictions corresponded well to those listed as "trout streams" and "Blue Ribbon trout streams" (www.trailstotrout.com/blueribbon.html) by the Michigan Department of Natural Resources (MDNR 2010). Brown Trout were predicted to occur at low relative biomass in streams throughout most of the LP, with patchy areas of higher biomass. Panfishes, a warmwater group, were predicted to be most abundant in small and large streams across the southern portion of LP, particularly in the southeast. Smallmouth Bass were predicted to be limited to main-stem habitats in larger rivers of the state, where warmer waters predominate. Walleye were predicted to occur at low biomass relative to the other species and to be limited primarily to main-stem rivers of the UP and western LP, but to inhabit smaller tributary systems bordering Saginaw Bay, Lake St. Clair, and Lake Erie.

Maps showing the uncertainty of our predictions enabled us to determine the streams and landscape contexts for which our predictions were least and most precise (Figure 6). The SDs of Brook Trout and Brown Trout biomass estimates were relatively low (<0.5 kg/ha) for coldwater habitats of the northern LP and parts of the UP, whereas SDs were higher in the southern portion of the LP, where trout are generally known to be scarce. The majority of panfish standing crop estimates fell within ±0.25 kg/ha of the predicted value, particularly within main-stem rivers. Smallmouth Bass standing crop estimates tended to have SDs less than 0.5 kg/ha, except for small tributary streams at the margins of their occupied habitats. There was slightly greater variation around the mean predictions of Walleye standing crop, which was expected because the Walleye model was the least precise of the models we examined (Table 2). The low precision of the Walleye model may result from the fact that Walleyes are sampled when they migrate into river habitats to spawn, so their abundances in resident and migratory habitats have a high degree of spatiotemporal variability (Pritt et al. 2013).

DISCUSSION

We used statistical models to map the capacity of riverine habitats in Michigan to support fish biomass. Our models explained a relatively high proportion of variation in training (50–87%) and test (22–56%) data sets; despite their limitations (discussed below), the models may provide a useful tool for spatially extensive fisheries valuation, management planning, or other applications. Maps of reach-specific standing crop predictions for Michigan showed spatially structured patterns of predicted fish biomass that corresponded to spatial patterns in water temperature, land cover, and nutrient availability. Water temperatures are colder in the UP and northern LP, where trout were predicted to have higher standing crops, whereas temperatures are warmer in the southern LP, where Smallmouth Bass and panfishes occurred at high biomass densities.

Our results corroborate the findings of other studies that have examined ecological controls on fishes. Those studies established that stream temperature and hydrology (Fausch

TABLE 4. Summary statistics for the predicted standing crop of game fishes across all stream reaches in Michigan (Min = minimum; Q25 = 25th percentile; Q75 = 75th percentile; Max = maximum). Percentage occupancy is given in parentheses.

		Predicted standing crop (kg/ha)					
Fishery	Occupancy (km)	Min	Q25	Median	Mean	Q75	Max
Brook Trout	30,321 (31)	0.00	0.73	3.25	4.40	6.95	25.42
Brown Trout	39,488 (43)	0.00	0.31	0.73	2.47	2.47	53.91
Panfishes	39,943 (44)	0.03	2.30	5.92	6.28	8.52	30.18
Smallmouth Bass	6,022 (7)	0.00	1.06	2.41	3.34	4.77	25.87
Walleye	10,694 (12)	0.01	0.16	0.22	0.34	0.283	2.22

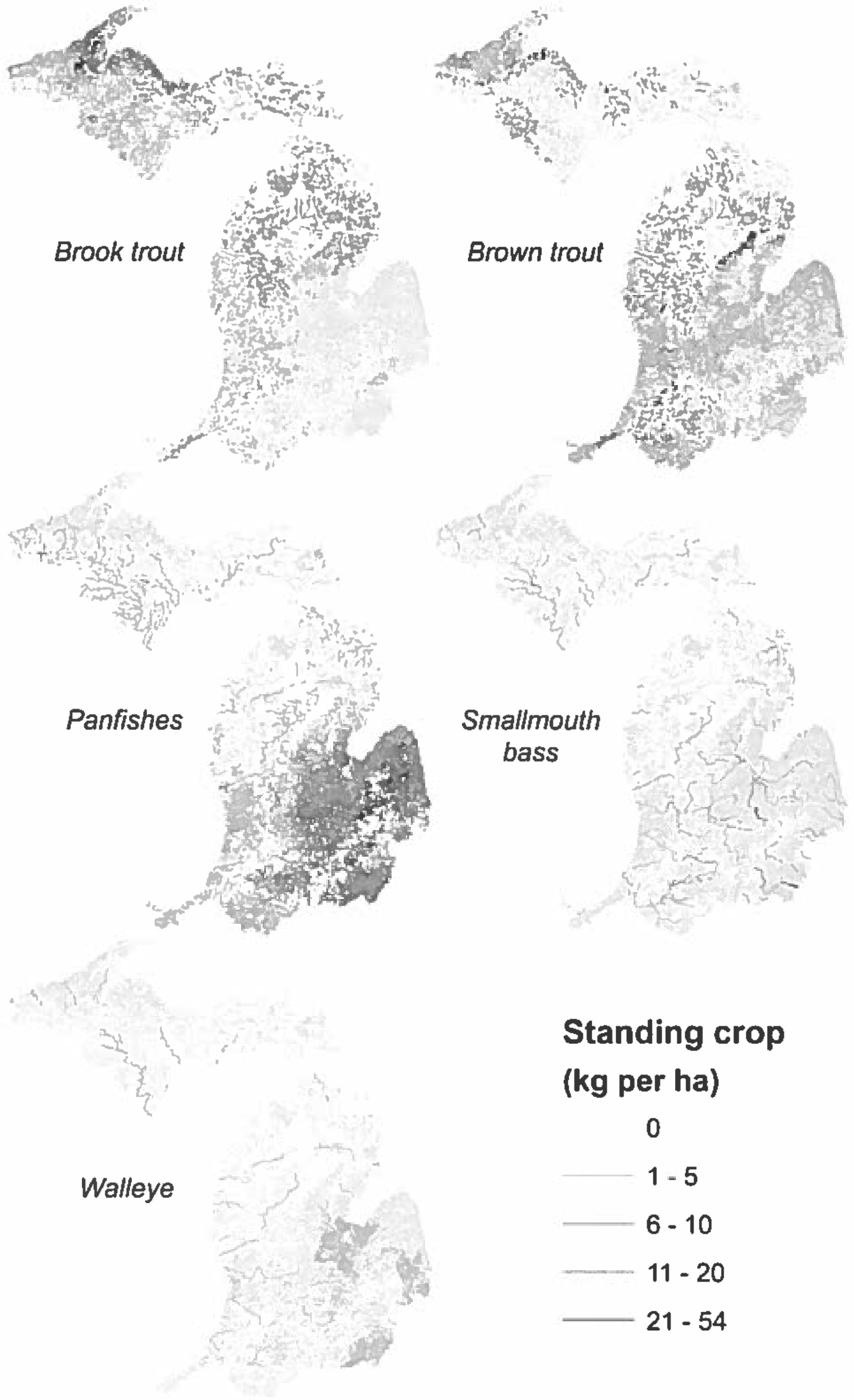

FIGURE 5. Spatial expression of model predictions mapped to individual stream segments in Michigan. Standing crops for each game fish are displayed on a common scale to allow direct comparison of biomass estimates. Reaches with zero predicted biomass and those predicted to be unoccupied by Steen et al. (2008) are not shown.

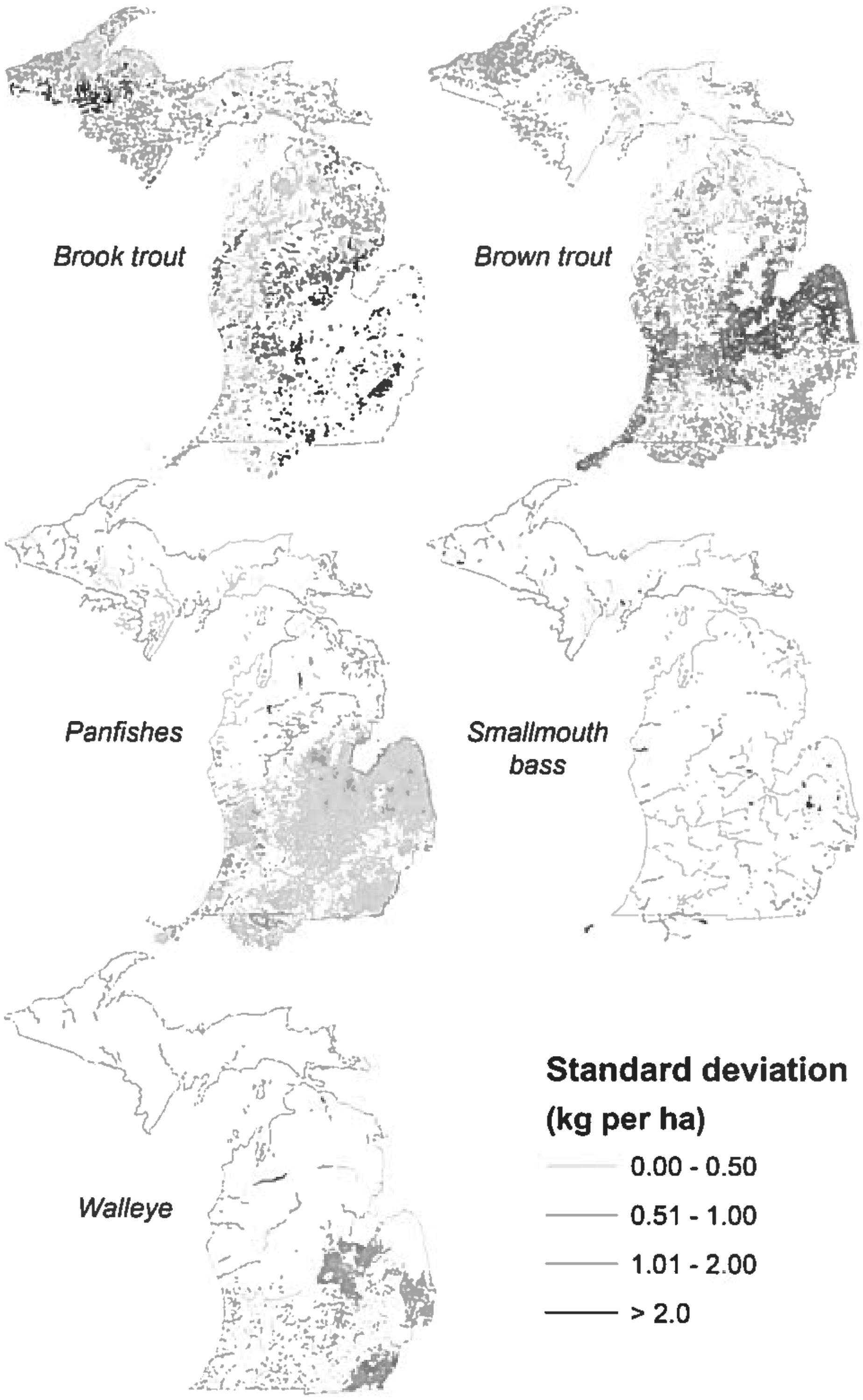

FIGURE 6. Estimated precision of game fish standing crop predictions for individual stream segments in Michigan, calculated as the SD around the mean predicted standing crop from 1,000 bootstrap samples of the training data. Reaches with zero predicted biomass and those predicted to be unoccupied by Steen et al. (2008) are not shown.

et al. 1988; Lyons et al. 1996; Peterson and Kwak 1999; Stoneman and Jones 2000; Zorn et al. 2002; Creque et al. 2005; McRae and Diana 2005; Steen et al. 2008; Brewer and Rabeni 2011) as well as concentrations of limiting nutrients (Johnston et al. 1990; Hoyer and Canfield 1991; Waite and Carpenter 2000) are important influences on fish distributions and biomass across broad spatial extents. The fact that stream temperatures, hydrology, and nutrient concentrations were all modeled as local-scale variables emphasizes an important point made by de Groot et al. (2010): that the supply and management of ecosystem services must be approached as a problem that incorporates drivers across a range of scales. Our results suggest that incorporating reach-specific information—even if the information is modeled—can be advantageous for the accuracy and ecological realism of predictive models.

Modeled fish responses to TP and other predictors (water temperature, hydrology, drainage area, and riparian land cover) were frequently nonlinear, exhibiting threshold, asymptotic, and hump-shaped responses (Figures 4, S.1). For instance, hump-shaped responses to TP concentration were evident for both Brook Trout and Smallmouth Bass, suggesting that TP subsidizes productivity to an optimum level after which stress effects become evident. A positive asymptotic relationship between panfishes and nutrient concentrations was apparent, suggesting subsidy effects only and a tolerance of high nutrient conditions (Figure 4). Previous studies have documented significant subsidy effects of growth-limiting nutrients on fishes, but few studies have documented stress effects. Strong experimental (Johnston et al. 1990; Peterson et al. 1993; Slaney et al. 2003), isotopic (deBruyn et al. 2003), and observational (Merron 1982; Askey et al. 2007) evidence supports bottom-up energetic subsidies as the likely mechanism by which nutrient enrichment benefits fish in rivers by increasing available food resources. In a study of Ohio streams, Miltner and Rankin (1998) observed the highest fish abundances at intermediate nutrient concentrations, whereas abundances of sensitive species were reduced at higher concentrations. Smallmouth Bass and Brook Trout have both been shown to be sensitive to habitat degradation (Sowa and Rabeni 1995; Argent and Flebbe 1999; Curry and MacNeill 2004; Stranko et al. 2008; Brewer and Rabeni 2011; Brewer 2013), pointing to one mechanism by which nutrient enrichment could be a stressor on fish. High concentrations of growth-limiting plant nutrients have been linked to an excessive growth of algae, macrophytes, and phytoplankton, which in turn can change habitat structure, flow velocities, dissolved oxygen concentration, and pH (Welch et al. 1992; Dodds and Biggs 2002). Other possible mechanisms for stress responses in Brook Trout and Smallmouth Bass include changes in insect prey availability (Miltner and Rankin 1998) and/or increased abundances of fish pathogens (e.g., *Pseudomonas*, *Aeromonas*, and myxobacteria) in eutrophic waters (Snieszko 1974). Although plausible mechanisms exist to support the subsidy stress responses observed, our findings were not derived from a controlled study but from an observational study, so they must be interpreted with caution due to our inability to account for potentially confounding stressors (e.g., fine sediment and habitat simplification) that co-occur with elevated nutrient concentrations (Carpenter et al. 1998; Smith et al. 2003).

Although not framed from an ecosystem services perspective per se, several other studies have modeled game fish abundances or biomass by using landscape-scale data (Sowa and Rabeni 1995; Zorn et al. 2004; Creque et al. 2005; McKenna et al. 2006; Stanfield et al. 2006; Steen et al. 2008; McKenna and Johnson 2011). Our study differed from these prior studies in terms of methods and response variables as well as the modeling approaches used. Choices of sampling methods and response variables are potentially important because not all methods for quantifying fishes are equally well suited to measure fish productivity as a provisioning service of ecosystems. For instance, Stanfield et al. (2006) used fish numeric densities (number per unit area) from single-pass electrofishing without any corrections for inefficient sampling. Numeric density is known to have higher interannual variation than biomass, and single-pass electrofishing provides a minimal estimate of the total abundance of each species at a site. Incomplete abundance estimates add an element of uncertainty to predictions of fish as a provisioning service and therefore would make maps less reliable. The depletion estimates, mark–recapture, and rotenone sampling used for this study and other studies (Sowa and Rabeni 1995; Zorn et al. 2004; Creque et al. 2005; Steen et al. 2008) provide estimates of total numeric abundance or biomass of the sampled population and thus offer a more objective basis for drawing conclusions about fish availability to anglers. Several authors (Steen et al. 2008; McKenna and Johnson 2011) chose to discretize continuous fish densities into log-scale abundance categories (0, 1–10, 10–100, and >100 fish/unit area). Although this approach may lead to improved goodness of fit by reducing variation in the response variable, modeling of continuous responses provides the potential for a better contrast in biomass between segments (Stanfield et al. 2006).

Our models performed favorably in comparison with other landscape models of abundances for the same game fish species (Sowa and Rabeni 1995; Zorn et al. 2004; Creque et al. 2005; Stanfield et al. 2006). Our Brook Trout model (training $R^2 = 0.68$; cross-validation $R^2 = 0.43$) explained more variation than the models of Creque et al. (2005; adjusted $R^2 = 0.23$) and Stanfield et al. (2006; adjusted $R^2 = 0.30$) and was comparable to the model of Zorn et al. (2004; $R^2 = 0.47$). Like other investigators, we found that Brown Trout were more difficult to model using landscape data than were Brook Trout. The performance of our Brown Trout model (training $R^2 = 0.58$; cross-validation $R^2 = 0.30$) and those of Stanfield et al. (2006; adjusted $R^2 = 0.12$) and Zorn et al. (2004; $R^2 = 0.36$) was low relative to the performance of the other models tested in each of the studies. Brown Trout may be challenging to model because they are nonindigenous fish that are actively stocked in some, but not all, places. Stocking of Brown Trout could lead to inflated standing crop estimates in some locations and therefore could increase the error variance for landscape models of trout productivity. Without spatially explicit information about where and how many Brown Trout were stocked, it was not possible for us to accommodate this aspect of their distribution and biomass. In contrast to our Brown Trout model, relatively strong Smallmouth Bass models were specified in our study (training $R^2 = 0.87$; cross-validation $R^2 = 0.43$) and in the studies by Zorn et al. (2004; $R^2 = 0.51$) and Sowa and Rabeni (1995; adjusted $R^2 = 0.49$). Neither our study nor the Zorn et al. (2004) study was able to specify a strong model for Walleye distributions.

Although our models compared favorably with other published models, they have several notable biases and weaknesses. For instance, our models tended to overpredict standing crops at sites where sampling yielded zero biomass of game fishes (Figures 2, 3). This problem was also experienced by Zorn et al. (2004), who used a similar response data set. To avoid mapping biomass to unoccupied areas, we masked our predictions to only those reaches predicted to be occupied based on the work of Steen et al. (2008). It is possible that the inclusion of additional fish population stressors in future models could account for some of the observed zero values in the data set. Other models specifically formulated for such zero-inflated data (e.g., zero-inflated Poisson models; Lambert 1992; Wenger and Freeman 2008) may also be useful. However, zero-inflated Poisson models were not appropriate for the current study because of our interest in exploring possible nonlinear subsidy and stress responses to which BRTs are very well suited. For interpretation of our maps, the implication of overpredicting zero values is that low biomass values may in reality represent zero-biomass values and thus should be interpreted conservatively. In contrast, intermediate and high biomass values were relatively accurate for panfishes and Smallmouth Bass and were generally conservative for Brook Trout and Brown Trout. Therefore, intermediate and high values on our maps can be interpreted more reliably as average or conservative estimates of biomass density.

Two issues associated with our predictor and response data sets have implications for model accuracy. First, our response data were collected over a 13-year time span and thus give only a general picture of the capacity of habitats to support fish biomass that is not referenced to a specific time or population year-class. In reality, cohort density of some species (e.g., Smallmouth Bass) can fluctuate as much as 500% between years in relation to environmental conditions during the first year of life (Coble 1975). The fish biomass density in a specific river reach on a specific day may not correspond to our prediction because we could not account for year-class variation or other temporal effects. Second, our use of modeled predictor variables (water temperature, hydrology, and TP) introduces an additional source of error and unexplained variance. For instance, temperature model predictions were generally within 1°C or 2°C of actual weekly mean temperatures (Wehrly et al. 2003), but given the strong nonlinearities observed in response to temperature and several other variables, this amount of error could affect the accuracy of our mapped model predictions.

In addition to issues associated with model specification and data sets, fish life histories and interspecific interactions can create challenges for modeling fish biomass with high precision and accuracy. For example, Brook Trout and Brown Trout are known to make long-distance movements from the Great Lakes to river habitats to spawn in the fall (Horrall 1981). Migratory Brook Trout were likely absent from our samples because their remnant populations are primarily found in Lake Superior, where no samples were gathered. Migratory behavior by Brown Trout would tend to decrease the accuracy of our models, which assume that the fish reside (and are thus available to anglers) at the location where they were sampled. Interspecific competition is potentially important for models of Brook Trout and Brown Trout because competition for space and food between these species has been documented (Fausch and White 1981; McKenna et al. 2013). We did not model this potential biotic interaction for three reasons. First, in order to generalize from a model with biotic interactions included, we would have had to use modeled Brook Trout and Brown Trout abundances, both of which had substantial prediction error. Second, Zorn et al. (2004) found that incorporating Brook Trout into a Brown Trout model or vice versa explained little additional variability in standing stocks. Third, landscape-scale abundances are largely controlled by abiotic gradients that limit the fitness of populations. Incorporating a competitor with a similar niche would have obscured these important relationships and our ability to learn from them. One implication of not accounting for potential competitors is that trout biomass may be overestimated in areas where the species co-occur. The nonuniform distribution of Brown Trout relative to Brook Trout (i.e., due to stocking) may also contribute to model inaccuracies.

Although there has been much focus on mapping the biophysical supply of ecosystem services (Chan et al. 2006; Gimona and van der Horst 2007; Egoh et al. 2008; Meyer and Grabaum 2008; Kienast et al. 2009) and/or service value (Naidoo and Ricketts 2006; Nelson et al. 2009), relatively few studies in the ecosystem services literature have used robust field data, subjected their models to validation, quantified the uncertainty in their biophysical or ecosystem service estimates, or provided "a sound basis for the conclusions they draw" (Seppelt et al. 2011). Our study did use robust field data with reliable population estimates, thus providing a snapshot of the system over time. We mapped model uncertainty in a spatially explicit way (Figure 6) that can help managers to determine where our model predictions are highly precise and where additional sampling may be needed to strengthen the model results. Maps of uncertainty suggested that our model predictions were most precise for habitats that were most suitable to fisheries.

This result further reinforces the notion that our moderate to high biomass estimates are reliable, whereas our low estimates should be interpreted conservatively, particularly for the trout species. The internal cross-validation procedure that we used could be improved (1) if independent field data become available or (2) through targeted sampling for the express purpose of model validation (sensu McKenna and Johnson 2011). Notwithstanding future improvements, our models are transparent and, more importantly, do not rely on overly simplified relationships, assumed production functions, or indirect proxies for the service of interest, as is common in the ecosystem services literature (Chan et al. 2006; Naidoo and Ricketts 2006; Troy and Wilson 2006; Egoh et al. 2008).

Our models and maps have numerous potential uses for fisheries managers to examine the productive potential of streams, describe geographic patterns of fisheries, and identify habitats that are candidates for stocking or restoration of locally extirpated stocks (Brewer et al. 2007). Our models also have utility for landscape nutrient management. Excessive anthropogenic nutrients in surface waters are a water quality management priority throughout the world because they are a primary source of impairment to freshwater ecosystems (Plessis and Veelen 1991; USEPA 1996; Smith et al. 1999; Davies and Jackson 2006). In North America, nutrient levels are regulated under the Clean Water Act of 1972 to be protective of designated stream uses such as "fish, shellfish, and wildlife" (USEPA 2000). Nutrient management targets are often set for streams according to the effects they have on aquatic life, and these targets must be quantitatively justified (Dodds and Welch 2000; USEPA 2000). Our results suggest that the biomasses of Brook Trout and Smallmouth Bass in Michigan streams may be maximized at TP concentrations of 13 and 34 μg/L, respectively, and that higher concentrations may have detrimental effects on biomass. Our models also suggest that panfish biomass is maximized at about 45 μg/L, whereas higher concentrations confer no additional production benefit upon the fishery. These concentrations could potentially serve as benchmarks that provide some level of desired protection to streams in support of fisheries management and management for ecosystem services (Davies and Jackson 2006; Stevenson et al. 2008). Future efforts will be necessary to distinguish among the indirect effects of phosphorus and covarying factors (e.g., fine sediment) as causal mechanisms for the game fish declines associated with higher nutrient concentrations in our study.

Developing a predictive understanding of landscape controls on spatial variability in game fish productivity is a critical research endeavor that can support economic valuation, examination of tradeoffs between ecosystem services, and spatial planning for efficient species conservation and exploitation (Heal et al. 2005). We trained BRT models for defining ecological production functions that predict an output of ecosystem services produced by Michigan rivers. However, societal benefits of fish biomass availability in Michigan rivers can only be determined by considering human demand for the service (Tallis and Polasky 2009). Until our fish standing crop estimates are connected to beneficiaries, we cannot draw detailed conclusions about the benefit or value of this ecosystem service to society. Thus, the essential next step for this research is to quantify angler behaviors relative to fish biomass availability and to assign values to biomass in the rivers where it is produced (see companion paper by Melstrom et al. 2015). With biophysical and economic information in hand, sport fishery managers should be able to utilize new spatial knowledge to improve fisheries management to the benefit of anglers.

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