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Abstract Anthropogenic impairment of water bodies represents a global environmental concern, yet few attempts have successfully linked fish performance to thermal habitat suitability and fewer have distinguished co-varying water quality constraints. We interfaced fish bioenergetics, field measurements, and Thermal Remote Imaging to generate a spatially-explicit, high-resolution surface of fish growth potential, and next employed a structured hypothesis to detect relationships among measures of fish performance and co-varying water quality constraints. Our thermal surface of fish performance captured the amount and spatial-temporal arrangement of thermally-suitable habitat for three focal species in an extremely heterogeneous reservoir, but interpretation of this pattern was initially confounded by seasonal covariation of water residence time and water quality. Subsequent path analysis revealed that in terms of seasonal patterns in growth potential, catfish and walleye responded to temperature, positively and negatively, respectively; crappie and walleye responded to eutrophy (negatively). At the high eutrophy levels observed in this system, some desired fishes appear to suffer from excessive cultural eutrophication within the context of elevated temperatures whereas others appear to be largely unaffected or even enhanced. Our overall findings do not lead to the conclusion that this system is degraded by pollution; however, they do highlight the need to use a sensitive focal species in the process of determining allowable nutrient loading and as integrators of habitat suitability across multiple spatial and temporal scales. We provide an integrated approach useful for quantifying fish growth potential and identifying water quality constraints on fish performance at spatial scales appropriate for whole-system management.

Keywords Fish performance · Water quality · Structured hypotheses · Water temperature · Eutrophication · Clean water act · Thermal remote imaging (TIR) · Bioenergetics

Introduction

The anthropogenic impairment of water bodies represents a global environmental issue (Parry 1998; Tilman 1999), yet our ability to identify mechanistic relationships between water quality and fish performance remains limited (Rose 2000). In the USA, response to impaired water bodies involves large-scale, often contentious and expensive total maximum daily load (TMDL; Clean Water Act" [CWA]; United States Code title 33, sections 1251–1387)) studies. Currently, >44,000 waterbodies are listed as impaired in the USA, and in every state, 'fish' or 'fisheries' are specifically listed as a primary beneficial use of their water bodies (Environmental Protection Agency (EPA) 2009). However, to date, research has struggled to link fish performance explicitly to thermal habitat suitability at spatial and temporal scales relevant for whole-system management (Davies and Jackson 2006). Similarly, given the

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strong natural seasonal effects of temperature and hydrology on the observed physical conditions and productivity of lentic systems, research has demonstrated even less success at distinguishing the effects of these co-occurring water quality constraints on fish performance (Rose 2000; Pilati and others 2009 *but see* Wazniak and others 2007).

The development of quantitative methods for measuring habitat suitability is a central, but challenging task for aquatic ecologists (Downing and others 1990; Boisclair 2001; Rosenfeld 2003), a task made more difficult by the heterogeneity often present in large lentic systems. Ultimately, a measure of habitat quality is necessary to accurately predict predator-prey relationships, fish distributions and production, and sustainable stocking or harvest quotas (Baldwin and others 2000; Mazur and others 2007). One such metric of habitat suitability is fish growth potential, which can be generally defined as the expected growth rate of a fish in a specified volume of water of known biological and physical characteristics, a metric that can be determined using a balanced energy budget within a bioenergetics framework (e.g., Brandt and others 1992; Hewett and Johnson 1992; Mason and others 1995). Temperature, a key abiotic variable, and food availability, a key biotic variable, act in concert with species-specific physiological processes to directly influence the individual growth rate of a fish (Kitchell and others 1974; Stewart and Ibarra 1991; Hanson and others 1997). Slight temperature deviations above or below the physiological thermal optima of a species can result in increased metabolic demands and physiological stress, subsequently resulting in a reduction of individual growth rates (Jackson and others 2001). As a result, fish growth potential describes a fish's response to both biological and physical conditions of their environment and thus can serve as a mechanistic and integrated index of habitat suitability and link to environmental management (Fausch and others 1990; Davies and Jackson 2006).

Despite the strength of bioenergetics as tool for estimating fish performance, coarse resolution spatial and/or temporal estimates of temperature and food availability represent some of the greatest sources of uncertainty for predicting fish growth potential, especially in large, heterogeneous water bodies (Brandt and others 1992; Brandt and Kirsch 1993; Rose 2000). To address this challenge, fisheries scientists have increasingly moved from the simple, deterministic approaches where temperature and food availability are generally static and homogenous (e.g., Winberg 1956), to models that attempt to more explicitly account for the heterogeneity of aquatic habitats and the individual differences in physiology and behavior within and among fishes. This incorporation of system-wide, higher resolution thermal and consumption data into models predicting fish growth rate, fish production, predator-prey interactions, and habitat quality have substantially increased the relevance and applicability of model predictions (e.g., Goyke and Brandt 1993; Mason and Brandt 1996; Niklitschek and Secor 2005). Furthermore, in shallow two-dimensional aquatic environments, Boisclair (2001) describes a spatially-explicit bioenergetics approach where each distinct patch of habitat is represented as a separate habitat unit, or tile; the merging of these tiles constitutes a habitat mosaic. In combination with Geographic Information Systems (GIS) and empirical data describing fish and habitat, bioenergetics has been used to create detailed and innovative maps of growth potential (Brandt and others 1992; Goyke and Brandt 1993). Further, Thermal Infrared Imaging (TIR) offers a system-wide approach to describing the temperature available to a fish in a given environment by facilitating the collection of high resolution thermal data surfaces (Torgersen and others 2001). This degree of thermal resolution is important, as fish are not restricted or exposed to "mean" temperatures across a reach, rather they can and do move and behaviorally thermoregulate (e.g., Zimmerman and others 1989). As such, TIR imaging provides a tool capable of capturing and integrating fine-scale spatial temperature fluctuations that can be incorporated into spatially-explicit bioenergetics modeling at both the relevant temporal and spatial scales that drive variability in fish performance.

Once thermal habitat suitability is linked to integrated measures of fish performance, interpreting thermal constraints in the context of other potential water quality effects presents additional challenges. Distinguishing co-occurring water quality effects is complicated by the role that seasonal climate plays in determining many biotic (e.g., primary and secondary production), and abiotic (e.g., discharge, oxygen) variables through hydrologic processes and autotrophic productivity (Sanborn and Bledsoe 2006; Riseng and others 2004; Wazniak and others 2007). These confounding effects on fish management are so pressing and ubiquitous that Rose (2000) explicitly categorizes six types of issues that limit our ability to identify quantitative relationships between fish populations an environmental quality ranging from habitat complexity to sublethal and cumulative effects. Teasing apart such interactions likely requires greater integration than exhibited by past bioenergetic analysis.

Food web studies and ecosystem simulation models do provide opportunities for investigating temperature-water quality effects, linking fish to lower trophic levels and abiotic factors. However, most food web studies are focused on web structure and energy flow rather than parsing environmental drivers (e.g., Carpenter and Kitchell 1993, and see review in Kasprzak and others 2002). In this well-developed literature, moderate increases in productivity that do that not exceed system thresholds (e.g., anoxia, dead zones etc.) are typically associated with increased fish density, biomass, and diversity. Under this scenario, eutrophication is viewed as having a positive effect on fish performance, rather than a constraint imposed by impaired water quality as under the CWA. Conversely, while numerous lake ecosystem models quantify biogeochemical dynamics, few include biotic components such as fish (see review in Mooij and others 2009). When included in ecosystem models, fish are typically integrated only as an "effect" (e.g., re-suspending sediment; Carpenter and others 1999) not as a response variable (e.g., fish performance).

To overcome these hurdles, we present an innovative approach that mechanistically links fish performance to thermal habitat suitability and then identifies potential water quality constraints within a spatially and temporally dynamic aquatic landscape. We used a novel, three-tiered combination (Fig. 1) of: (1) bioenergetics modeling of fish growth potential as a measure of fish performance, (2) spatial analysis of continuous, remotely-sensed thermal data within a GIS interface to map fish performance across a heterogeneous landscape of thermal habitat suitability, and, (3) a path analysis (Wootton 1992; Bollen 1989; Shipley 2000; Grace 2006) to decompose covariance among environmental variables and identify potential water quality constraints across focal species. For Tiers 1 and 2, we focused on temperature as a primary driver of fish growth potential because temperature is a primary component of aquatic habitat (Crowder and Magnuson 1982; Stewart and Ibarra 1991), because it can be quantified with a high degree of spatial precision, and because previous work indicates that temperature, rather than food, is the limiting bioenergetic factor for species in eutrophic systems (e.g., *this study*; Dahle 2009). For Tier 3, identifying potential water quality constraints, we statistically explored patterns of relationship among a broader suite of environmental variables and fish performance.

We completed this study in Cutler Reservoir, Utah, an extremely heterogeouous and dynamic reservoir currently on the U.S. Environmental Protection Agency (EPA) 303(d) list as an impaired water body and the focus of a total maximum daily load (TMDL) study; the overall goal of the TMDL process for Cutler Reservoir is to restore and maintain water quality to a level that protects and supports the designated beneficial uses for these waters, including fishes. We chose to use three common fish species to capture the range of available physiological and ecological differences in fish performance response. We hypothesized walleye (*Sander vitreus*) would be most sensitive to both spatial and temporal variation in thermal habitat suitability and potential water quality constraints, followed by black crappie (*Pomoxis nigromaculatus*) and channel catfish (*Ictalurus punctatus*), respectively.

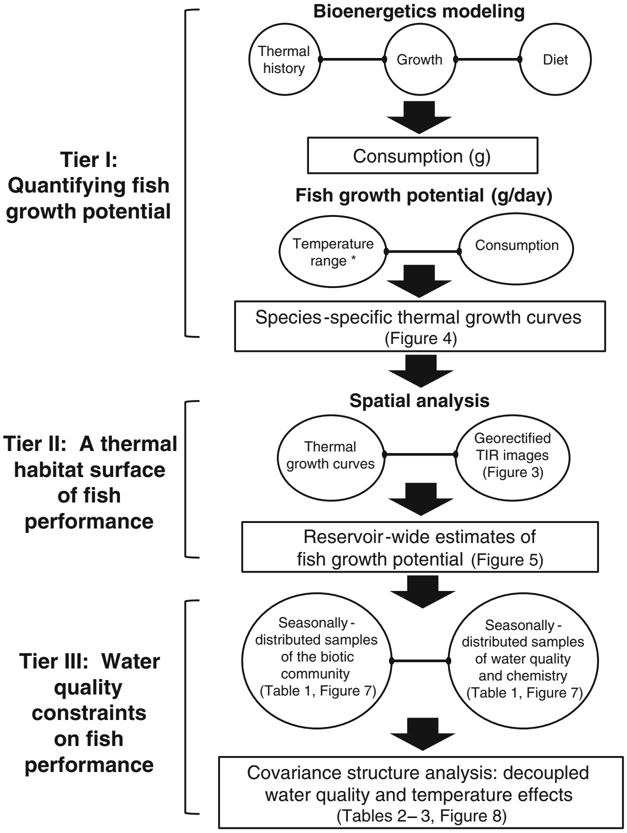

Fig. 1 Schematic representation of the three tiers of analysis: the primary inputs at each tier, and the primary output at each tier, with associated references to tables and figures where applicable. All data and derived inputs and outputs are species- ($n = 3$) and segment- ($n = 5$) specific, and are originally based primarily on data collected in Cutler Reservoir during 2006. An *asterisk* represents the temperature range experienced by our focal species during the modeling period. Georectification and reclassification were completed with ArcGIS 9.2. Covariance structure analysis was completed using a combination of regression tree, Random Forest, and path analysis of structured equations. See text for further details

Methods

Site Description

Cutler Dam, located in northern Utah, impounds the waters of the Bear, Logan, and Little Bear rivers, as well as several other small tributaries creating Cutler Reservoir (Fig. 2). Cutler Reservoir reached its current full pool in 1927, with a capacity of 29,359,335 m^3 and a surface area of 9,601,200 m^2. Cutler Reservoir is a shallow (average depths of less than 2.5 m), run-of-the river reservoir highly influenced by the natural hydrograph of the primary tributary inflows and extremely heterogeneous on even short temporal scales (e.g., diel). Flow through the reservoir is restricted by several causeways and bridges, naturally dividing the reservoir into several segments with distinct inflow and outflow properties. Seasonal discharge follows a

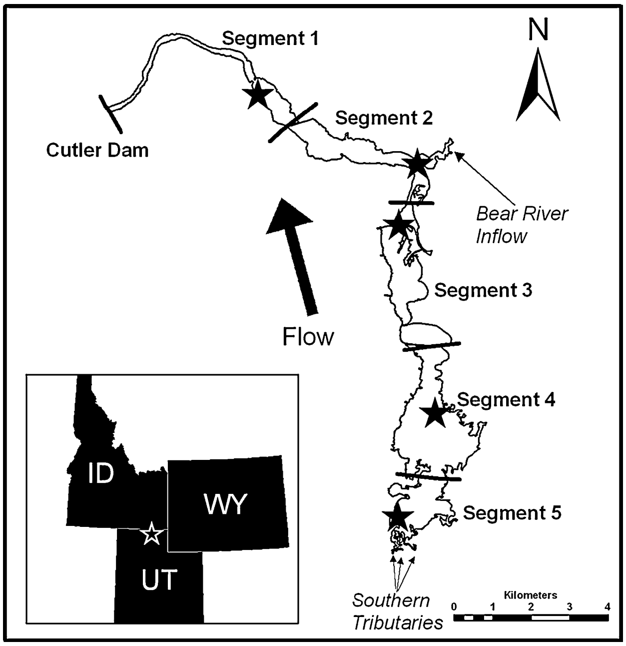

Fig. 2 Map of Cutler Reservoir, the study area; segments *1–5* were sampled intensively during spring, summer, and autumn of 2006 and summer and autumn of 2005. Segment boundaries are defined by *black bars*, and *black stars* indicate temperature-logger locations

single pulse hydrograph typical of the intermountain west, with average daily discharges ranging from 148 m^3/s during May and June snowmelt to 0.7 m^3/s during September low flows. Under current operation water levels are maintained so the reservoir fluctuates less than 0.5 m annually, with a mean surface elevation of 1343.6 m.

Cutler Reservoir is a warm-cool, polymictic system that mixes frequently during mild to moderate wind events. Stratification, if present at all, generally persists less than three days and occurs only in the upper 0.5 m (*this study*; Utah Department of Environmental Quality, Division of Water Quality (UDWQ) 2009). Winter-time lows of 0–1°C and ice cover are common, while mid-summer surface temperatures reach 20–30°C depending upon location. Shoreline habitat is predominated by inundated macrophytes, specifically cattails (*Typha latifolia)* and hard stem bulrush (*Schoenoplectus acutus*). The reservoir is eutrophic with summertime chlorophyll *a* concentrations exceeding 50 µg/L. In addition, isolated reports of summertime fish kills during low runoff years and night-time anoxia indicate that dissolved oxygen depletion may occur periodically and concentrations are often below water quality thresholds for larval or juvenile fishes during warm, summer months, a primary tenant of the TMDL study and impaired status of the reservoir (Utah Department of Environmental Quality, Division of Water Quality (UDWQ) 2009). The zooplankton biomass of Cutler Reservoir is diverse and is dominated by moinids during all seasons followed by *Daphnia* spp., and copepods, respectively.

Cutler Reservoir is designated as a warm-water fishery (Utah Department of Environmental Quality, Division of Water Quality (UDWQ) 2009) and currently contains multiple desired sport fish species, including our three focal species: (1) walleye, a cool-water, top piscivore and popular sport fish, (2) black crappie, a cool to warm-water, generalist predator, and (3) channel catfish, a warm-water, omnivore (Dahle 2009; Fig. A1). All fishes present (except 1 native sucker) in Cutler Reservoir are non-native, were sporadically introduced or invaded naturally at some time in the past (no fishes have been stocked since 1990; Utah Division of Wildlife Resources, *pers. comm.*), and reproduce naturally in the reservoir; the reservoir is not currently actively managed by the state (UDWR) for fisheries.

To capture the range of abiotic and biotic conditions, as well as the distribution of fish within Cutler Reservoir, we divided the reservoir into five segments, with a goal of maximizing the degree of internal homogeneity within each segment. Each segment is characterized by a distinct morphology and associated with its own unique tributary inflows, separated by a causeway or other flow constriction. We sampled fish and environmental variables at one randomly-placed sampling station within each segment (Fig. 2; see details below). We then implemented a standardized intensive sampling protocol, sampling each station one time during summer (July) and autumn (October) of 2005 and spring (May), summer (July), and autumn (October) of 2006 (each sampling event required 3–5 days per station). This study design resulted in a total fish and environmental data set of five time periods and five sample stations ($n = 25$), for each of three focal species.

Field Data Collection: Fish, Limnology, and Water Quality Indices

Our fish standardized sampling protocol consisted of a combination of the following gear types: (1) three experimental gill nets (1.8 m × 40 m; 8 panels containing 19–64 mm bar mesh in 6 mm intervals), (2) three trap nets (1.8 m × .8 m rectangular mouth, multiple baffle, with 30 m leads attached), (3) boat electrofishing (Coffelt VVP 15 boat electrofisher), and (4) beach seining (1.2 m × 10 m, 4 mm mesh). We distributed each gear type and sample station randomly within each reservoir segment and sampled for one night with each gear type during each sample period. We placed all passive sampling gear before sunset, recorded its location using a handheld GPS unit, and retrieved nets the following morning, thereby encompassing two crepuscular periods. In addition, we conducted beach seining during both morning and evening time periods, typically conducting 4–8 seine hauls in each segment during each sample period. Lastly, we conducted all electro-fishing at night by shocking 3–6, 100 m transects in each reservoir segment during each sample period. We identified captured fish to species, weighed, measured (nearest mm total length), and released each fish after retaining a sub sample of captured fish for laboratory aging and diet analysis. Estimation of fish growth, a primary bioenergetic driver, is described below. For each sample station, we also used an index of composite catch per unit effort of non-target fish as a potential explanatory variable ('Other fish CPUE index'), calculated as the total # of fish captured, of species other than the target species, per gear type, per unit time.

To identify physical water quality constraints (i.e., temperature and dissolved oxygen) on fish growth potential and assess relationships between fish species and biota at lower trophic levels (i.e., zooplankton and phytoplankton), we collected limnological data at the closest open-water site within each sample station during all sample events. We measured and recorded water temperature (°C), conductivity (µS/cm^3), total dissolved solids (TDS), pH, salinity (% solution), turbidity, dissolved oxygen (DO; mg/L; discrete measurements, see also *minDO* below) every 0.5 m from the surface to the bottom; observations represent integrated, water column averages. From each site and on each date, we took a water clarity (Secchi depth, m) measurement and collected a nutrient grab sample, later analyzed for chemical measures of nitrogen (TKN, NO_3-NO_2 and NH_4) and phosphorous (TP, SRP, and DP). We sampled phytoplankton using an integrated tube sampler to collect water from a depth just off the bottom to the surface and used the concentration of chlorophyll a (chl *a*; µg/L) as an index of phytoplankton biomass (Welschmeyer fluorometric method; Welschmeyer 1994). During the same sampling event, we sampled pelagic zooplankton and collected triplicate zooplankton samples from each index site using a 1.5-m integrated tube sampler with a 7.5 cm inside diameter (6.5 L total volume). We sampled and filtered 13 L of water with each replicate, depending on depth. We sieved samples through both 500- and 80-µm mesh zooplankton nets, preserved them in a Lugol's solution, and brought samples back to the laboratory for identification, enumeration, and measurement. We determined zooplankton density (number/L) for each species, and estimated biomass (µg/L) based on established length-to-weight relationships (Dumont and others 1975; McCauley 1984; Pauli 1989). More detailed limnological methods and data are available in Dahle (2009) and UDEQ (2009).

Water Quality Indices

In this type of reservoir, water quality, and both primary and secondary production are all strongly forced by seasonal differences in discharge and water residence time in each segment (see *Results*; Soballe and Kimmel 1987). Thus, we also calculated indices of minimum DO and mean water residence time for each segment and each season (spring, summer, and autumn) to help parse seasonal temperature and water quality effects in our limnological data. Based solely on our discrete (snapshot) measurements of dissolved oxygen (DO), conditions did not appear to be limiting fish ($DO > 4$ mg/L; Table 1) over the duration of this study. Therefore, our index of minimum DO (*minDO*) was based on continuous DO measures collected and made available as part of the TMDL study. Dissolved oxygen data (mg/L) were continuously recorded over selected time periods within the same habitat segments identified above from spring 2005 through autumn of 2006, the time period of our study (Utah Department of Environmental Quality, Division of Water Quality (UDWQ) 2009). We estimated *minDO* as the lowest recorded DO measurement for the same spring, summer and autumn seasons, 2005–2006.

Quantification of mean water residence time (*WRT*) was greatly simplified by mandated maintenance of near-constant water levels and by use of the same reservoir segments by other studies. We estimated *WRT* by dividing bathymetric surveys of segment volume by seasonal outflow discharge (Chapra and Reckhow 1983). Estimates of tributary inputs to each reservoir segment from a recent hydrologic study (Utah Department of Environmental Quality, Division of Water Quality (UDWQ) 2009) were employed to calculate discharges (by difference) as a proportion of the total outflow discharge at Cutler Dam. *WRT* (d) within the entire reservoir was interpreted as a cumulative weighted average of the daily discharge fractions (m^3/d) passing through each successive reservoir segment (m^3). For each reservoir segment, seasonal tributary inputs were combined with inputs from upstream segments to calculate outflow discharge. Tributary input WRT was conditioned solely by the segment in question, yet the WRT of inputs from upstream segments was a cumulative function of time spent in each successive segment.

Thermal Data Collection

We used three forms of sampling techniques to describe the thermal characteristics of Cutler Reservoir (Fig. 1). First, we placed one digital temperature logger 0.5 m below the surface in a representative location of each sample segment ($n = 5$) and set each logger to record temperature every 0.5 h. To ensure that selected logger locations were representative of each reservoir segment, in collaboration with related water quality sampling (Utah Department of Environmental Quality, Division of Water Quality (UDWQ) 2009), we compared the data from our fixed sample sites to the data recorded from a sub-set of temporary loggers

Table 1 Complete set of potential response and predictor variables used in exploratory analyses of patterns of relationships among environmental variables and fish performance

Segment	Response variables			Potential explanatory variables			Limnological and water quality data								
	Growth potential (average g/day)			Other fish (CPUE index)			Conductivity (µS/cm)	NO_3–NO_2 (ppb)	TP (ppb)	Chl *a* (µg/L)	Total zoop biomass (µg/L)	Moina biomass (µg/L)	Water temp mean (°C)	*WRT* (days)	min DO (mg/L)
	Catfish	Crappie	Walleye	Catfish other	Crappie other	Walleye other									
Spring season															
1	2.122	0.350	1.159	1.852	1.724	1.790	323.0	174.0	148.0	14.96	0.308	0	18.03	1.73	7.69
2	1.866	0.356	1.844	3.339	3.362	3.582	331.8	194.0	150.0	11.19	1.539	0.564	17.57	1.56	6.26
3	1.678	0.342	1.877	3.527	4.494	4.389	284.7	124.0	213.0	9.033	0.026	0	17.53	1.20	7.14
4	1.501	0.326	1.952	5.580	5.870	5.789	243.0	81.0	71.0	2.121	0.051	0.026	15.06	2.17	7.55
5	1.816	0.352	1.862	1.555	1.502	1.555	248.6	229.0	95.0	3.156	0.051	0	13.13	0.15	7.58
Mean	1.797	0.345	1.739	3.171	3.390	3.421	286.2	160.4	135.4	8.091	0.395	0.118	16.26	1.36	7.24
SD	0.231	0.012	0.327	1.605	1.851	1.783	41.0	58.4	55.2	5.422	0.650	0.250	2.10	0.76	0.59
Summer season															
1	3.089	0.064	−12.999	5.797	6.718	6.511	586.7	4.0	223.0	53.83	4.487	3.795	25.59	41.01	6.80
2	3.118	0.101	−12.111	5.184	6.767	6.302	592.7	2.0	227.0	61.67	2.051	1.436	26.53	36.98	4.55
3	3.205	0.133	−12.373	9.505	10.199	9.910	539.5	2.0	246.0	48.88	5.026	3.590	26.37	28.53	4.90
4	3.184	0.180	−6.898	5.328	6.281	6.265	417.7	38.0	215.0	64.83	1.615	1.205	24.39	51.49	4.58
5	2.964	0.222	−4.400	5.004	5.573	5.469	500.2	1881	228.0	17.20	0.154	0.154	20.62	3.55	6.10
Mean	3.112	0.140	−9.756	6.163	7.108	6.891	527.4	385.4	227.8	49.28	2.667	2.036	24.70	32.31	5.39
SD	0.095	0.063	3.866	1.891	1.793	1.733	71.9	836.2	11.4	19.01	2.042	1.589	2.43	18.07	1.01
Fall season															
1	0.828	0.227	1.486	3.325	4.446	4.072	547.3	675.0	175.5	23.02	0.154	0	11.17	4.20	7.20
2	0.789	0.219	1.435	6.491	7.006	6.491	570.7	727.0	147.0	18.81	0.077	0	10.60	3.79	9.90
3	0.759	0.213	1.393	3.617	4.441	4.497	494.2	704.0	235.0	20.04	0.026	0	11.03	2.92	12.12
4	0.687	0.198	1.289	8.859	9.453	9.545	314.0	165.0	56.5	3.177	0.077	0	9.79	5.28	12.21
5	0.778	0.217	1.418	3.836	3.891	3.891	428.0	2093	162.0	4.733	0.000	0	9.10	0.36	8.49
Mean	0.768	0.215	1.404	5.226	5.847	5.699	470.8	872.8	155.2	13.96	0.067	0	10.34	3.31	9.98
SD	0.052	0.011	0.073	2.395	2.351	2.386	103.4	720.9	64.5	9.275	0.059	0	0.88	1.85	2.21

Catch-per-unit-effort (CPUE) index is calculated as a function of the number of nets per set time (e.g., gill nets) or length of time sampled (e.g., electrofishing) according to each gear type (Dahle 2009). Other fish CPUE index) refers to the sum of the CPUE for all fish other than the focal species identified

SD standard deviation

distributed randomly throughout the segment. Second, to capture the spatial heterogeneity of the thermal environment, we used two forms of remote sensing, which allowed us to expand our thermal data into a continuous, spatially explicit data surface (Fig. 1). During summer sampling we used helicopter-mounted Thermal Infrared Imagery (TIR) to capture a synoptic, one time view of the thermal habitat of the reservoir with extremely high resolution (3 m pixels). We ground-truthed ($n = 12$) aerial TIR data using in-situ temperature loggers (Torgersen and others 1999; Torgersen and others 2001, Faux and others 2001). Lastly, we obtained Landsat 5 National Landsat Archive Processing System (NLAPS) band six data (thermal; 30 m pixels) corresponding to our spring and autumn sampling dates. We converted Landsat thermal band data to degree celsius using the algorithm developed by Barsi and others (2003) and cross-validated this data with in-situ temperature loggers to test and correct for systematic bias.

Tier 1: Quantifying Fish Growth Potential

As a mechanistic measure of fish performance, we evaluated overall growth potential for Cutler Reservoir as well as relative differences in growth potential across segments given inherent differences in thermal history and diet proportions using the Wisconsin Bioenergetics model 3.0 (Hanson and others 1997; Fig. 1).

To obtain the necessary fish growth (g) inputs for bioenergetics modeling, we first generated length frequency histograms in order to determine annual growth rates for walleye, black crappie, and channel catfish for each reservoir segment. Size-at-age data was then validated for black crappie and walleye using scale and otolith aging, respectively. Catfish sample sizes were sufficiently large, and cohorts were well defined using length frequency data requiring no additional age validation. We assumed fish attained 80% of their annual growth during the time period from April 1 to October 1, representing the summer growing season and the period of time when water temperatures exceed 10°C (Vatland and others 2008).

To obtain the necessary fish diet inputs for the bioenergetics modeling, we analyzed stomach contents for prey composition for each segment of the reservoir. We enumerated fish and zooplankton remains on a sub-sample of target fish collected in each segment, and identified fish prey items to species when possible. We enumerated terrestrial and aquatic invertebrates and identified individual specimens to order. After identification and enumeration, we measured and weighed all stomach contents (blot-dry wet weights to nearest 0.001 g) to quantify the size fraction of prey items selected by fish and to calculate diet proportion by wet weight.

We modeled walleye growth using physiological parameter values for bioenergetic metabolic rates from Madon and Culver (1993), and we synthesized these parameters for black crappie by substituting adult bluegill parameters (Kitchell and others 1974) with adjusted optimal and thermal maximum respiration and consumption temperatures (Jobling 1981) as recommended by Hanson and others (1997). Channel catfish physiological properties were generated by substituting flathead catfish physical parameters (Roell and Orth 1993) with adjusted optimal and maximum temperatures for channel catfish (McMahon and Terrell 1982), as described above.

We first ran bioenergetic model simulations (at an annual time step) for each individual species and reservoir segment incorporating site-specific growth, seasonal diet composition, and thermal history using temperature data collected with temperature loggers (Fig. 1). We used the output of estimated (g/individual) from these segment-specific model runs to parameterize consumption rates (g/g/day) for the target species (hereafter referred to as *field-estimated consumption*). Second, we generated species-specific thermal growth potential curves by running bioenergetics simulations on a 1 day time step for the complete range of temperatures present in Cutler Reservoir (Fig. 1; 0–35°C). We then modeled the average individual growth potential of each target species (channel catfish 400 g, black crappie 100 g, and walleye 1000 g), by holding individual consumption as a fixed variable, as estimated and averaged across the segment-specific model runs described above, and allowing the bioenergetic model to scale growth potential (g/day) based on thermal conditions. To evaluate the sensitivity of the model to consumption rates, we bracketed the *field-estimated consumption* by ±20% (the range observed across segments) and re-ran the simulations to generate upper and lower error estimates for our thermal growth potential curves.

Tier 2: A Thermal Habitat Surface of Fish Performance

We used these species-specific thermal growth curves to classify the growth potential of the TIR data for each of the three target species. Daily growth curves provide an estimate of growth potential in g/individual/day based on temperature and field-estimated consumption. We converted the TIR units from temperature (°C) to growth potential (g/individual/day) within ArcGIS 9.2 (ESRI, Inc.) by reassigning each pixel based on the relationship between these two variables on a daily time step, as generated using the bioenergetics model (Fig. 1). Using this approach we were able to generate synoptic maps of reservoir-wide (3-30 m pixel size) growth potential estimates for the three target species. In addition, we calculated the reservoir-wide and segment-specific seasonal mean and standard deviation of predicted growth potential for each of the target species. We generated reservoir-wide Cumulative Frequency Distributions (CFD) of available habitat versus modeled growth potential to quantify the effects of seasonal shifts in habitat quality for the three target species. We used segment-specific averages of growth potential for each season in statistical analyses of Tier 3 (below).

Tier 3: Water Quality Constraints on Fish Performance

At the last tier of our study, we statistically explored patterns of relationship among a broader suite of environmental variables and fish growth potential to better identify potential water quality constraints on fish performance. In this sub-analysis, we limited our dataset to represent a single year where the data were symmetrical and available for each of three seasons, and thus further reduced our sample size ($n = 15$). We initiated our statistical analyses with graphical data exploration of a comprehensive set of abiotic and biotic environmental variables (Table 1) using species-specific, seasonal and segment averages of fish growth potential growth. Interpretation was limited by sample size and also, in some cases, by the way the variables were measured. Thus, we attempted to reduce the predictor set under consideration to a feasible and biologically-meaningful sub-set of candidate variables that would allow us to maintain model parsimony. We first assessed correlations among candidate explanatory variables to identify groups of potentially redundant measures. Next, we used non-parametric recursive partitioning within Random Forests (RF; Breiman 2001) to assess potential relationships among fish growth potential and this smaller series of candidate explanatory variables. Random Forest allowed comparison of average prediction error, variable importance, and potential for interaction among predictors. The RF procedure consists of growing a large number of trees from bootstrapped samples, and using unselected (i.e., "out of bag") observations to evaluate predictive error in bootstrapped trees and calculate indices of variable importance (e.g., variable importance plots; VIPs) as the change in predictive error (measured as nodal purity) when that variable is permuted. Based on RF analysis of five sampling stations measured across 3 seasons we identified the strongest explanatory variables as well as a number of potential interactions from highly correlated predictors.

We next used path analysis fit by maximum likelihood within Amos 18 (SPSS, Inc 2009) to explore direct and indirect relationships between environmental factors and fish growth potential while accounting for covariance among predictors (Shipley 2000). Path analysis is a special case of structural equation modeling (Bollen 1989, Grace 2006) that allows decomposition of correlations in a multivariate system into both causal (as implied by user-defined model structure) and non-causal effects (Mitchell 1992) when all variables are measured (i.e., none are latent). Such models do not prove causality, rather they allow us to assess whether covariance implied by a model structure is consistent with our observations, and whether parsing of direct and indirect effects alters interpretation of observed correlations (Mitchell 1992, Shipley 1997). Correspondence between implied and observed covariance matrices is typically tested with a Chi-Square discrepancy and various measures of fit (Bollen 1989), thus power to detect significant departures from the hypothesized causal structure as well as significant effects within the model are a function of, and limited by, sample size (N). Further, path analysis is a linear modeling technique and is thus subject to assumptions of univariate and multivariate normality (Petraitis and others 1996).

Our hypothesis was that *WRT* influenced temporal and spatial patterns of both observed water temperature and eutrophication, and that a simple model might be used to explain patterns of fish performance. We chose chl *a* concentrations as our eutrophication proxy (Soballe and Kimmel 1987) because, as a direct result of elevated nutrients, it is more likely to be independent of spatiotemporal patterns of temperature within a season than dissolved oxygen. We used standardized coefficients linking WRT to fish performance via the effects of temperature and chl *a*, across focal species, to compare both thermal and eutrophication pathways, and examined differences among total (either direct or indirect) 'causal' effects and observed correlations. Because the sample size within this Tier was small ($n = 15$), there was increased potential for our specific sample to distort underyling of population parameters and produce poor representations of effect strength. Therefore, we used a bootstrap of 1000 replicates within Amos to assess whether changes to our sample had a substantial impact on the significance of observed effects.

Results

We were able to reliably capture all three target species using a combination of active and passive fish sampling techniques. In sum we handled and measured more than 135 walleye, 378 channel catfish, and 560 crappie and evaluated diets on a minimum of 10 species per sample date and site. The total catch per unit effort varied considerably between sample dates with summer catch rates nearly double that of spring and autumn catch. In general, growth rates and other indices of performance (e.g., PSD—proportional stock density) of target fishes in Cutler Reservoir are similar or exceed (e.g., walleye) those observed in comparable systems. More information describing the general diversity, distribution, demographics and abundance of the fish community is available in Dahle (2009).

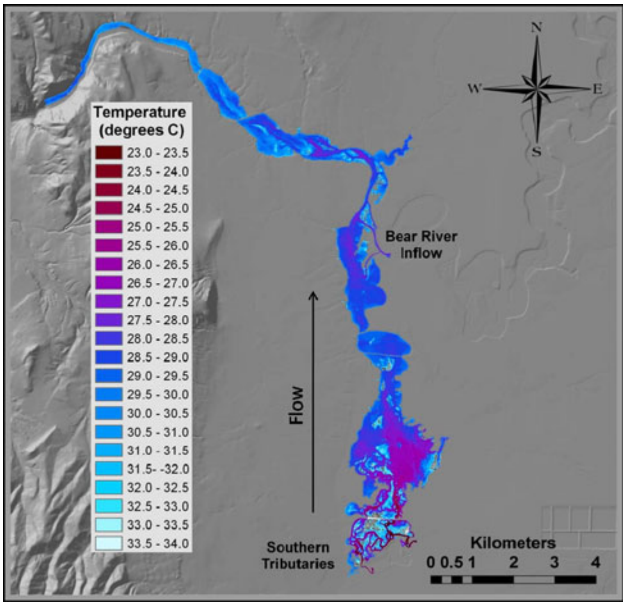

Fig. 3 Synoptic, 3-m resolution, Thermal Infra Red (TIR) image of Cutler Reservoir taken on 30 July 2006, and showing temperature variation within the study area

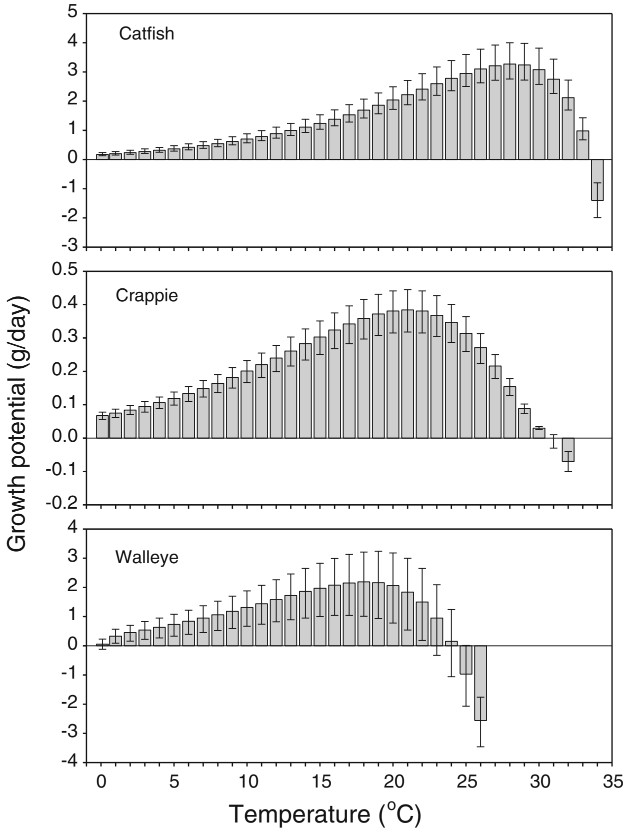

Fig. 4 Species-specific growth potential curves (g/day) of focal piscivores generated using the Bioenergetics model and calculated using the complete temperature range in Cutler Reservoir and coupled with field-estimated consumption (g/g/day), *Error bars* represent sensitivity analysis of ±20% field-estimated consumption (the range observed across segments)

Tier 1: Quantifying Fish Growth Potential

Cutler Reservoir demonstrates an extremely dynamic and spatially heterogeneous thermal environment. Daily average temperatures, as recorded at temperature loggers, ranged from 6.7°C (segment 5, April 1) to 28.7°C (segment 3, July 23). Diel temperature fluctuation was considerable during the sampling period, with up to 5°C per day. However, daily average temperatures corresponded with TIR thermal data (average difference = −0.5°C, 1 SE = 0.69°C), and daily average temperatures from dispersed, randomly-placed, temperature loggers within each segment paralleled the daily averages from our fixed logger stations in the corresponding reservoir segment. Based on the general level of agreement between the TIR thermal data and the temperature logger data, no adjustments were made to the TIR data sets prior to their use in bioenergetics modeling. On July 30, 2006 alone, reservoir-wide TIR temperatures ranged from 18 to 34°C demonstrating the extreme spatial heterogeneity of this system (Fig. 3).

All TIR images display a general warming pattern in water temperature moving from south to north (direction of water flow) within the reservoir. Cool inflowing water from the Logan and Little Bear rivers are clearly visible in the southern portions of the water body (Fig. 3). These two streams enter the reservoir at 20–23°C during summer and warm to 27–28°C within 2 km of their inflow point as they spread across the broad, shallow, southern portion of the water body (Segments 4 and 5). Additionally, although to a lesser extent, cool water inflows from the Bear River can be observed mixing with warm reservoir waters from the confluence of the Bear River at Segment 3, north of the upstream boundary of Segment 1.

Under our scenario of field-estimated consumption (±20%) the daily growth potential of the target species varied widely according to modeled thermal conditions (Fig. 4). Channel catfish growth potential peaked at 29°C, and at this temperature catfish growth potential ranged from 2.75 g/day to 4.0 g/day. Black crappie growth potential was greatest at 22°C and ranged from 0.32 g/day to 0.45 g/day at this temperature. Peak walleye growth potential depended more strongly on the modeled consumption rate and ranged from 1.04 g/day at 17°C to 3.24 g/day at 20°C.

Tier 2: A Thermal Habitat Surface of Fish Performance

Growth potential varies widely by season for all three of the target species, indicating that thermal habitat suitability changes substantially across seasons within Cutler

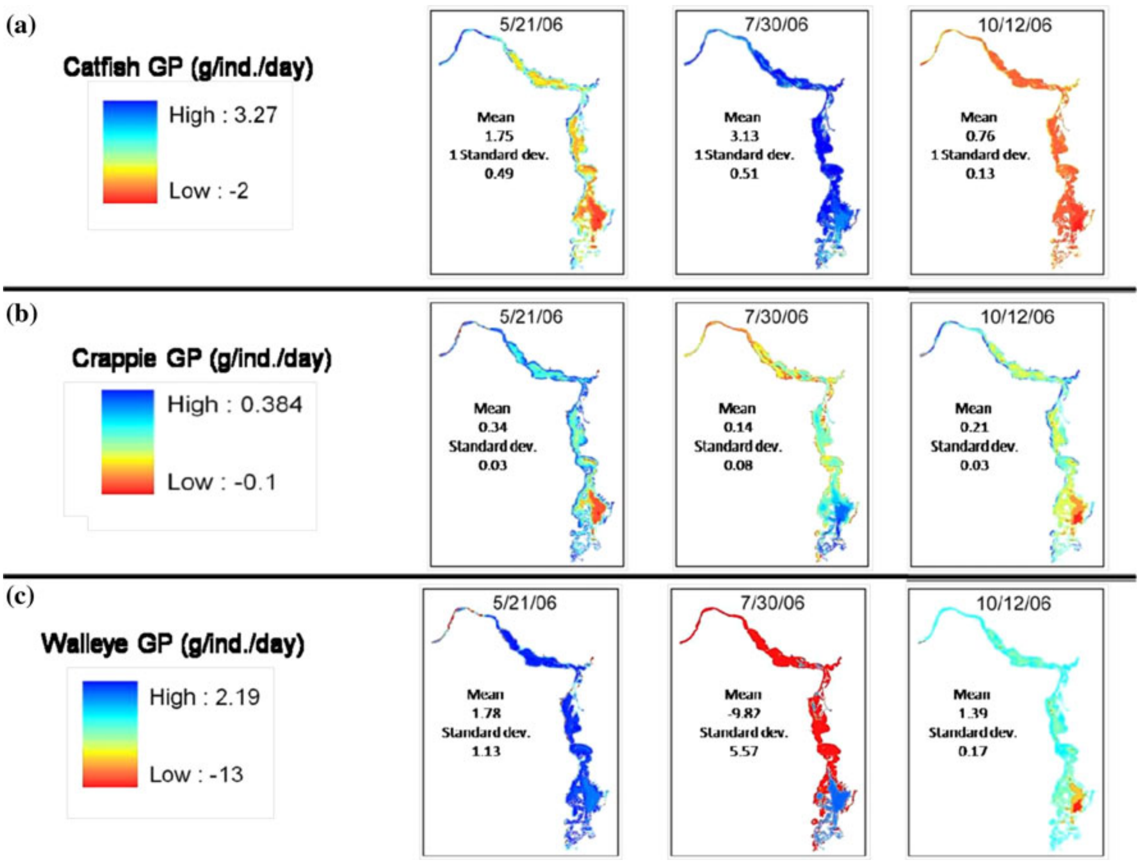

Fig. 5 Seasonal growth potential of focal species in Cutler Reservoir. Reservoir-wide growth potential (g/individual/day) maps for spring, summer, and autumn of 2006. The model output represents and average individual of each focal species (see text)

Reservoir (Fig. 5). Black crappie and walleye growth potential peaked during spring with a second, lower peak during autumn. Both walleye and crappie experienced reductions, 103 and 99% respectively, in their average daily growth potential (g/day) from May 21 to July 30, as thermal conditions became limiting for these species. Conversely, channel catfish average daily growth potential increased by 78% during this same period, achieving the highest rates during the summer as temperatures reached the optimal range for this species across most of the reservoir.

In May channel catfish growth potential averaged 1.75 g/day (Fig. 5a) and was greatest in shallow shoreline habitats, where water temperatures were warmest. In July, catfish growth potential reached its peak with an average of 3.13 g/day, and nearly 100% of the reservoir offered optimal growth potential for catfish during this time period. By October, thermal conditions had cooled below the optimal range for channel catfish throughout the water body and habitat that offered low growth potential dominated.

In contrast to the model results for channel catfish, black crappie growth potential averaged 0.34 g/day on May 21, the highest average of the modeling efforts for this species (Fig. 5b). As with catfish, spring growth potential for black crappie was highest along warm shoreline habitats and lowest in the cool southern tributary inflow area. Interestingly, crappie growth potential dropped to an average of 0.14 g/day by July 30. On this date, habitat providing high growth potential did exist for crappie, but it was confined to the cool southern tributary inflow area that displayed the lowest growth potential during the spring. In a pattern similar to the spring, crappie growth potential was again highest along warm shoreline habitats in October.

Walleye growth potential reached its highest average, 1.78 g/day, in May (Fig. 5c) and was high across most of the reservoir with few areas exhibiting sub-optimal thermal conditions. By July however, walleye growth potential had dropped to an average of −9.82 g/day, and most of the reservoir displayed negative growth potential for walleye (except for the southern tributary segment). Walleye growth potential increased moderately again in autumn and was greatest along warm shoreline habitats.

Cumulative Frequency Distribution (CFD) plots of species-specific thermal suitability quantify the system-wide effects of seasonal shifts in habitat quality for the

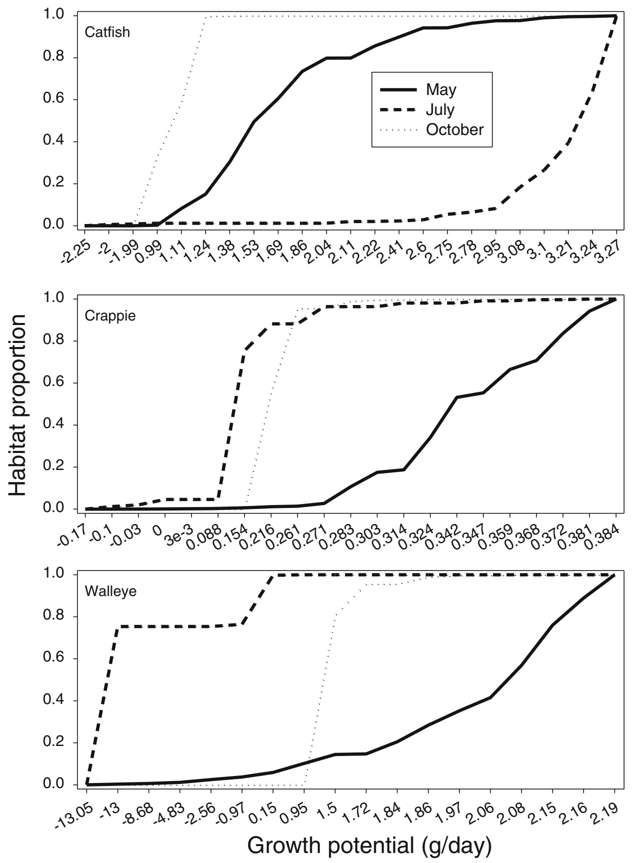

Fig. 6 Cumulative frequency distributions relating the proportion of habitat area suitable in Cutler Reservoir for the three target species and their estimated seasonal growth potential (g/day) in those areas. Note change in *x*-axis scales

three target species (Fig. 6). In May, 60% of available habitat offered channel catfish a growth potential range of 1.24–2.04 g/day representing an intermediate habitat quality between the extremes of summer and autumn. Summer growth potential for catfish was high with greater than 90% of available habitat providing a growth potential above 3 g/day. Autumn catfish growth potential provided less than 20% of available habitat with a growth potential above 0 g/day. Black crappie and walleye CFD plots are similar, with May providing the majority of suitable habitat in the medium to high growth potential range. However, walleye experience considerably less suitable habitat available than do crappie during July, a function of their limited physiological ability to perform in warm water conditions.

Tier 3: Water Quality Constraints on Fish Performance

In general, nearly all environmental variables showed strong correspondence with fish growth potential due to their common seasonality. Variable importance analysis revealed strong seasonal patterns in the relationship between specific environmental conditions and fish performance. Overall, categorizing fish growth potential by season consistently reduced variability in model predictions across all three species; however the reason this occurred appeared to vary among species. *WRT*, a seasonally-influenced variable that likely influences water temperature and productivity, also scored near the top for two of the three focal fishes (Fig. 7). Catfish growth potential was most strongly associated with average water temperatures (*avgT*), and only secondarily associated both with indicators of chemical water quality (*minDO*). Crappie growth potential appeared to be closely related to seasonal patterns of *WRT*, and to a lesser degree to *avgT* and measures of nutrient concentration or productivity. Walleye growth potential was strongly associated with *avgT*, but also with *WRT*. These results highlight the strong seasonal covariance among environmental conditions characterizing the system and the potential dependence of many variables on the flux of water through the system. However, it remained unclear whether the observed correlations were simply an artifact of the strong seasonality or whether it was possible to distinguish different effects across space and time.

Thus we next used a common model structure to test relationships among environmental measures and fish growth potential (Fig. 8). In all three models, *WRT* was an exogenous predictor, whereas *avgT* and chl *a* concentrations, respectively, were endogenous (physical) variables predicted by WRT and mediating its effects on fish growth potential. Indices of fit suggested excellent correspondence between hypothesized models of catfish, walleye, and crappie growth potential and field observations (Table 2; Chi-square P-values = 0.455, 0.503, 0.491, respectively). There were no notable departures from normality (skewness and kurtosis < 2.5, critical ratio (C.R.) < 2.0 for all variables, multivariate normality < 2.5 for all models, twice < 1.0) and bootstrap replicates supported the pattern found in observed fits. In all models, *WRT* was strongly and positively associated with *avgT* and chl *a* concentrations (Fig. 8). However, *avgT* showed no significant association with chl *a* concentration after accounting for their covariance with *WRT*. In the crappie and walleye models, chl *a* exhibited a significant negative direct effect on fish growth potential. In contrast, the direct effect of *avgT* was positively related to both catfish and crappie growth potential, and negatively related to walleye growth potential.

Decomposition of observed correlations provides further evidence that strong patterns of covariance influence this system. All models demonstrated good correspondence between observed and implied correlations with fish growth potential and the total effects of the exogenous

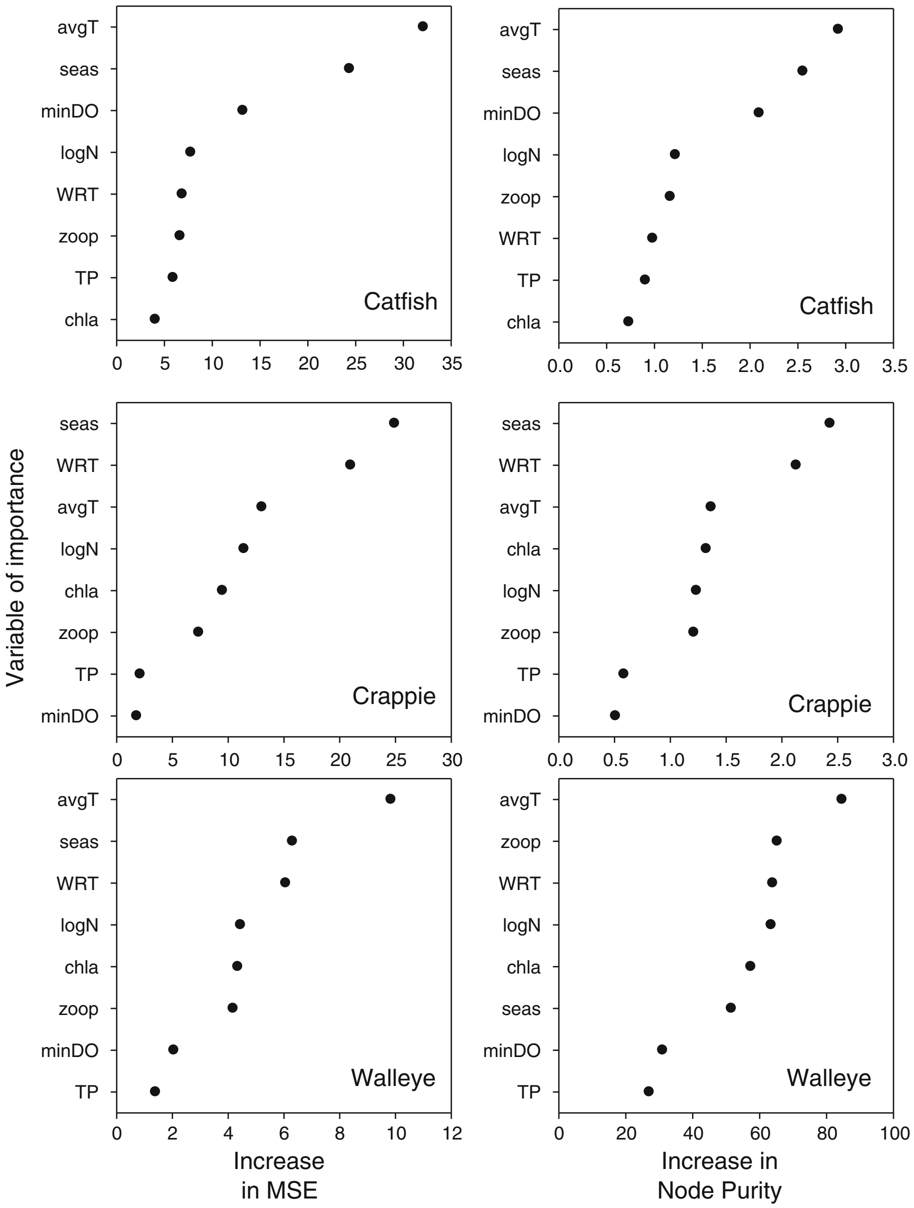

Fig. 7 Variable importance plots (VIP) from Random Forests models used to determine average prediction error, assess variable importance, and identify potential for interaction among a candidate set of predictor variables. The same set of candidate variables was explored for each focal fish species. Increase in mean square error (accuracy) explained by each variable is shown in *left panels*; the increase in node purity for each variable is shown in *right panels*

forcing variable *WRT* were no exception (Table 3). However, as implied by the model structure (Fig. 8), several observed correlations between proximal environmental predictors and fish growth potential were non-causal (i.e., spurious) and occurred solely due to shared correlation with *WRT*. In the catfish model, the observed correlation between chl *a* and fish growth potential was almost entirely a result of its dependence on *WRT*, and the resulting correspondence with *avgT*. *avgT* had a positive (although apparently insignificant) direct effect on crappie growth potential, even though the observed correlation was significant and negative. In contrast, the negative direct effects of both *avgT* and chl *a* on walleye were amplified in the observed correlation matrix by their common dependence on *WRT*. In each case, important patterns were obscured by the strong seasonality and non-causal correlation of the system.

Discussion

Our multi-tiered approach allowed us to develop an integrated response metric of fish performance (fish growth potential) to quantify thermal habitat suitability and identify potential water quality constraints in a shallow, mixed reservoir listed as impaired under the CWA. In Tier I of our analysis, mechanistic bioenergetic modeling quantified the growth potential of three predominant sport fishes representing a range of physiological and behavioral differences as well as potential water quality sensitivity. This

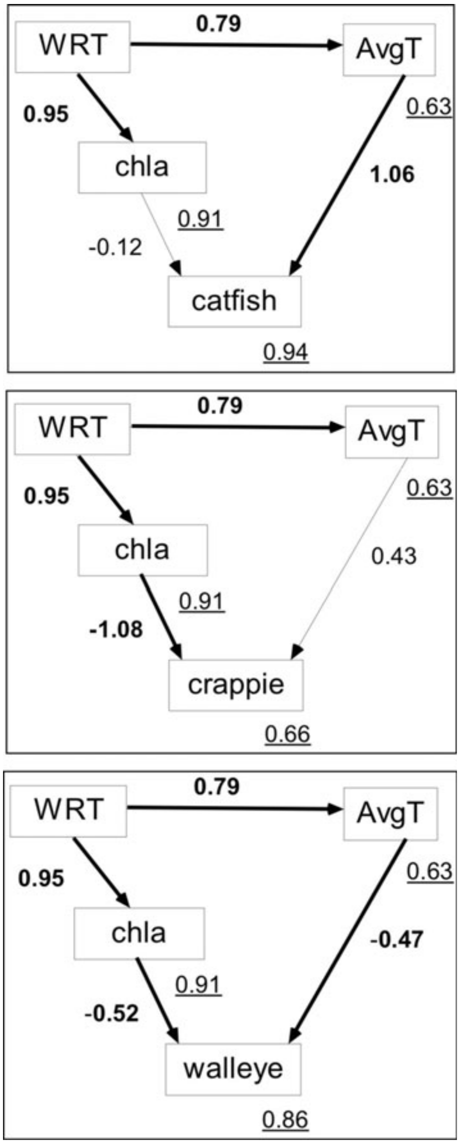

Fig. 8 Path diagrams for each focal species under the structural hypothesis that *WRT* exerts a causal influence over temporal and spatial patterns of both observed water temperature and a eutrophication proxy (chl *a*); these endogenous variables were used to explain patterns of fish performance across focal species. *Thick arrows* and *bold* coefficients represent statistically significant ($P < 0.05$) paths; *thin arrows* represent non-significant paths. Path coefficients are presented adjacent to path arrows; total variance explained by each endogenous variable is *underlined* and shown adjacent to the *right corner* of each endogenous variable box

Table 2 Measures of fit between modeled fish performance and observed covariance structure from path analyses; catfish, crappie, and walleye structured equation models

Fit index	Catfish	Crappie	Walleye
χ^2 discrepancy	1.57	1.42	1.37
d.f.	2	2	2
P-value	0.455	0.491	0.503
Goodness of fit index	0.958	0.955	0.959
Normalized fit index	0.982	0.977	0.982
Comparative fit index	1.000	1.000	1.000
Root mean square error of approx.	<0.001	<0.001	<0.001

See also Fig. 8

Table 3 Decomposition of correlation among environmental variable and fish growth potential into direct, indirect, total, causal, and spurious effects

	avgT	*WRT*	Chl *a*
Catfish			
Direct effects	**1.060**	0.000	−0.122
Indirect effects	0.000	**0.723**	0.000
Total effects	**1.060**	**0.723**	−0.122
Non-causal	−0.091	0.000	0.799
Implied R	0.969	0.723	0.677
Observed R	**0.969**	**0.741**	**0.738**
Crappie			
Direct effects	0.426	0.000	**−1.082**
Indirect effects	0.000	**−0.693**	0.000
Total effects	0.426	**−0.693**	**−1.082**
Non-causal	−0.824	0.000	0.320
Implied R	−0.398	−0.693	−0.762
Observed R	**−0.458**	**−0.735**	**−0.758**
Walleye			
Direct effects	**−0.472**	0.000	**−0.517**
Indirect effects	−0.190	**−0.866**	0.000
Total effects	**−0.472**	**−0.866**	**−0.517**
Non-causal	−0.389	0.000	−0.356
Implied R	−0.861	−0.866	−0.873
Observed R	**−0.877**	**−0.869**	**−0.886**

Significant direct effects and observed correlations ($P < 0.05$) are shown in bold text

quantification incorporates both biotic and abiotic variables that may impact each fish species uniquely and often fluctuate widely across space and time (Crowder and Cooper 1982; Romare and others 2003).

In Tier II, we capitalized on multiple scenes of readily available Landsat TM data to estimate fish performance across both space and time (reservoir-wide) from bioenergetics model output. We relied more heavily upon thermal condition than previous spatially-explicit bioenergetics models, which may have resulted in a better description of the thermal surface of fish performance reservoir-wide (Wildhaber and Crowder 1990; Höök and others 2004b; Power and Attrill 2007). In addition, our modeling approach benefited from advanced and recently validated remote sensing technology to describe the thermal habitat of aquatic systems (Handcock and others 2006). In a similar approach (the only one we know of), Höök and others (2004a) used Advanced Very High Resolution Radiometer

(AVHRR) data to generate spatially-variable growth potential estimates for steelhead (*Oncorhynchus mykiss*) in Lake Michigan. Yet our model differs from the Höök and others (2004a) approach in several important ways. First, we were able to define our model results at a much higher resolution (9 m^2 cells instead of 234,000,000 m^2; but note the relative size differences of these two systems). Second, we were able to extend the model output to include the entire water column due to the lack of thermal stratification in Cutler Reservoir. Finally, we used a combination of satellite and aerial TIR imaging validated by in-situ temperature loggers. These differences allowed us to generate continuous thermal data sets that captured fine-scale spatial temperature fluctuations, incorporate these fine-scale spatial temperature fluctuations into bioenergetics modeling, and build a thermal surface of fish performance for the entire reservoir.

The thermal surface of fish performance revealed large differences in the amount and spatial-arrangement of thermally suitable habitat for the three focal species. In particular, our results demonstrate the effect of high water temperature on habitat quality for cool-water fishes (e.g., walleye) in contrast to effects on a warm water generalist species (e.g., channel catfish). Given these inherent thermal requirements, it is perhaps not surprising that we found the peak growth potential of our target species occurred at different times of the growing season. The model results show that black crappie and walleye growth potential peaked during spring and autumn, while channel catfish growth potential reached its highest levels during the summer period. Spatially, peak growth potential shifted from shallow shoreline habitats during spring and autumn to localized thermal refugia during summer for walleye and crappie. In contrast, catfish growth potential was high throughout the reservoir during the summer modeling period. This diversity in species-specific growth potential emphasizes the dynamic nature of fish growth potential and, ultimately, the care one must exercise when defining habitat suitability (e.g., Costanza and others 1992) or designating the boundaries of fisheries protected areas based on these metrics (e.g., Friedlander and others 2007).

Despite these species-specific differences, in general we found that the growth potential of the three focal fish closely tracked the thermal characteristics of the habitat available in Cutler Reservoir, a pattern that has been noted by others in both similar and dissimilar systems (Goyke and Brandt 1993; Hughes and Grand 2000; Friedland and others 2000). Assuming food resources were generally sufficient to support high growth rates within the study area, we expected the peak in mean growth potential of our target species to coincide with the time period when Cutler Reservoir provided the greatest amount of habitat that matched the thermal preferences of our target species. The results from our field observations and modeling support this hypothesis. Interestingly, for both crappie and walleye, we found that a single location within the study area, the southern tributary inflow, oscillated between the lowest growth potential in the reservoir to the most energetically beneficial, providing the highest growth potential, depending on the season modeled. Our results confirm that fish performance is tightly coupled with the thermal regime of a water body (Brandt and others 1992; Mason and others 1995), and to a large extent this coupling defines the habitat quality available for a specific species of fish and during a particular time-window or season (Power and Attrill 2007).

The seasonal effects of hydrology and productivity, and influence of these processes on water temperature and water quality resulted in the widest fluctuation in fish performance for walleye, the focal species we chose a priori as the most sensitive measure of fish performance. For walleye, the summer season was marked by large-scale negative growth potential, and this cool-water piscivore experienced a period of thermal stress; more than 95% of the water body demonstrated negative growth potential during the warmest portion of the summer growing period. Despite this finding, walleye within Cutler Reservoir maintain above-average yearly growth rates when compared to other North American recreational walleye fisheries (Radant and Sakaguchi 1979; Minnesota Department of Natural Resources (MNDNR) 2006; Quist and others 2002). This discrepancy between model predictions of negative growth potential during warm periods and high growth rates measured in the field has been observed elsewhere (Luecke and others 1999; Höök and others 2004a), with several plausible explanations and implications. First, spatially-explicit bioenergetics models may be inaccurate due to errors in species physiological parameters, inaccurate estimation of consumption estimates, imprecision in thermal data, or a combination of these measures (Ney 1990, 1993; Boisclair 2001). Second, the duration of the time period of negative growth potential may be too short to be of consequence, such that fish may endure a short period of negative growth while growth over the entire season remains positive (Headrick and Carline 1993). Third, fish may be capable of locating and utilizing thermal refugia that are not identified in modeling efforts (Torgersen and others 1999). Lastly, as also demonstrated here, fish may be extremely adept at utilizing complex habitat mosaics in a manner that minimizes or eliminates periods of low growth (Luecke and others 1999). Any one, or a combination of these factors, may explain the tendency for fish to demonstrate positive growth overall despite periods of predicted low growth potential (Tyler and Brandt 2001, Höök and others 2004a). Regardless of the cause of this discrepancy, managers are left with the difficult decision of whether to manage the water body of interest for isolated periods of low fish performance, or based on their performance overall, across a year or a life-span. Those two different management objectives would clearly result in different and potentially conflicting water quality management plans and associated TMDL requirements.

Despite the improved ability of spatially-explicit bioenergetics models to facilitate the understanding of complex patterns in habitat quality and fish habitat use that emerge across varying spatial and temporal scales, these models still remain generally static in structure and cannot completely predict the dynamic nature of fish habitat selection (Tyler and Brandt 2001, but see Nislow and others 2000; Hartman and Kitchell 2008). Future bioenergetic models that incorporate competitive interactions, deduct the costs of movement between forage patches, and document localized forage production could improve predictions of fish habitat selection (Tyler and Brandt 2001; Railsback and Harvey 2002). Similarly, our approach assumes a uniform distribution of prey and uses the physiological response of a fish to temperature to estimate consumption rate. The model results would undoubtedly change, and could improve in accuracy with the incorporation of more descriptive prey availability information and the inclusion of a foraging module (Brandt and others 1992). Nonetheless, foraging models also require many simplifying assumptions and may not accurately represent prey availability and concomitant consumption estimates of target species (Persson and Greenberg 1990; Giske and others 1998; Mazur and Beauchamp 2006). In contrast to the direct physiological mechanisms modeled using bioenergetics alone, the incorporation of more dynamic interactions may result in models that are unwieldy and that predict patterns that realistically cannot be corroborated, validated, or applied in management (Ginzburg and Jensen 2004; Hartman and Kitchell 2008). As such, progress in describing thermal habitat at a much finer resolutions and the enhanced understanding of suitable habitat available for fish use should not be overlooked (Hansen and others 1993; Miranda and others 2010).

Does Water Quality Constrain Fish Performance?

Cutler Reservoir is just one of thousands (>44,000) of water bodies in the USA currently listed as impaired under the CWA, the focus of a large and expensive TMDL study, and for which fish or fisheries is listed as a designated beneficial use (Environmental Protection Agency (EPA) 2009). Yet in Cutler Reservoir, as elsewhere, mechanistic linkages between fish performance (growth, survival) and water quality have yet to be established (Davies and Jackson 2006). Our study revealed several important misconceptions regarding the relationships between measures of fish performance and water quality in this system as well as providing an approach to explore potential relationships among dynamic spatio-temporal patterns of water quality and fish growth potential. First, while historical information regarding the fish community within this system is limited, previous spot sampling and anecdotal accounts suggested that water quality in the reservoir has been impaired resulting in simplified fish community composition dominated by 'rough' fish and with low overall fish abundance (Dahle 2009; Utah Department of Environmental Quality, Division of Water Quality (UDWQ) 2009). In contrast to this anecdotal information, we captured 14 fish species, fish biomass was relatively high, and we found that a considerable percentage of biomass was comprised of highly desired sport fish (Dahle 2009). Not only was the fish community diverse and composed of many desired fishes, crappie and walleye demonstrated growth rates at the upper range of reported values for these species (e.g., Carlander 1969; Quist and others 2002).

Although difficult to categorize as this system is completely artificial and dominated by non-native fishes, we attempted to place Cutler Reservoir on the Biological Condition Gradient (Davies and Jackson 2006). The diversity of fishes is relatively high for a western reservoir (e.g., Haddix and Budy 2005; Vatland and others 2008), there are some sensitive species present (e.g., walleye, occasionally brown trout); however, tolerant species (e.g., carp) are dominant (>50%) and are likely affecting function to some degree (suspending sediment; Weber and Brown 2009). Thus conceptually, this system appears to score, on average, between four and five indicating a mid-level biological condition and degree of stress (Davies and Jackson 2006), as compared to the purported state of severe degradation and high stress. Collectively these field results confirm the assertion that below certain thresholds, metrics of fish density, biomass, and diversity typically increases with eutrophication (e.g., Carpenter and Kitchell 1993, *and see review in* Kasprzak and others 2002, *but see* Miranda and others 2010). This pattern represents a generality that complicates the role of fish or fisheries as a designated beneficial use, potentially driving TMDL standards under the CWA. At the high eutrophy levels observed in Cutler Reservoir (e.g., chl $a > 50$ µg/L) some desired fishes appear to suffer from the combination of excessive cultural eutrophication in the context of elevated temperatures (e.g, walleye) whereas others appear to be largely unaffected or even enhanced by elevated productivity (e.g., catfish). Thus our overall findings do not necessarily indicate that Cutler Reservoir is degraded by pollution; however, our results do suggest that fish "in general" or a single species of fish alone, may not be the best justification for implementing TMDL standards.

Nonetheless, our results generally supported our *a prior* hypothesis that that walleye would be most sensitive of our focal species to both spatial and temporal variation in thermal habitat suitability and potential water quality constraints, followed by black crappie and channel catfish, respectively. These results make sense, as walleye, for example, are a cool-water species and require relatively high levels of DO. Therefore whereas a broadly tolerant, warm-water fish such as catfish is unlikely to contribute significantly to our understanding of the potential constraints imposed on fishes by eutrophication, walleye and their cool-water relatives represent useful and sensitive measures of fish performance for use in TMDL standard determination in warm-water lentic systems. Using a sensitive focal species within this context may provide biological relevance to the process of determining allowable nutrient loading and as integrators of habitat suitability across multiple spatial and temporal scales (Landres and others 1988, Fausch and others 1990; Dale and Beyeler 2001).

The relative vulnerabilities of focal species demonstrated here, however, were strongly and differentially affected by seasonal patterns between environmental variables, driven by hydrology and productivity, and fish performance. The small sample size ($n = 15$) available for Tier III of our analysis limits strong inference in this case (Griffith and others 2009). For example, the Chi-square discrepancy and other fit statistics have limited power to detect potential differences between observed and implied covariance matrices; significance of all coefficients are similarly vulnerable to Type II error. However, such analyses do offer additional opportunities to quantitatively explore potential water quality effects as distinct from the strong seasonality of the system, which might otherwise mask water quality signals (e.g., Livingston 2007; Wazniak and others 2007). Using structured causal hypotheses to decompose correlations among environmental predictors helped us to detect patterns otherwise obscured by strong spatial and seasonal covariance. Nevertheless, inferences drawn from such models are only useful if our hypotheses provide an adequate characterization of the causal system (Petraitis and others 1996; Shipley 2000).

When we categorized fish performance by season, variability in model predictions of fish growth potential was consistently reduced across all three species, but interestingly not for the same reasons. While variation in *WRT*, *avgT*, and chl *a* were all strongly influenced by season and each had significant correlations with fish growth potential, much of this correlation appears to result from an indirect, causal dependence on seasonal changes in *WRT*. Elevated productivity throughout our system meant that catfish growth depended solely on temperature constraints, whereas primary productivity (chl *a*) had a greater effect on crappie, because crappie growth potential was less sensitive to temperature variation throughout the year. Both predictors were negatively related to walleye growth potential, but pairwise correlations with walleye growth were amplified by failure to account for a shared dependence on *WRT*. Griffith and others (2009) similarly used a comparable path approach to explore parallel pathways in headwater agricultural streams and identified that periphyton (also an index of primary productivity) mediated indirect pathways of increased nutrients and open canopy on invertebrates and fish in a complex variety of directions (both +/−). Based on our exploratory analysis, we cannot reject the hypothesis that water quality constrains crappie and walleye performance. Notably there have recently been considerable advances in attempts to make similar linkages, but primarily in coastal lagoons and estuaries (e.g., Wazniak and others 2007; Livingston 2007, and other contributions in this Special Supplement).

Overall Implications

Our study demonstrates a novel three-tiered approach to overcome some of the challenges in quantifying fish performance as a function of habitat suitability across large, heterogeneous lentic systems. In addition, our approach allows us to explicitly link a mechanistic and fitness-related measure of fish performance to potential water quality constraints. As such our approach represents a distinct advancement over previous efforts where: (1) the extremely heterogeneous nature of reservoir temperature has generally been ignored despite direct links to fish growth—fish are not exposed to average temperatures, rather they are free to move and pick and choose in order to maximize their growth, and (2) negative water quality effects on fish are either simply assumed and/or obscured by strong co-variation with other factors (e.g., the potentially overwhelming effects of temperature).

Each tier of our analysis demonstrates the potential application of this approach to overcoming some of such challenges and highlights generalities among fish and habitat suitability that span impaired lentic water bodies world-wide. Our study required a moderately comprehensive field effort tied to both mechanistic modeling of fish growth potential and structured statistical analysis of water quality constraints. Despite this effort, our inference is still somewhat limited by the small final sample size across species, time and space and by strong natural, seasonal effects of hydrology and productivity; limitations common in many such studies. Nevertheless, while substantial challenges may limit our ability to better understand and manage impaired water bodies specifically for fish, we provide an overall approach that we believe is: (1) useful for quantifying fish performance mechanistically and at a large spatial scale appropriate for whole-system management, and (2) feasible and promising for exploring and identifying the water quality factors most likely to constrain fish performance (a common designated beneficial use; CWA). Furthermore, our approach provides an efficient and quantitative means of monitoring changes in habitat quality and consequent fish production potential for economically-important fishes as well as providing guidance for conservation efforts dealing with sensitive or imperiled populations alike.

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