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Modeling white sturgeon movement in a reservoir: the effect of water quality and sturgeon density[☆]

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Abstract

We developed a movement model to examine the distribution and survival of white sturgeon (*Acipenser transmontanus*) in a reservoir subject to large spatial and temporal variation in dissolved oxygen and temperature. Temperature and dissolved oxygen were simulated by a CE-QUAL-W2 model of Brownlee Reservoir, Idaho for a typical wet, normal, and dry hydrologic year. We compared current water quality conditions to scenarios with reduced nutrient inputs to the reservoir. White sturgeon habitat quality was modeled as a function of temperature, dissolved oxygen and, in some cases, suitability for foraging and depth. We assigned a quality index to each cell along the bottom of the reservoir. The model simulated two aspects of daily movement. Advective movement simulated the tendency for animals to move toward areas with high habitat quality, and diffusion simulated density dependent movement away from areas with high sturgeon density in areas with non-lethal habitat conditions. Mortality resulted when sturgeon were unable to leave areas with lethal temperature or dissolved oxygen conditions. Water quality was highest in winter and early spring and lowest in mid to late summer. Limiting nutrient inputs reduced the area of Brownlee Reservoir with lethal conditions for sturgeon and raised the average habitat suitability throughout the reservoir. Without movement, simulated white sturgeon survival ranged between 45 and 89%. Allowing movement raised the predicted survival of sturgeon under all conditions to above 90% as sturgeon avoided areas with low habitat quality.
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1. Introduction

When faced with suboptimal water quality, fish typically migrate to areas with more favorable conditions. A number of lab and field studies have documented fish avoidance behavior in response to sublethal or lethal levels of dissolved oxygen and temperature (Whitmore et al., 1960; Neil, 1979; Magnuson et al., 1985; Coutant, 1986; Suthers and Gee, 1986; Claireaux et al., 1995a,b; Schurmann et al., 1998). This avoidance behavior moves fish away from areas

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with stressful or lethal conditions of temperature or dissolved oxygen.

Avoidance behaviors are important at both the individual and population level. They benefit individual fish by helping them survive in environments with variable water quality conditions. At the community level, avoidance responses can transform aquatic communities when the affected fish migrate away from one environment to another (Atchison et al., 1987). For instance, avoidance behavior is thought to be one reason for decreased fish populations in polluted surface waters (e.g. Woodward et al., 1995). Likewise, avoidance of areas with poor water quality can increase fish density in areas with acceptable water quality (Coutant, 1985). Depending on the spatial location and extent of high temperature and low dissolved oxygen, access to essential habitat areas, such as spawning or feeding grounds, can be blocked. For many years, areas of low dissolved oxygen in the Delaware River blocked anadromous fish, such as American shad (*Alosa sapidissima*), from reaching their traditional upstream spawning grounds (Maurice et al., 1987). Low levels of dissolved oxygen in portions of the San Joaquin Delta of California impeded upstream migration of chinook salmon (*Oncorhynchus tshawytscha*) (Alabaster, 1989).

In this modeling study, we examined the effect of movement in response to temperature and dissolved oxygen on the distribution and survival of adult white sturgeon (*Acipenser transmontanus*) in a reservoir with strong spatial and temporal variation in temperature and dissolved oxygen. We used temperature and dissolved oxygen information from years with high, normal, and low flow conditions to compare movement responses under different hydrologic conditions, and we examined the effect of reducing nutrient inputs to the reservoir. Finally, we considered the effect of including other factors, besides water quality, that likely influence the habitat preferences of white sturgeon.

2. Background information

2.1. White sturgeon

The white sturgeon is a semi-anadromous, bottom-feeding fish found in rivers and ocean environments from the Aleutian Islands to central California. Populations in the Columbia and Snake Rivers have been affected by the building of dams, which have isolated populations and altered physical habitat conditions such as water depth and velocity (Parsley et al., 1993; Jager et al., 2001). White sturgeon populations are vulnerable to alterations of large rivers and over-exploitation because they are long-lived (more than 100 years), slow to reach sexual maturity (15–32 years old), and spawn infrequently (every 2–11 years).

Seasonal migration related to spawning activity accounts for some movements by sturgeon. Because information on the rates, locations, and timing of seasonal spawning migration in impoundments is far from complete, this type of movement was not addressed in this model. In the few free-flowing rivers that remain, sturgeon are thought to migrate to upstream areas in the springtime as they prefer to spawn in fast, turbulent habitat, and broadcast their eggs over rocky substrates (Beamesderfer and Farr, 1997). Factors that have been linked to the rate, timing, and direction of these migratory movements for various sturgeon species include water temperature, sturgeon size, and sexual maturity (Haynes and Gray, 1981; McKinley et al., 1998; Bramblett and White, 2001). These long-range migratory movements are not represented in this movement model; instead, we simulate daily movements by sturgeon in response to local environmental habitat characteristics and sturgeon density.

There is little direct evidence regarding the levels of dissolved oxygen and temperature that produce avoidance movement in white sturgeon. However, there have been a few studies that give some insight into preferred, stressful, and lethal levels of dissolved oxygen and temperature for this and other sturgeon species. Khakimullin (1987) found that in the temperature range of 17.2–21.5 °C, Siberian sturgeon (*Acipenser baeri*) preferred dissolved oxygen levels between 5.9 and 13.2 mg/l. In a study in the Bliss Reach of the Snake River upstream of Brownlee Reservoir, white sturgeon were caught from waters with dissolved oxygen levels ranging from 8 to 16 mg/l and temperatures from 10 to 22 °C (Lepla and Chandler, 1995). In addition, several sonic-tagged sturgeon ($n = 4$) were tracked. When they encountered low levels of dissolved oxygen (w6 mg/l), sturgeon moved laterally onto elevated ledges where dissolved oxygen levels exceeded 6 mg/l.

Jenkins et al. (1993) conducted 6-h tests at 22.5 °C for shortnose sturgeon (*Acipenser brevirostrum*) and found that young sturgeon were more sensitive than adults to low levels of dissolved oxygen. At 2.5 mg/l dissolved oxygen, 100% of 25-day-old fish, 96% of 32-day-old fish, and 86% of 64-day-old fish were killed, while only 12% of 104 and 310-day-old fish were killed. Secor and Gunderson (1997) found complete mortality of juvenile Atlantic sturgeon (*Acipenser oxyrinchus*), in five out of six replicates at 26 °C and 3 mg/l of dissolved oxygen. Klyashtorin (1976) developed relationships describing changes in sublethal and lethal levels of dissolved oxygen as a function of temperature for several species of young sturgeon; at 10 °C the sublethal and lethal levels of dissolved oxygen were 3.30 and 1.33 mg/l, respectively.

Limited information is available to document upper temperature tolerances for sturgeon. For white sturgeon embryos, temperatures above 20 °C were found to be lethal (Wang et al., 1985). The Idaho state temperature standard for cold-water biota is 22 °C or less with a maximum daily average below 19 °C. The Idaho state dissolved oxygen criterion is above 6.0 mg/l. However, for reservoirs that stratify, the oxygen standard does not apply to the hypolimnion (bottom waters of the lacustrine zone).

2.2. Area description

Brownlee Reservoir, impounded in 1958, is located on the Snake River in west-central Idaho and receives drainage from 189,000 km². There are three sections of Brownlee (Fig. 1): a riverine zone (River Kilometer (RK) 539–518), a transition zone (RK 528–486), and a lacustrine zone (RK 505–458). The exact boundaries of these zones vary depending on flow. The basin hydrology is dominated by snowmelt runoff with peak flows from March through June.

Spatial and temporal variation in dissolved oxygen and temperature is a common feature of reservoirs in temperate regions. Patterns of dissolved oxygen concentrations are affected by factors such as temperature, flow, reservoir morphology, allochthonous input of nutrients and organic matter, photosynthesis and respiration, and mixing by wind (Cole and Hannan, 1990). In-situ heating, the temperature of inflowing waters, and the release of water from the outflow affect local
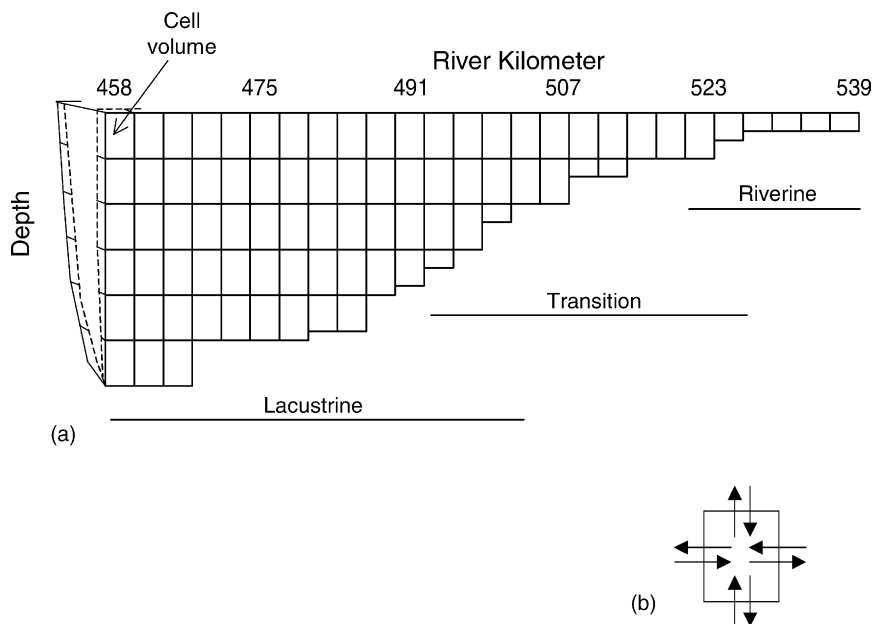

Fig. 1. (a) The model movement grid (not to scale) for Brownlee Reservoir. Locations of the lacustrine, transition, and riverine zones are noted. The dam is located at river kilometer 458. (b) Possible directions of sturgeon movement into and out of a representative cell.

temperature. For instance, in a bottom-discharging reservoir the release of cold waters from the hypolimnion allows replacement by warmer waters from above. Complex temperature gradients often form in reservoirs due to temperature and density differences through the water column (Petts, 1984).

Brownlee Reservoir generally remains stratified from March until November. The temperature generally cools with depth—as much as a $10\,^{\circ}\text{C}$ change within 18 vertical meters during the summer months (Harrison et al., 1999). Temperatures in the hypolimnion are usually below $10\,^{\circ}\text{C}$, while surface waters in summer can reach $28\,^{\circ}\text{C}$. The thermal stratification in Brownlee Reservoir discourages vertical mixing and contributes to anoxic conditions in the hypolimnion (Harrison et al., 1999). Areas of low dissolved oxygen also occur in the transition zone, although higher dissolved oxygen is typical in the riverine zone.

The duration and strength of thermal stratification is strongly influenced by reservoir inflow and dam operations. Stratification is typically weaker and shorter in duration during high flow years, and in general, dissolved oxygen levels are lowest, and temperatures highest, in years with low flow. In July 1990, a low flow year, at least 28 white sturgeon were killed in and near the transition zone because of low dissolved-oxygen levels (Harrison et al., 1999).

Tributary inflows also exert some control on water quality conditions in Brownlee. The influx of nutrients and organic matter allows high concentrations of phytoplankton to flourish in the transition zone of the reservoir, which contributes to the dissolved oxygen patterns seen in Brownlee (Harrison et al., 1999). Inflowing waters also often have elevated temperatures (Myers et al., 1998).

3. Model

3.1. Modeling fish movement

We used a population level approach to simulate fish movement based on water quality parameters and other factors that influence the spatial location of white sturgeon in Brownlee Reservoir. Our approach is similar to that used by Reyes et al. (1994) and Bertignac et al. (1998), who modeled the movement and distribution of estuarine and oceanic fish in response to environmental gradients. Our model also operates over a discrete grid of cells, and we assume that adult fish move away from cells with poor habitat or high density to areas with better habitat or lower density. Other researchers have modeled fish interactions with water quality at the individual level and aggregated the results to examine population-level dynamics (DeAngelis, 1978; Tyler and Rose, 1994). A general overview of fish movement models can be found in Zabel (1996).

To produce observed responses to habitat conditions, we required an index of habitat quality that combined water quality and other habitat preferences for each location on each day. We defined a water quality index (WQI) to quantify the suitability of dissolved oxygen and temperature conditions, based on our knowledge of lethal and sublethal levels for white sturgeon. We also calculated a second habitat index that incorporated depth and feeding location preferences. The formulation of these indices was similar to that of Reyes et al. (1994) and U.S. Fish and Wildlife Service (1981). We used these two indices to simulate advective fish movement away from areas with low quality towards locations with higher quality. These advective movement preferences were constant and did not change over time. However, the spatial distribution of temperatures and dissolved oxygen levels, changed on a daily basis.

Density-dependent movement was simulated, in addition to advective movement, in areas where water quality was not lethal. This component acted to distribute fish density and simulated exploratory movement by fish into areas with poor water quality. In other environmental models, diffusion methods are often used as the main equations to model animal movements. However, basic diffusion models assume that the environment is constant and homogeneous, and they are therefore relatively insensitive to environmental conditions (Folse et al., 1989; Reyes et al., 1994; Bertignac et al., 1998) unless some bias is incorporated into the diffusion process.

3.2. Model description

Because sturgeons are bottom-dwelling fishes, we only modeled Brownlee Reservoir's bottom perimeter

volume, consisting of the bottom 2 m of the water column throughout the reservoir. We divided this bottom perimeter volume into a spatial grid of 164 cells (Fig. 1). As the reservoir was assumed to be symmetrical, only one side of the reservoir (82 cells) was represented. A resurvey of reservoir bathymetry to account for sedimentation produced a slightly different grid with only 65 cells, which was used in the 1997 CE-QUAL-W2 model runs. Each cell was 3.2 km (2 miles) long, 2 m into the water column, and the depth along the side of the reservoir ranged from 10.0 to 12.2 m (33–40 feet). Simulated white sturgeon could move through this grid, into and out of adjacent cells. The model recalculated the volume of each cell daily to determine the volume of the perimeter, which was used to compare sturgeon density against an upper limit of 5.92×10^{-4} fish per perimeter m^3 (0.73 fish per perimeter acre-ft) (Ken Lepla, personal communication, Idaho Power Co., Boise, ID). The simulated collection of sturgeon was initialized with 165 individuals—an estimated population size in Brownlee Reservoir, which we distributed evenly throughout the reservoir, (Ken Lepla and Jim Chandler, personal communication).

Water quality information used to produce the habitat indices consisted of temperature and dissolved oxygen output from a CE-QUAL-W2 model that was developed for the reservoir (Harrison et al., 1999), and calibrated against monitoring data collected in Brownlee Reservoir. CE-QUAL-W2 integrates hydraulic and water quality components in two dimensions to evaluate dissolved oxygen budgets, nutrient cycling and organic matter processes in reservoirs. The movement model used daily temperature and dissolved oxygen from CE-QUAL-W2 simulations of:

1. Baseline years with low, normal, and high flow (1992, 1995, and 1997, respectively).
2. For 1995 with 30, 50, and 90% reduction in organic matter inputs.
3. For 1995 with an 81% reduction in both organic matter and phosphorus to meet a draft target of 0.07 mg/L total phosphorus TMDL in the Snake River.

We developed two slightly different versions of the model, which differ in the way the habitat index is calculated (see the flow diagram in Fig. 2). The first version was designed largely to examine the effect of water quality on movement. It used the WQI to
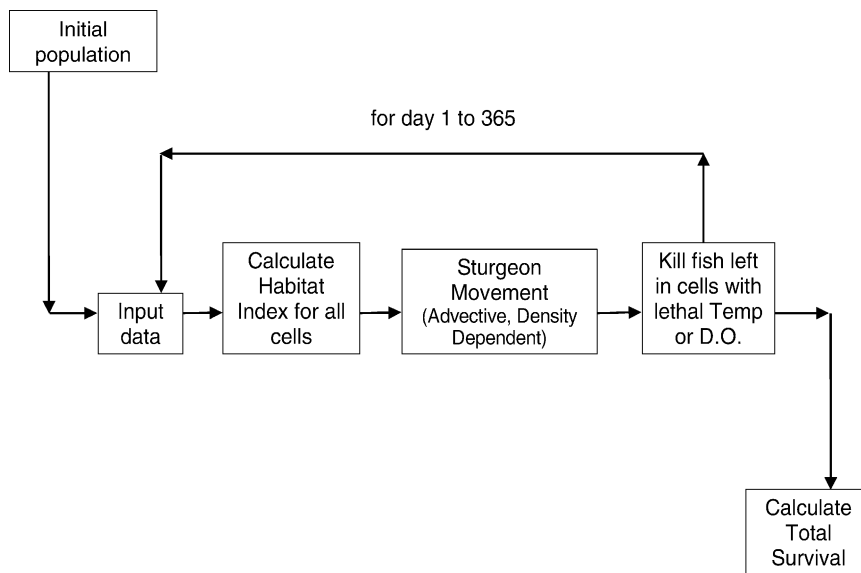

Fig. 2. Model flowchart. Version 1 of the model uses the water quality index to produce advective movement, while version 2 uses the combined habitat index.
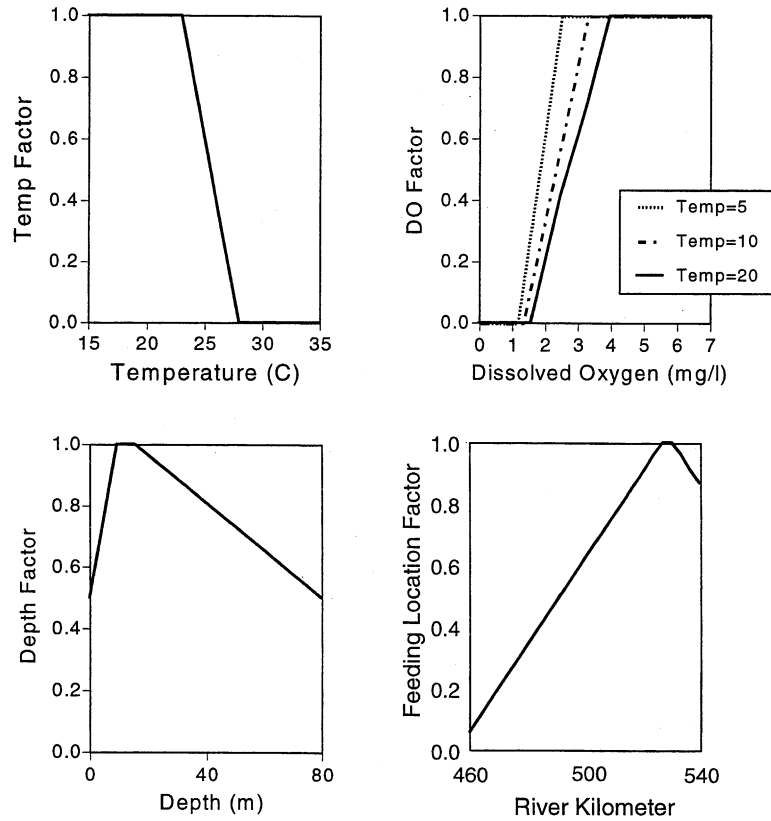
Fig. 3. Temperature, dissolved oxygen, depth and feeding location preference factors used in the calculation of habitat indices.

produce advective movement and allowed for density dependent movement in areas with non-lethal water quality. The second version of the model was designed to account for other habitat preferences of white sturgeon in Brownlee by expanding the habitat index to include depth and feeding location preferences in addition to water quality.

3.2.1. Version 1: water quality only

The model defined lethal and stressful temperature and dissolved oxygen levels (see Section 2.1) and calculated a WQI (0–1) to quantify the suitability of temperature and dissolved oxygen for white sturgeon (Fig. 3) in each cell on each day using CE-QUAL-W2 output. The factor was set to 1 for levels that were ideal. At lethal conditions, the factors were set to 0. For values between lethal and ideal conditions, a proportional value between 0 and 1 was used to represent stressful, sublethal levels:

$$T_F = \begin{cases} 0, T > T_L \\ \dfrac{(T_L - T)}{(T_L - T_S)}, & T_S \leq T \leq T_L \\ 1, T < T_S \end{cases}$$

$$DO_F = \begin{cases} 0, DO < DO_L \\ \dfrac{(DO - DO_L)}{(DO_S - DO_L)}, & DO_L \leq DO \leq DO_S \\ 1, DO > DO_S \end{cases}$$

The stressful temperature $T_S = 23\,°C$, lethal temperature $T_L = 28\,°C$, stressful dissolved oxgyen $DO_S = -0.0015T^2 + 0.115T + 2.28$, and lethal dissolved oxygen $DO_L = -0.0006T^2 + 0.0431T + 0.95$.

We combined the temperature (T_F) and dissolved oxygen factor (DO_F) into one WQI that weights the two factors equally:

$$WQI = (T_F \cdot DO_F)^{1/2}$$

An index of 1 indicated satisfactory water quality conditions for sturgeon, while an index of 0 indicated lethal conditions due to either temperature or dissolved oxygen. An index between 0 and 1 indicated stressful conditions of either temperature or dissolved oxygen.

The advection rate between adjacent cells was the difference between the water quality indices of two adjacent cells. The greater the difference, the more movement occurred. For a grid cell located at depth i and river mile j, the advection rates (K) between cell i, j and adjacent cell $i + p$, $j + q$ with pairs of integers (p,q) drawn from the interval $[-1, 1]$ under the constraint that the distance $|p + q| = 1$ step would be:

$$K_{i,j/i+p,j+q} = WQI_{i,j} - WQI_{i+p,j+q}$$

This advection rate was used to calculate population changes (ΔN) between cells by multiplying the advection rate by the population (P) in the adjacent cell at the previous timestep:

$$\Delta N_{i,j}^A = \begin{cases} K_{i,j/i+p,j+q}P_{i+p,j+q}, & \text{if } K_{i,j/i+p,j+q} > 0 \\ K_{i,j/i+p,j+q}P_{i,j}, & \text{if } K_{i,j/i+p,j+q} < 0 \end{cases}$$

The total population change by advection for a cell would then be:

$$\Delta N_{i,j}^A = \Delta N_{i,j/i+1,j}^A + \Delta N_{i,j/i-1,j}^A + \Delta N_{i,j/i,j+1}^A + \Delta N_{i,j/i,j-1}^A$$

There would be no advective migration between two cells with the same habitat indices, and the relative amount of population change was based on the difference between the habitat indices in adjacent cells. For instance, if a cell with a habitat index of 0 (lethal) was located next to a cell with a habitat index of 1 (ideal), all fish would migrate away from the cell with lethal water quality, unless the density limit was reached.

The second type of movement invoked in this version of the model was density-dependent movement. For each timestep, this movement occurred when the habitat index in two adjacent cells was nonzero. For example, density-dependent population change in one cell from one direction was calculated by:

$$\Delta N_{i,j}^D = -k \cdot \left(\frac{P_{i,j}}{S_{i,j}} - \frac{P_{i+p,j+q}}{S_{i+p,j+q}} \right),$$

where k was a diffusion coefficient and S is cell volume. This simulated density dependent migration and worked to spread populations out spatially when the water quality was non-lethal.

After calculating each component of movement, we determined the total population change in each cell based on the fluxes of sturgeon into and out of the cell. The model includes a check for negative fish populations. If it ever occurs, those "negative" fish are distributed to adjacent cells proportionally based on the WQI. Finally, the population changes were added to the original populations in each cell.

$$N_{t+1} = N_t + \Delta N_{i,j}^A + \Delta N_{i,j}^D$$

After movement in each timestep, sturgeon remaining in areas with a lethal WQI were killed. Simulated sturgeon might be unable to move away from areas with lethal water quality if the density limit in adjacent cells was reached, or if a block to migration existed between suitable areas.

We calculated the total survival of sturgeon for each year by comparing the fish population at the end of the year to the initial population. To examine the effect of behavioral avoidance on survival, the model was also run without allowing any movement by the fish.

3.2.2. Version 2: water quality and other habitat preferences

The second version of this model used an expanded habitat index, incorporating other observed habitat preferences of white sturgeon in Brownlee Reservoir. The first additional habitat factor was depth (D_F) (Fig. 3), where the preference was based on field surveys of white sturgeon habitat use (Ken Lepla and Jim Chandler, personal communication). The feeding factor (F_F) takes into account the biological productivity of the transition zone as a food source for sturgeon. Reservoir transition zones are distinguished by slowing of the water current as the river enters the lacustrine part of the reservoir. This change in water velocity leads to increased sedimentation of organic matter and silt, which together make good substrate

for benthic invertebrates. Bacteria, phytoplankton and zooplankton, eggs and larvae of chironomids, and mollusks are found in these zones. This area of biological productivity generally attracts fish to this zone (Poddubny, 1971). The combined index (CI) takes the form:

$$CI = (T_F \cdot DO_F \cdot D_F \cdot F_F)^{1/4}$$

Migration parameters (K) then become a function of the CI instead of the WQI: As in version 1, we only used the WQI to determine whether fish were killed due to poor water quality. Density-dependent movement was also invoked by this version of the model in areas where the CI was nonzero.

4. Results

4.1. Water quality index

The white sturgeon WQI showed significant temporal and spatial variation in Brownlee Reservoir. Under 1995 baseline water quality conditions (Fig. 4), the WQI was 1 throughout the reservoir from Jan-

uary through April. Areas with poor water quality developed in May and persisted through summer. The average quality in Brownlee did not improve until September. Reducing organic matter inputs by 90% increased the WQI during most of the year (90% R scenario in Fig. 4), as did decreasing total phosphorus and organic matter by 81% in the Snake River to meet TMDL standards (PR scenario in Fig. 4). Decreasing total phosphorus and organic matter also increased the number of days in the spring with good water quality (i.e. an average WQI of 1; Fig. 4).

Risk-free areas (WQI = 1) provided refuge for white sturgeon when water quality conditions in other areas of the reservoir dropped to stressful or lethal levels. The average risk-free perimeter volume was smallest in the low flow year (1992), and larger in normal (1995), and dry (1997) years (Table 1). Low values of minimum risk-free area in 1992 and 1997 (Table 1) were caused by a combination of low dissolved oxygen levels in the hypolimnion and deep transition zone and high temperatures in shallow surface waters. Each of the reductions in nutrient inputs for 1995 increased risk-free sturgeon habitat and decreased lethal sturgeon habitat. Reducing nutrient inputs also
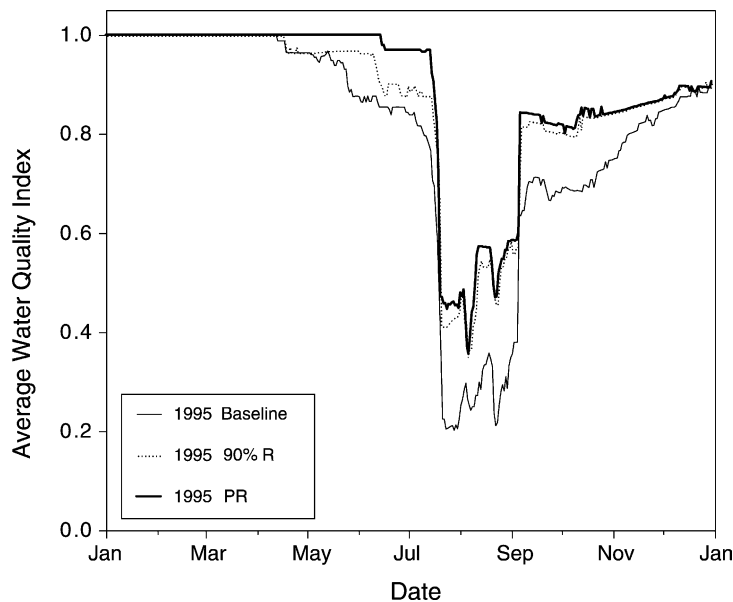

Fig. 4. Average daily water quality index in Brownlee for 1995, the normal hydrologic year. Baseline conditions are shown as well as 90% reduction in organic matter (90% R) and 81% reduction in both phosphorus and organic matter (PR) to simulate a 0.07 mg/total phosphorus TMDL draft target for the Snake River.

Table 1

Average and minimum risk-free perimeter volumes (water quality index = 1) and lethal perimeter volumes (water quality index = 0) for Brownlee Reservoir for 1992, 1995, and 1997

	1992	1995					1997
	Baseline	Baseline	30% R	50% R	90% R	PR	Baseline
Risk-free perimeter volume							
Average	0.73	0.80	0.82	0.84	0.87	0.88	0.81
Minimum	0.02	0.20	0.26	0.34	0.35	0.36	0.004
Date for minimum	19 August	28 July	29 July	8 August	5 August	6 August	13 August
Number of risk-free days (average WQI = 1)	116	103	104	103	107	166	136
Lethal perimeter volume							
Average	0.19	0.10	0.08	0.07	0.05	0.04	0.11
Maximum	0.55	0.30	0.22	0.17	0.14	0.11	0.36
Date for maximum	21 August	05 August	1 October	2 October	4 November	29 October	28 August

For 1995, simulations of 30, 50, and 90% reduction in organic matter input to the reservoir, and 81% reduction in both phosphorus and organic matter (PR) were also run.

delayed the timing of the maximum proportion of lethal perimeter volume from August to October/November.

The spatial distribution of habitat with good water quality showed seasonal shifts. Brownlee began the year with ideal water quality conditions for sturgeon throughout the reservoir (top panel in Fig. 5). Areas of poor sturgeon habitat developed in the deep transition zone and in the hypolimnion of the lacustrine zone in late spring. During the summer months, sturgeon habitat quality deteriorated near the surface as the surface temperature warmed. In some simulations, an area with poor sturgeon habitat developed above the lacustrine hypolimnion as anoxic water from the transition zone was drawn towards the reservoir outflow; this is seen in the July 30 snapshot in Fig. 5. The riverine zone of Brownlee generally had good water quality, with adequate concentrations of dissolved oxygen and moderate temperatures. The riverine zone experienced episodes of high water temperatures during some days in summer. By late fall, much of the

reservoir had returned to a WQI of 1, with some remnant areas of poor WQI in the deep hypolimnion (bottom panel in Fig. 5).

4.2. Version 1: movement and survival due to water quality

When avoidance behavior (i.e. movement) was not allowed, sturgeon mortality occurred in the transition zone and the hypolimnion where the WQI decreased to reflect lethal conditions in summer. Survival was highest in high flow year and lowest in the low flow year (Table 2). Sturgeon survival increased in all scenarios with reduced nutrient inputs when no movement was allowed.

Allowing avoidance behavior improved survival in all scenarios as sturgeon moved to areas of the reservoir with more suitable habitat. This behavior is illustrated graphically in Fig. 6 showing predicted fish distribution on several days in 1995. On January 1, sturgeon were distributed evenly throughout the

Table 2

Simulated sturgeon survival for different years and for reduced nutrient simulations in 1995

	1992	1995					1997
	Baseline	Baseline	30% R	50% R	90% R	PR	Baseline
Survival, no movement	0.45	0.59	0.66	0.80	0.87	0.89	0.69
Survival, movement, version 1	0.94	1.00	1.00	1.00	1.00	1.00	0.91
Survival, movement, version 2	1.00	1.00	1.00	1.00	1.00	1.00	1.00

Results are compared for no movement, and with movement produced by the two versions of the simulation model.
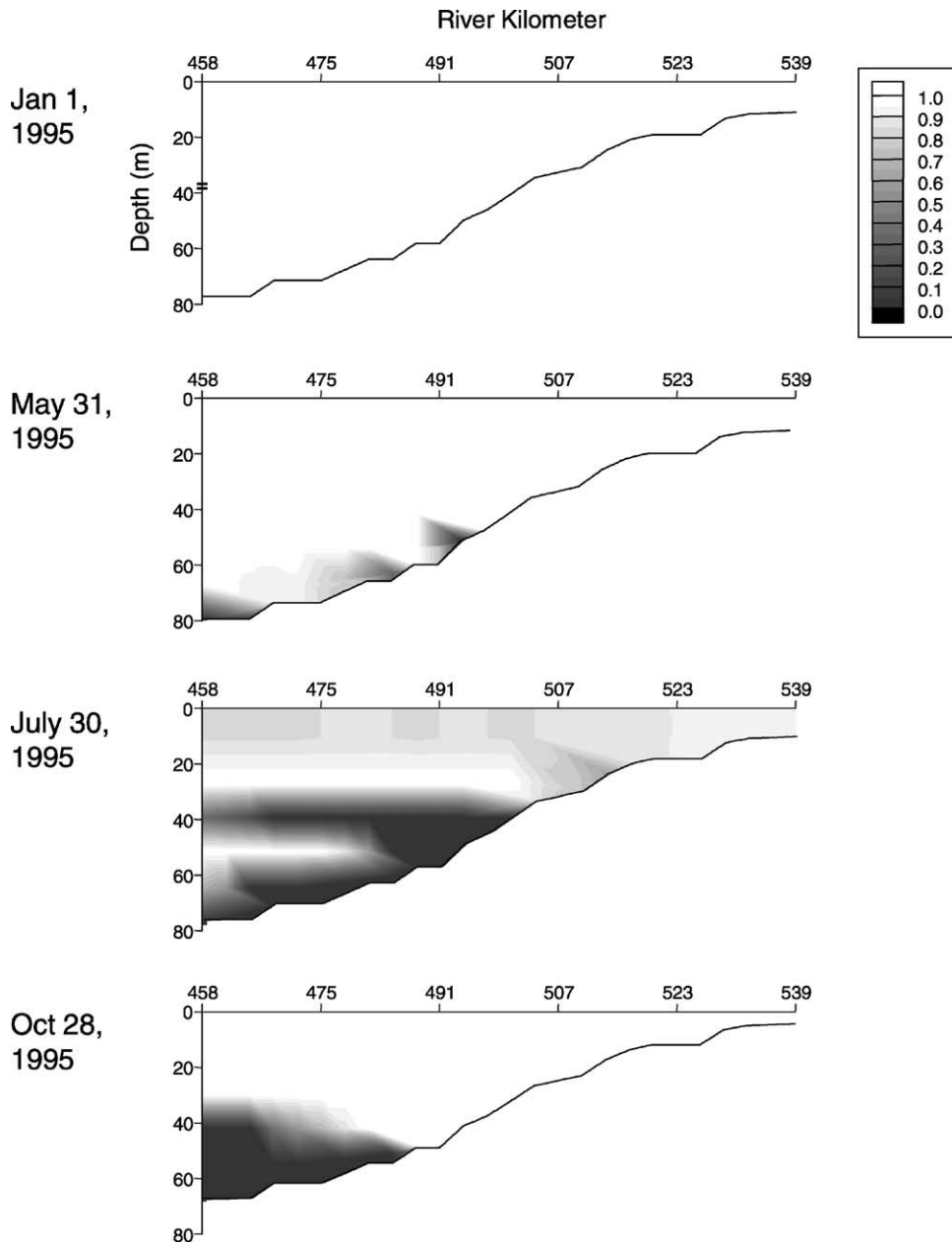
Fig. 5. Temporal changes in water quality index in Brownlee Reservoir in 1995, showing conditions on January 1, May 31, July 30, and October 28. The depth axis illustrates conditions in perimeter cells that line the bottom of the reservoir on one side, where shallow cells are near the shoreline, and deep cells are near the middle of the channel. The lacustrine zone is located from RK 458 to 505, the transition zone from RK 486 to 528 and the riverine zone from RK 518 to 539. An index of 1 indicates ideal conditions for adult white sturgeon and an index of 0 indicates lethal conditions.
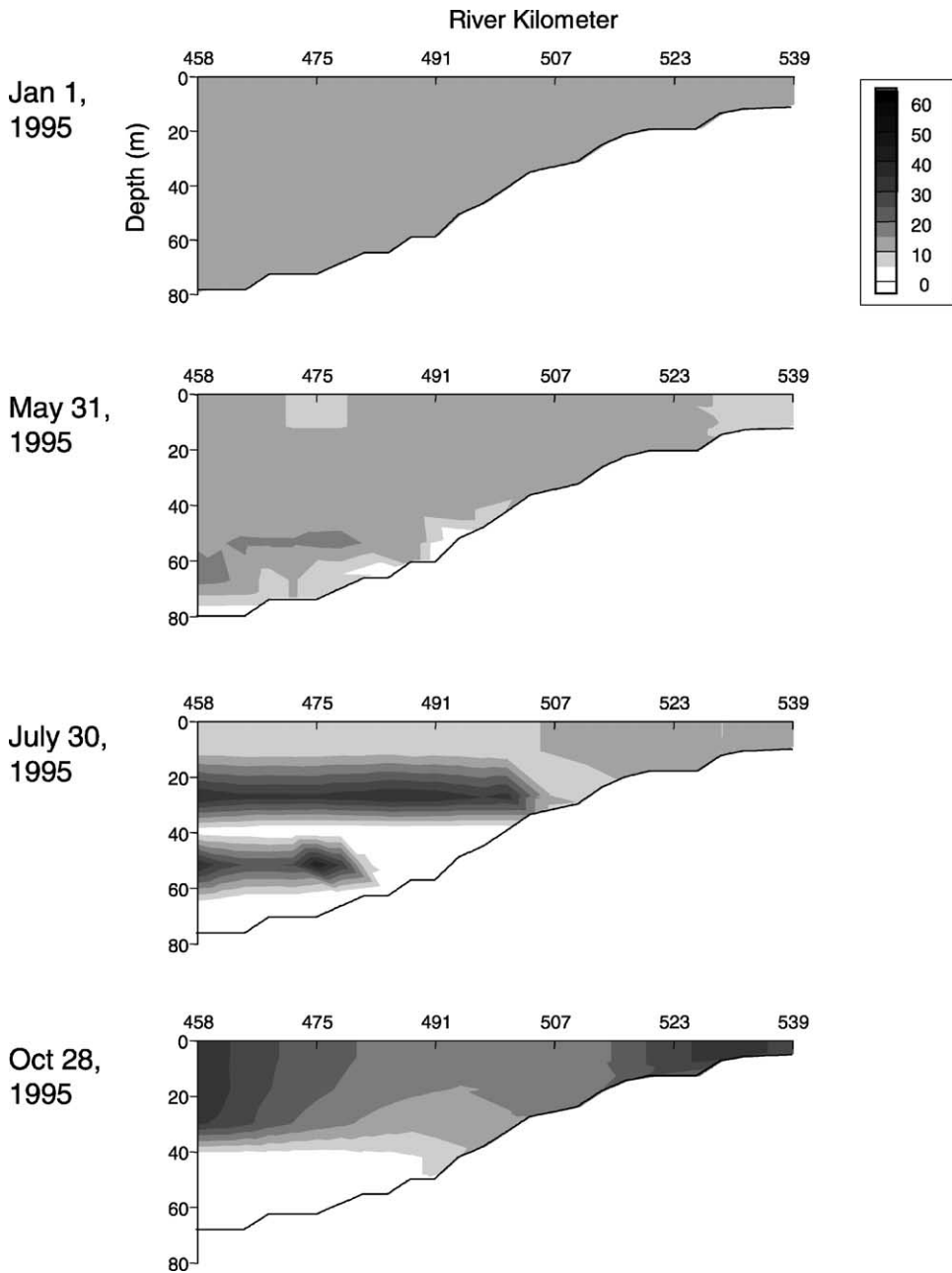
Fig. 6. Predicted spatial distribution of the white sturgeon population in Brownlee Reservoir in 1995, using version 1 of the simulation model for January 1, May 31, July 30, and October 28. Units of sturgeon density are fish per perimeter $m^3 \times 10^6$. The depth axis illustrates conditions in perimeter cells that line the bottom of the reservoir on one side, where shallow cells are near the shoreline and deep cells are near the middle of the channel. The lacustrine zone is located from RK 458 to 505, the transition zone from RK 486 to 528 and the riverine zone from RK 518 to 539.
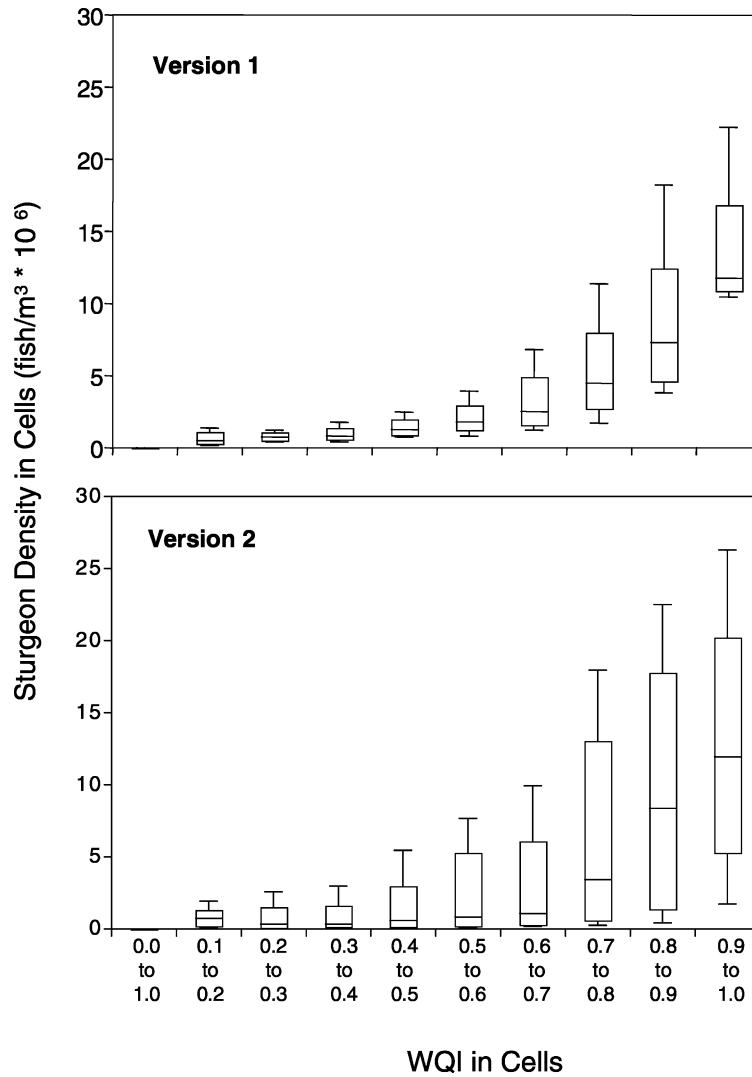
Fig. 7. Comparison of fish density to habitat index in grid cells for 1995 for version 1 and version 2 of the model.

reservoir (top panel in Fig. 6). As areas of low WQI developed in late spring and summer, sturgeon moved away from those areas in the transition zone and hypolimnion and concentrated in other areas of the reservoir (July 30 panel in Fig. 6). In two of the years, 1992 and 1997, some sturgeon became trapped in a high WQI refuge above the hypolimnion and below the outflow. Later in the year, when the WQI in that refuge dropped to lethal values, those sturgeon were killed in the simulation. When the WQI recovered in fall of each year, reflecting good water quality

throughout most of the reservoir, sturgeon moved in response to density dependent mechanisms through the areas with a WQI of 1.

Average sturgeon densities were higher in cells with higher quality for both versions of the model (top panel, Fig. 7). No simulated sturgeon stayed in cells with a WQI of 0—if they failed to move to better areas, they were killed by the model. The variance in sturgeon density was higher in cells with high quality, showing the influence of other factors such as density on simulated movements.
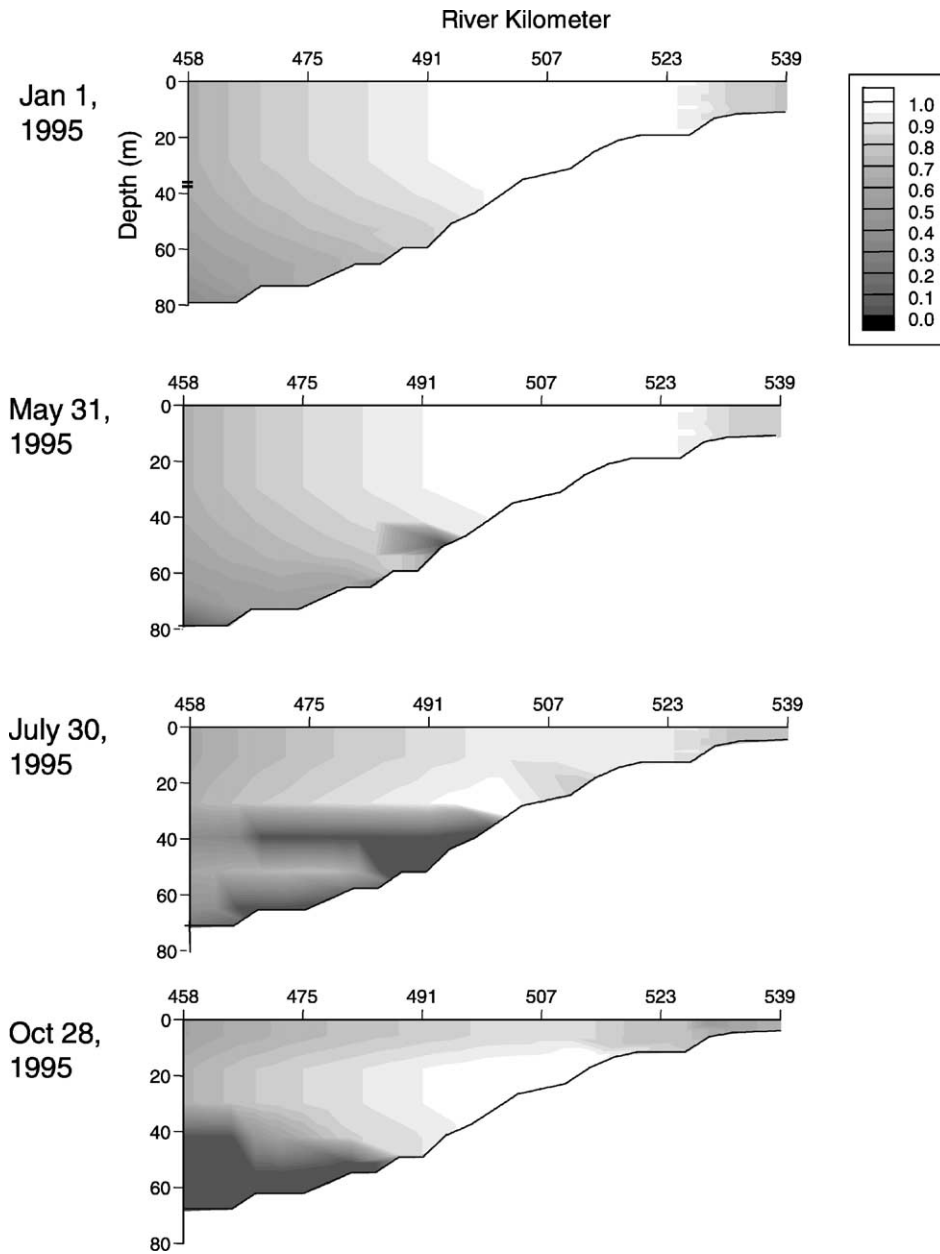
Fig. 8. Temporal changes in the augmented habitat index in Brownlee Reservoir in 1995, showing conditions on January 1, May 31, July 30, and October 28. An index of 1 indicates ideal conditions for adult white sturgeon and an index of 0 indicates lethal conditions. The depth axis illustrates conditions in perimeter cells that line the bottom of the reservoir on one side, where shallow cells are near the shoreline and deep cells are near the middle of the channel. The lacustrine zone is located from RK 458 to 505, the transition zone from RK 486 to 528 and the riverine zone from RK 518 to 539.

4.3. Habitat index including water quality and other habitat preferences

The spatial distribution of habitat with good water quality and preferred depth and position for foraging shifted from one season to the next. In contrast to the pattern of water quality alone (Fig. 5), quality was not uniform in Brownlee Reservoir at the beginning of the year. Rather, the index was highest in the transition zone because of feeding preferences for this area (white area in Fig. 8). Areas of poor sturgeon habitat began to develop in the deep transition zone and in the hypolimnion of the lacustrine zone in late spring, and these increased in area through summer and fall. During summer and fall, quality as measured by this index was best for sturgeon at intermediate depths in the transition zone (white patch in the bottom panel of Fig. 8). However, worsening conditions in the riverine zone may prevent sturgeon from moving upstream.

4.4. Version 2: movement and survival due to water quality and other habitat preferences

Simulated sturgeon were evenly distributed through the reservoir at the start of the year (top panel in Fig. 9). By late spring, sturgeon had moved away from the dam and the deep hypolimnion. This movement continued through the summer, and by late fall, the sturgeon were concentrated in the transition and riverine zones. Although they were initially placed everywhere, simulated sturgeon moved away from, and did not occupy, reservoir areas nearest the dam in any season (Fig. 9).

Sturgeon survival was 100% in all years (Table 2). Because sturgeon moved towards the transition zone early in the year, none were trapped in areas of poor water quality and killed, as they were in version 1 simulations.

As in version 1, no sturgeon were found in locations with a WQI of 0 (Fig. 7), and most sturgeon were found in cells with a WQI above 0.8. Average sturgeon density increased with increasing water quality. Because factors other than water quality determined sturgeon location in this version of the model, low densities did occur in some cells with a WQI of 1. This explains the variance in simulated sturgeon density predicted in cells with high water quality (Fig. 7).

5. Discussion

Simulating avoidance behavior as an advective component of white sturgeon movement generally increased survival. One interesting finding of this study was that average water quality conditions throughout the reservoir did not necessarily correspond to model predictions of survival. This is because the spatial configuration and juxtaposition of high and low quality habitat was important. Model predicted survival depended on whether sturgeon were located between areas of poor water quality that converged as the summer progressed. Such spatial water quality "traps" consisted of localized areas of high water quality that were surrounded on all sides by low water quality. Neil (1979) also found this trapping effect in his temperature-induced movement model. If the localized area of high water quality in the trap eventually reached lethal conditions, the fish had no escape and were killed by the model. This trapping occurred to some extent because the model assumed that fish were only able to choose between adjacent cells for each timestep. This is similar to the model of Bertignac et al. (1998), and they speculate that survival results would be different if fish were able to sample larger areas and cross regions with poor habitat in order to reach areas of refuge.

Interestingly, water quality traps were not predicted to occur in the transition zone, where the 1990 sturgeon kill in Brownlee was located. One possible reason for this is that the spatial and temporal patterns of water quality in the years used in this model simulation differed from those in the year when mortality was observed. It could also be an issue of scale, as this model works to predict white sturgeon distribution at fairly large spatial scales. Biogeochemical processes could produce water quality traps at scales finer than those addressed by this model.

Reducing nutrient inflows into Brownlee Reservoir increased the proportion of reservoir perimeter volume with ideal water quality habitat conditions for white sturgeon, and also reduced the volume with lethal water quality conditions. Because the model did not predict any sturgeon mortality in the baseline case, we did not observe a change in survival associated with reducing nutrient inflows. However, if we considered years with worse water quality conditions (e.g. 1991, when the sturgeon kill occurred), it is likely that the
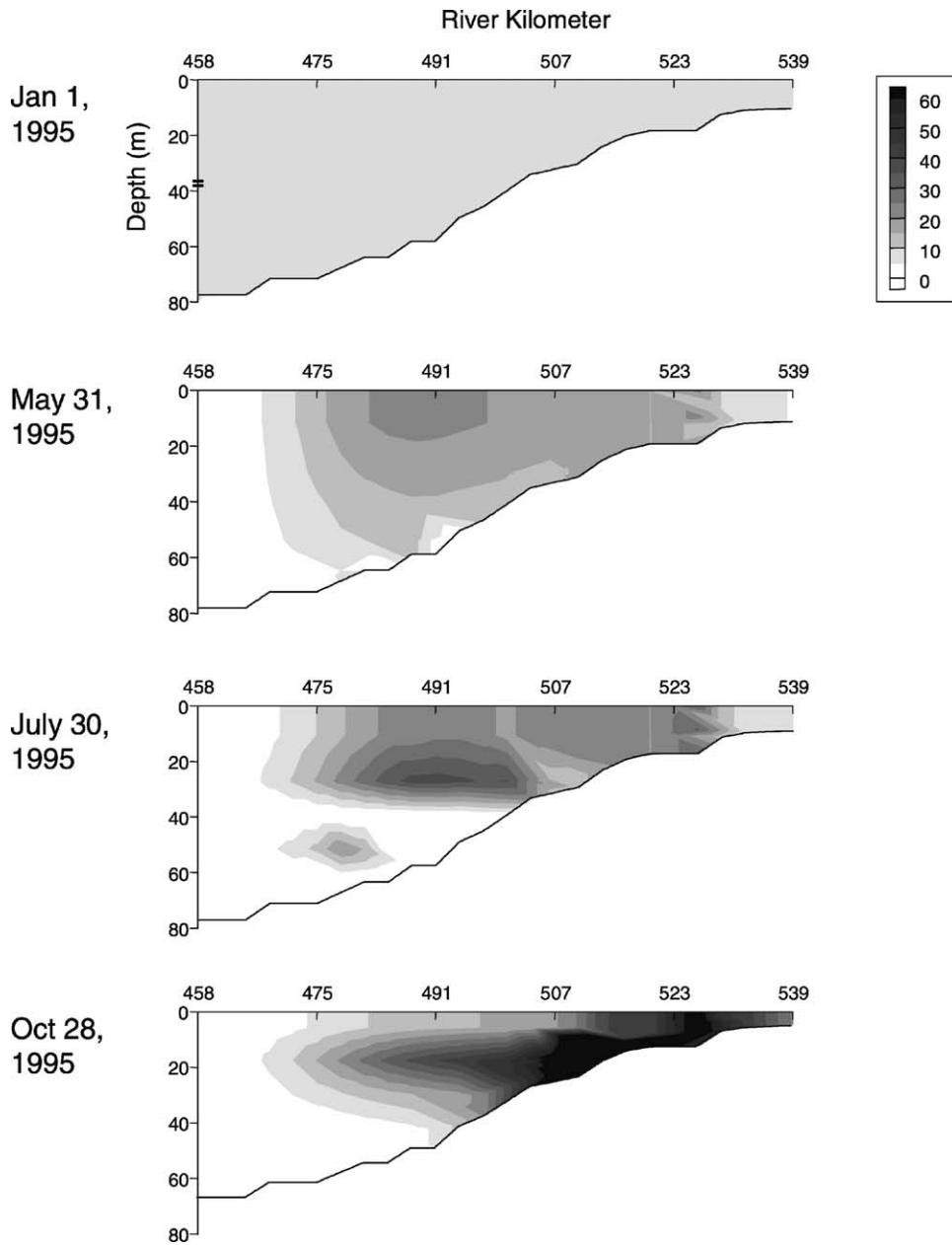
Fig. 9. Predicted white sturgeon population in Brownlee Reservoir in 1995, using version 2 of the simulation model and showing conditions January 1, May 31, July 30, and October 28. Units of sturgeon density are fish per perimeter $m^3 \times 10^6$. The depth axis illustrates conditions in perimeter cells that line the bottom of the reservoir on one side, where shallow cells are near the shoreline and deep cells are near the middle of the channel. The lacustrine zone is located from RK 458 to 505, the transition zone from RK 486 to 528 and the riverine zone from RK 518 to 539.

model would predict an increase in sturgeon survival in response to reduced nutrient inputs.

Our comparison of wet, normal, and dry hydrologic years was not definitive. The general expectation is that dry years would have the lowest habitat index and correspondingly low sturgeon survival, and the high flow years would have overall higher habitat index and high survival rates. Our model predictions supported this trend when behavioral avoidance was not allowed. However, when movement was allowed in version 1, we found that the wettest year (1997) had the lowest predicted survival. That year had a very low minimum risk-free volume due to a combination of summer low dissolved oxygen conditions and high temperatures in the shallow surface regions.

There are several areas for future expansion and development for this sturgeon movement model. For instance, we assumed that the stressful and lethal levels of temperature and dissolved oxygen that triggered movement did not change through the year. There is some speculation that the behavioral avoidance response to dissolved oxygen conditions may vary temporally (Davis, 1975). A behavioral response may be triggered at higher oxygen levels when the fish are active and metabolic requirements are large, compared to when the fish are resting and oxygen requirements are lower. Whitmore et al. (1960) found that chinook salmon avoided dissolved oxygen levels between 1.5 and 4.5 mg/l in summer, but did not avoid 4.5 mg/l in autumn.

In addition, bioenergetic considerations could be an important next step in model development, as the current model does not consider the effects of avoidance behavior or water quality on sturgeon growth and fecundity. The US EPA (1986) has suggested that avoidance behavior could affect fish almost as seriously as direct mortality if the supply of space or food was limited. Crowding of fish in limited areas with ideal water quality conditions can lead to the spread of disease and the decline of the local food supply (Coutant, 1986).

Results from model calculations show that even with avoidance movement, a number of fish were predicted to spend time in areas with suboptimal conditions (Fig. 7) and it would be useful to consider the effect of chronic sublethal conditions. Cech et al. (1984) have found that areas of hypoxia reduced the growth of juvenile white sturgeon at all temperature levels. Crocker and Cech (1997) found that juvenile

white sturgeon can reduce their dissolved oxygen consumption during hypoxic events, which is achieved partly by reduced activity. However, reduced activity over long periods would increase the risk of starvation and reduce fecundity. Linking the movement model to a spatially explicit bioenergetic model of sturgeon growth such as those described by Brandt et al. (1992), Brandt and Kirsch (1993), and Mason et al. (1995) would allow for all of these considerations. Linking this movement model to models of sturgeon bioenergetics and population dynamics will provide a useful management tool that can be used to increase the survival of sturgeon in impounded regions of the Snake River.

Acknowledgements

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