ARTICLE

Consequences of seasonal variation in reservoir water level for predatory fishes: linking visual foraging and prey densities

Stephen L. Klobucar and Phaedra Budy

Abstract: In reservoirs, seasonal drawdown can alter the physical environment and may influence predatory fish performance. We investigated the performance of lake trout (*Salvelinus namaycush*) in a western reservoir by coupling field measurements with visual foraging and bioenergetic models at four distinct states (early summer, mid-summer, late summer, and fall). The models suggested that lake trout prey, juvenile kokanee (*Oncorhynchus nerka*), are limited seasonally by suitable temperature and dissolved oxygen. Accordingly, prey densities were greatest in late summer when reservoir volume was lowest and fish were concentrated by stratification. Prey encounter rates (up to 68 fish·day^{-1}) and predator consumption are also predicted to be greatest during late summer. However, our models suggested that turbidity negatively correlates with prey detection and consumption across reservoir states. Under the most turbid conditions, lake trout did not meet physiological demands; however, during less turbid periods, predator consumption reached maximum bioenergetic efficiency. Overall, our findings demonstrate that rapid reservoir fluctuations and associated abiotic conditions can influence predator–prey interactions, and our models describe the potential impacts of water level fluctuation on valuable sport fishes.

Résumé : Dans les réservoirs, l'abaissement saisonnier du niveau d'eau peut modifier le milieu physique et influencer la performance des poissons prédateurs. Nous avons étudié la performance des truites grises (*Salvelinus namaycush*) dans un réservoir de l'Ouest en combinant des mesures de terrain à des modèles d'approvisionnement et de bioénergétique pour quatre états distincts du réservoir (début de l'été, milieu de l'été, fin de l'été et automne). Les modèles donnent à penser que l'abondance saisonnière des proies des truites, les saumons rouges (*Oncorhynchus nerka*) juvéniles, est limitée par la température et l'oxygène dissous. Ainsi, les densités de proies étaient les plus grandes à la fin de l'été, quand le volume du réservoir était à son plus faible et les poissons étaient concentrés par la stratification. Il est également prédit que la fréquence des rencontres de proie (jusqu'à 68 poissons·jour^{-1}) et la consommation des prédateurs sont plus élevées à la fin de l'été. Cependant, nos modèles suggèrent une corrélation négative entre la turbidité, d'une part, et la détection et la consommation de proies pour tous les états du réservoir. Dans les conditions les plus turbides, les truites grises ne répondaient pas à leur demande physiologique; cependant, durant les périodes de plus faible turbidité, la consommation des prédateurs atteignait l'efficacité bioénergétique maximum. Globalement, nos résultats démontrent que des fluctuations rapides des réservoirs et les conditions abiotiques associées peuvent influencer les interactions prédateurs–proies et nos modèles décrivent les impacts potentiels des fluctuations du niveau de l'eau sur des poissons d'intérêt pour la pêche sportive. [Traduit par la Rédaction].

Introduction

Reservoir water quality and availability can change temporally and spatially as a result of climate-driven variation in physical, chemical, and biological conditions (Williamson et al. 2009; Carpenter et al. 2011*b*). Ecosystem-level changes may be natural, anthropogenic, or both (e.g., landscape position, exploitation, water use by humans, nutrient inputs; Poff et al. 1997; Landres et al. 1999; Meyer et al. 1999). Recent research on lakes and reservoirs has focused on predicting abrupt, long-lasting changes in ecosystem states (e.g., Biggs et al. 2009; Carpenter et al. 2011*a*), whereas short-term changes such as algal blooms and fish migrations are more predictable by season (Carlsson and Caron 2001; MacAvoy et al. 2001). However, humans often exploit or interrupt these seasonal patterns with little understanding of the implications for aquatic biota and ecosystem processes (Walters et al. 2000; Hobbs et al. 2006).

Water availability is altered via natural variation (e.g., precipitation, drought) and human use (e.g., irrigation diversions, reservoir drawdown), and associated changes in water volume or elevation can have direct and indirect effects on fishes (Lytle and Poff 2004; Xenopoulos et al. 2005). The effects of water-level fluctuations in the littoral zone of standing waters are easily recognized and increasingly understood and managed (Sass et al. 2012; Gaeta et al. 2014), but important physical and biological interactions in the pelagic zones of dynamic lakes and reservoirs are less understood (Schindler and Scheuerell 2002). Although predator–prey interactions have been quantified under a variety of physical and biological conditions (Adams et al. 1982; Horppila et al. 2004), and shifts in pelagic food webs can even induce changes in the physical environment (e.g., trophic cascades; see Carpenter and Kitchell 1993), predicting predator–prey interactions and the performance of predators when subjected to a pelagic zone influence by anthropogenic-driven variability in water quality and volume can be difficult.

In the western United States, many reservoirs are subjected to large-scale and dynamic seasonal fluctuations as a result of water availability and designated use (Cayan et al. 1999; Barnett et al. 2005). Water availability can be predicted by forecasting regional

S.L. Klobucar. Department of Watershed Sciences and The Ecology Center, Utah State University, Logan, UT 84322, USA.
P. Budy. U.S. Geological Survey, Utah Cooperative Fish and Wildlife Research Unit, Logan, UT 84322, USA; Department of Watershed Sciences and The Ecology Center, Utah State University, Logan, UT 84322, USA.

Corresponding author: S.L. Klobucar (e-mail: stephen.klobucar@gmail.com).

snowpack and precipitation; however, availability is still highly dynamic across years, creating extreme fluctuations in reservoir storage (Garen 1993). Consequently, biota in western reservoirs are often subjected to stressful temperature and dissolved oxygen conditions, especially during summer months when temperatures are warmest and water demand is greatest (Moss 1985; Feder and Hofmann 1999). Despite these dynamic conditions, many western reservoirs support extremely valuable salmonid fisheries that are often maintained via expensive stocking programs (Johnson et al. 1995). Seasonal fluctuations of these reservoirs may affect food web dynamics and sport fish condition (Johnson and Martinez 2012).

It is likely that the foraging success of fishes in fluctuating reservoir ecosystems will be limited by water temperature, turbidity, and prey density, which strongly vary seasonally with reservoir elevation. Salmonid visual foraging volume is often greatest during high light intensity and lowest turbidity, and visual foraging efficiency is greatest when prey densities are highest and reaction distance is not limited (Beauchamp et al. 1999). However, these limiting factors can change daily and across seasons based on water management practices. Providing a better understanding of predator–prey interactions in dynamic reservoirs is a challenge, but the ability to quantify and predict these interactions would allow for better management of fisheries and water resources alike (Renwick 2001; Cooke et al. 2005).

In this study, we tested for lake trout foraging success and growth potential in the pelagic zone of a reservoir in northeastern Utah exposed to extreme fluctuations in volume seasonally. We measured abiotic conditions in a low-water (typical) year and a high-water year. We then used these conditions coupled with field-based prey estimates in visual foraging and bioenergetics models to test the following hypothesis: growth potential of sport fishes is greatest when reservoir volume is stable. Alternatively, fluctuations in reservoir volume and, accordingly, prey densities could produce seasonal periods of high growth potential.

Methods

Study area

Impoundments of the Uintah and Ouray Reservation in northeastern Utah experience a wide range of seasonal water levels based on location in the landscape and designated use (e.g., irrigation, recreation). We monitored physical and biological factors in Twin Pots Reservoir during a typical water year (2010) in which reservoir levels fluctuated seasonally (Fig. 1; Table 1). For comparison, we also measured fall reservoir conditions in a year when water levels remained relatively stable throughout the summer (2011; e.g., 2011 mid-summer and late summer conditions similar to 2010 mid-summer conditions). Twin Pots Reservoir is a mid-elevation (2325 m), cool water, dimictic reservoir that usually stratifies from late June to late September. Water use is regulated by the Moon Lake Water Users Association as part of the Lake Fork canal system, while the fishery is managed by the Ute Tribe Fish and Wildlife Department. In a typical water year, Twin Pots Reservoir starts at maximum pool (capacity = 5.11×10^6 m^3), the water is clearest in late spring, and water levels decline throughout the summer, reaching minimum levels (approximate capacity = 1.27×10^6 m^3) just prior to the end of the water year on 1 October. The reservoir rapidly fills from an upstream canal system during the fall (October–November) to minimize winter kill of sport fish and still allow for storage of spring snowmelt (Fig. 2). This refill often initiates fall turnover; however, the rapid refill also creates extremely turbid water as organic sediments are resuspended. To track seasonal fluctuations in reservoir volume, we developed a bathymetric map of the reservoir at full pool using a survey GPS (shoreline) combined with transects from a boat-mounted depth sounder GPS (open water; e.g., Odhiambo and Boss 2004; Heyman et al. 2007). We then calculated reservoir volume using ArcGIS 10.1 (ESRI 2012) at distinct water levels across the year.

Fig. 1. Temperature (°C; solid line) and dissolved oxygen (mg·L^{-1}; dashed line) profiles measured in the field during each reservoir state (early summer = June, mid-summer = July, late summer = August, fall = October) in Twin Pots Reservoir, Utah, during 2010. Fall conditions of a high-water year (bottom panel) are from October 2011. Dissolved oxygen probe malfunctioned during early summer data collection and no data are available.
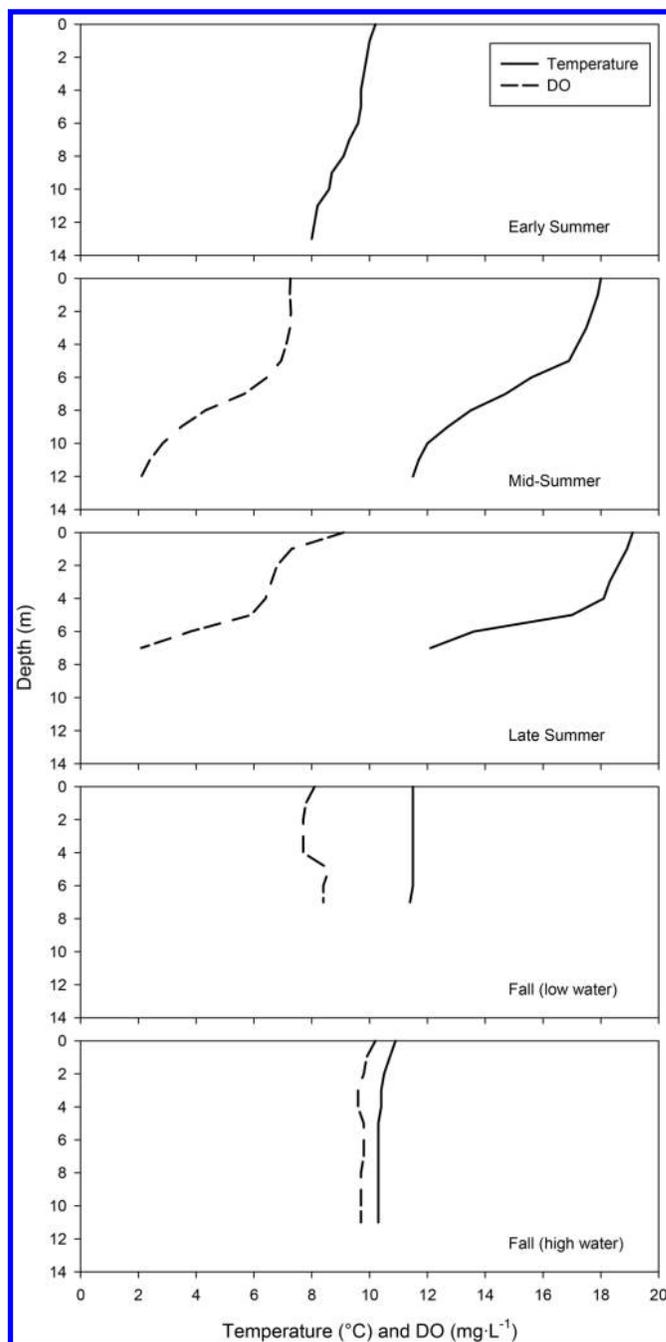

To examine potential physiological constraints for cold water fishes in Twin Pots Reservoir, we measured limnological factors during the 2010 and 2011 growing seasons (May–October). To minimize diel variability, we completed measurements between 1000 and 1400 h for monthly (2010) and biweekly (2011) sampling at the deepest point in the reservoir. We measured temperature (°C) and dissolved oxygen (mg·L^{-1}) at 1 m intervals throughout the water column using a temperature – dissolved oxygen probe. In addition, we deployed remote temperature loggers set to hourly recoding

Table 1. Physical conditions and water quality metrics of Twin Pots Reservoir, Utah, for four seasonal reservoir states in a typical year (2010).

	Early summer	Mid-summer	Late summer	Fall (low water)	Fall (high water)
Maximum depth (m)	13.0	12.0	7.0	8.0	11.0
Reservoir volume (m³ × 10⁶)	5.11	4.31	1.27	1.74	3.57
Utilized volume (m³ × 10⁶)	3.42	1.42	0.83	1.68	3.57
Surface T (°C)	10.2	18.0	19.1	11.5	10.9
DO (mg·L⁻¹)	n/a	2.11–7.26	2.10–9.10	7.70–8.60	9.60–10.20
Surface turbidity (NTU)	0.45	1.32	1.60	5.04	1.45
k	−0.47	−0.62	−0.59	−1.14	−0.55

Note: Fall (high water) measurements are made in October 2011 and represent an alternative state of fall during years when water is readily available. T, temperature; DO, dissolved oxygen; k, light extinction coefficient. Utilized volume is the amount of total reservoir volume that is available for lake trout and kokanee based on physiological constraints (T <17 °C, DO >3.0 mg·L⁻¹). DO probe malfunctioned during early summer sampling, but this event was prior to stratification so DO was not limiting.

Fig. 2. Bathymetric maps and schematic of Twin Pots Reservoir fluctuation in a typical low-water year. The left map is Twin Pots Reservoir at full pool; the right map is Twin Pots Reservoir in the late summer after reservoir drawdown. The polygons are representative of the water level and volume at this time, and the coloration in the fall represents turbidity caused by reservoir refill. Stars on the bathymetric maps indicate limnological sample sites.
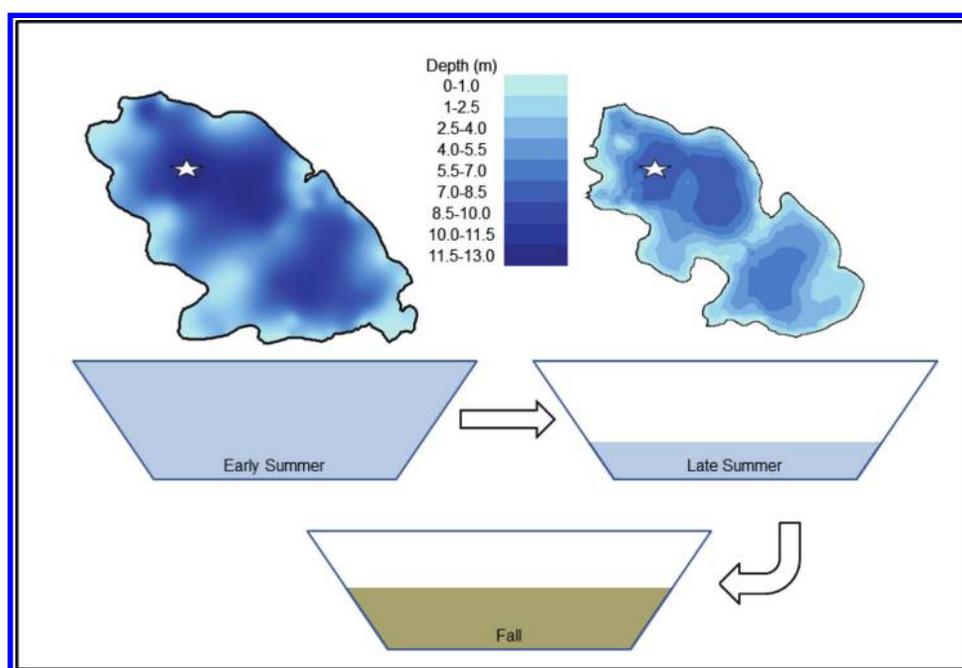
intervals at 1, 3, and 5 m below the surface and 1 m above the bottom in the deepest part of the reservoir from May to October each year. We measured surface turbidity (NTU) using a nephelometer.

The fish community of Twin Pots Reservoir contains a number of cold-water species (e.g., lake trout (*Salvelinus namaycush*) and kokanee salmon (*Oncorhynchus nerka*)) originating from historic stocking, recruitment from prior stocking, and illegal introductions, and is supplemented with annual stocking of rainbow trout (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*). Many of these other populations of fishes are naturally reproducing; thus, young-of-year and juveniles are available as prey for the largest predators. To establish baseline fish data and populate models, we sampled fish primarily via monofilament gill nets set perpendicular to shore (see Lester et al. 2009). Gill net sampling corresponded with limnology sampling events during the 2010 (monthly) and 2011 (biweekly) growing season (May–October). We set four nets on each sampling date, one within each quadrant of the reservoir. Benthic gill nets consisted of eight panels (3.1 m long × 1.8 m deep), each of different bar-mesh size (38, 57, 25, 44, 19, 64, 32, and 51 mm), and we randomly set the nearshore end of the net (38 or 51 mm). The nearshore end was set in water at a depth

of <2.0 m, and the offshore end was set 8.0–12.0 m deep, depending on location. As Twin Pots Reservoir is relatively shallow (<14.0 m), these net sets sampled the complete depth range of target species. To corroborate the hydroacoustics survey, we used vertical gill nets set immediately after the survey in addition to the nets set in each quadrant of the reservoir. Vertical nets consisted of two benthic nets stitched together and set in the deep areas of each basin in Twin Pots Reservoir. We modified these nets such that the total height of the vertical set approximately covered the entire water column (12.0–14.0 m), with each mesh panel of similar length and height (3.6 m wide × 1.5 m deep). We supplemented our fish catch with monthly angling and minnow trapping, May–October 2011. We identified, weighed (mass to nearest 1.0 g), and measured (total length; nearest 1 mm) all fish and released all live fish after tagging with a unique T-bar style anchor tag.

Prey density

We estimated the density of juvenile kokanee (number of fish·m⁻³) from a hydroacoustic survey completed during a new moon (25–26 July 2011), when prey fishes are most likely to be up in the water column and detected by the echo sounder. We defined prey fish as hydroacoustic targets calculated to be 50–150 mm in length. At

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the time of survey, maximum depth was 12 m, but hypolimnetic dissolved oxygen (<3 mg·L^{-1}) constrained fish to the top 7 m. We completed 10 nighttime transects on Twin Pots Reservoir over distances from 295 to 613 m with mean depths ranging from 6.9 to 10.5 m, and we evenly spaced the transects in the pelagic zone to cover a representative area of the reservoir. We completed surveys using a scientific echo sounder (model DE6000; Biosonics, Inc., Seattle, Washington) with a 420 kHz dual-beam transducer (6 × 15°), and the transducer was towed on a fin at a depth of 1 m while using Visual Acquisition processing software (Biosonics, Inc., Seattle, Washington) to record data. We received data at a rate of two pings per second traveling at a boat speed of 1–2 m·s^{-1} (2–5 km·h^{-1}). Pulse width of the signal was 0.4 ms. We processed acoustic targets and density data using Biosonics Visual Analyzer software and only selected echoes that met the single-target shape criteria used by the analysis software to calculate target strengths and densities. We verified targets via pelagic set gill nets. We treated transects as replicates in the analysis to produce mean fish per cubic metre with 1 standard error and expanded density of prey fish (fish·m^{-3}) into lake-wide abundance using reservoir volume.

As we did not have seasonal and diel acoustic data available, we estimated expected vertical distributions of prey fish from similar studies that accounted for seasonal temperature and dissolved oxygen limitations (e.g., Berge 2009; Hansen et al. 2013a), as well as diel distribution and schooling (e.g., Beauchamp et al. 1997). To account for diel distribution and schooling, we reduced daytime prey abundances to 10% of night estimates and crepuscular prey abundances to 33% of night estimates. When the reservoir was not stratified with suitable temperature and dissolved oxygen (>3 mg·L^{-1}) conditions, we assumed prey fish to be (i) normally distributed in mid-water during early summer and (ii) evenly distributed throughout the water column as schools for day hours and as individuals for night hours and normally distributed during dusk as schools begin to disperse, during the fall period. When the reservoir was stratified (mid- and late summer), we assumed that prey fish behaviorally thermoregulate and that their distributions would be skewed towards the thermocline as schools or individuals dependent on diel period. For example, the optimal temperature for juvenile kokanee is 15 °C (Brett 1971); thus, we would distribute the juvenile kokanee with the mode at the depth nearest 15 °C and dissolved oxygen greater than 3 mg·L^{-1}.

Visual foraging

As a metric of prey fish availability, we modeled prey encounter rates (ER$_{z,t}$, prey·h^{-1} at depth z and time t; see Beauchamp et al. 1999) as

$$\text{ER}_{z,t} = \text{SV}_{z,t}\text{PD}_{z,t}$$

where SV is predator search volume at depth z and time t and PD is prey fish (juvenile kokanee) density at depth z and time t. For this study, we modeled piscivorous lake trout (400 mm) at day, night, and crepuscular diel periods during typical early summer (June), mid-summer (August), late summer (September), and fall (October) time. We defined crepuscular as the 1.5 h period encompassing sunrise and sunset. We weighted hourly encounter rates by estimated temporal prey distributions and scaled to daily encounter rates based on day length for each time.

Search volume varied with predator swimming speed SS$_t$ (cm·s^{-1}; mean SS$_{\text{Day}}$ = 29.5 cm·s^{-1}, SS$_{\text{Crepuscular}}$ = 23.5 cm·s^{-1}, SS$_{\text{Night}}$ = 4.0 cm·s^{-1}; see Henderson and Northcote 1985) as

$$\text{SV}_{z,t} = \pi\text{RD}_{z,t}^2\text{SS}_t$$

where RD$_{z,t}$ (cm) is predator reaction distance to prey as a function of light intensity (lx) and prey size given water turbidity (NTU). We calculated light-dependent reaction distances as (but see Beauchamp et al. 1999 and references within)

$$\text{RD} = 25.49I_{z,t}^{0.4747}\cdot f(\text{NTU}) \text{ for } I_{z,t} \leq 17.8 \text{ lx and}$$
$$\text{RD} = \text{RD}_{\text{max}} = 101.2\cdot f(\text{NTU}) \text{ for } I_{z,t} > 17.8 \text{ lx}$$

where reaction distance reaches a maximum of approximately 101.2 cm for light intensity greater than 17.8 lx ($I_{z,t}$; Henderson and Northcote 1985), and light intensity is derived from

$$I_{z,t} = I_{0,t}e^{zk}$$

where k is the calculated light extinction coefficient, and the turbidity multiplier ($f(\text{NTU})$; Hansen et al. 2013b) is derived from

$$f(\text{NTU}) = P(\text{RD}_{\text{max}}) = 1.0 \text{ for } \leq 1.65 \text{ NTU}$$
$$f(\text{NTU}) = P(\text{RD}_{\text{max}}) = 1.49e^{(-0.240\cdot\text{NTU})} \text{ for } > 1.65 \text{ NTU}$$

where NTU is field measured turbidity (see Table 1 for seasonal measurements of k and NTU values). We measured daytime light intensity (PAR) at 1 m intervals using a LI-COR radiometer (LI-COR, Inc., Lincoln, Nebraska) equipped with deck and sea sensors and converted to lux based on a conversion factor of 54 (Thimijan and Heins 1982). We used crepuscular (50 lx) and night (0.005 lx) surface light intensities as defined by a previous study (Hansen et al. 2013a).

Predator consumption and growth potential

To assess the foraging efficiency of predators, we estimated predator growth potential (g·day^{-1}) and bioenergetic efficiency (proportion of maximum consumption, BioEff; Budy et al. 2013) using the Wisconsin Fish Bioenergetics model (Hanson et al. 1997). We designated the modeled prey fish at the smallest size class distinguished using hydroacoustics (50–150 mm) and used 50 mm prey with a mass of 3.07 g during bioenergetic simulations. The mass of prey fish was based on a length–mass regression of juvenile kokanee (see Luecke et al. 1999), which are abundant in Twin Pots Reservoir. Predator consumption was fit to bioenergetics from a light-dependent capture probability given estimated prey encounter rates as

$$C_{z,t} = \text{ER}_{z,t}P_c(I_{z,t})$$

where consumption $C_{z,t}$ (g·day^{-1}) is the product of the probability of capture success $P_c(I_{z,t})$ and encounter rate (Mazur and Beauchamp 2003). However, other studies have indicated that predators consume 2%–24% of prey fish biomass encountered (Savitz and Bardygula-Nonn 1997; Baldwin et al. 2000; Hansen et al. 2013a); thus, in this study, we estimated consumption for both low (2%) and high (24%) capture successes based on capture probability and encounter rate. We modified consumption parameters in the bioenergetics model (consumption eq. 3) for lake trout to allow for a temperature-dependent relationship for maximum consumption (see Luecke et al. 1999); otherwise, we used the default settings (Stewart et al. 1983). As we modeled piscivorous lake trout to obtain a metric of predatory performance, we ran models with prey fish (kokanee energy density = 5338 J·g^{-1}; Hewett and Johnson 1992) making up 100% of the simulated predator diet. Lake trout began simulations at a mass of 520 g and had a predator energy density of 7302 J·g^{-1}, based on a length–mass relationship for a 400 mm lake trout (Yule and Luecke 1993; Luecke et al. 1999). We calculated predator thermal history by averaging temperatures available in Twin Pots Reservoir within the suitable range of

temperature (<17 °C) and dissolved oxygen (>3 mg·L⁻¹), where we also estimated prey fish distributions. We conducted simulations over 11 days (early summer = day-of-year (DOY) 160–170, mid-summer = DOY 222–232, late summer = DOY 253–263, fall = DOY 283–293) encompassing the day of abiotic field measurements ±5 days.

Results

Prey density

Prey fish abundance in Twin Pots Reservoir was 71 000 (±24 000; 1 SE). In a typical year, prey fish distributions were limited by seasonal water temperatures > 17 °C and dissolved oxygen < 3 mg·L⁻¹ (Appendix A). Average prey densities were lowest during daytime hours in early summer, when the greatest volume of suitable water was available. As water levels decreased and temperatures increased in mid-summer, prey densities became more concentrated; depth-specific, diel maximum prey densities ranged from 6.8 to 34.2 fish·1000 m⁻³. We estimated the greatest susceptible prey densities (58.5·1000 m⁻³) during night in late summer, when reservoir water volume was lowest and the reservoir was stratified. During mixis in fall, prey fish were distributed across depths, and these densities were greater than in early summer.

Visual foraging

Turbidity had the greatest predicted effect on predator visual foraging efficiency and performance across diel and seasonal periods. Estimates of reaction distances varied during seasonal and diel periods (Fig. 3). As all summer period turbidity measurements were less than 1.65 NTU, maximum reaction distances (maximum RD = 101.2 cm) were calculated during day periods when light was also not limiting (>17.8 lx). We calculated the shortest reaction distances during fall (greatest RD = 45.0 cm), when turbidity levels were about 10-fold greater than early summer (5.04 vs. 0.45 NTU). During crepuscular hours, we calculated maximum reaction distances during summer periods near the surface, which then decreased with depth. At night, light was limiting and all reaction distances were greatly diminished regardless of season.

Predicted prey encounter rates were directly related to prey fish distributions and, thus, affected by seasonal abiotic conditions (Fig. 4). The greatest encounter rates occurred during late summer, again when prey fish were most concentrated by temperature, dissolved oxygen, and reservoir volume (maximum ER = 4.4 prey·h⁻¹). As encounter rates are largely dependent on reaction distances and strongly influenced by turbidity, the lowest encounter rates occurred during the fall (maximum ER = 0.03 prey·h⁻¹). Additionally, as reaction distances were highest during daytime, almost all prey encounters occurred during the day across summer seasons (93% of cumulative prey encounters), whereas daytime and crepuscular encounter rates were similar in fall. However, encounter rates were negligible in fall, and further, day length is shortest during the fall, which further reduced overall encounter rates. Under similar prey abundances, we predicted that a predator would encounter over 68 prey·day⁻¹ during late summer (clear water, low reservoir elevation), whereas a predator would encounter <1 prey fish·day⁻¹ under fall reservoir conditions (most turbid water; Table 2).

Predator consumption and growth potential

Estimates of predator consumption (g·day⁻¹) from bioenergetic models paralleled the number of prey encountered from visual foraging models. Lake trout encountered between 1.3 and 209.3 g of prey biomass each day (fall and late summer, respectively). Assuming predator's capture success between 2% and 24% (Beauchamp et al. 1999), maximum bioenergetic efficiency could be achieved by predators in all seasons except during the fall season (Table 3). Predators would need a capture successes of 6.6%, 2.5%, 1.6%, and >100% (early summer, mid-summer, late summer, and fall, respectively) for all prey biomass encountered to reach maximum efficiency. At 2% capture success, simulated predators

Fig. 3. Diel estimates of lake trout (*Salvelinus namaycush*) reaction distance (cm) to prey for the four different reservoir states in Twin Pots Reservoir, Utah.
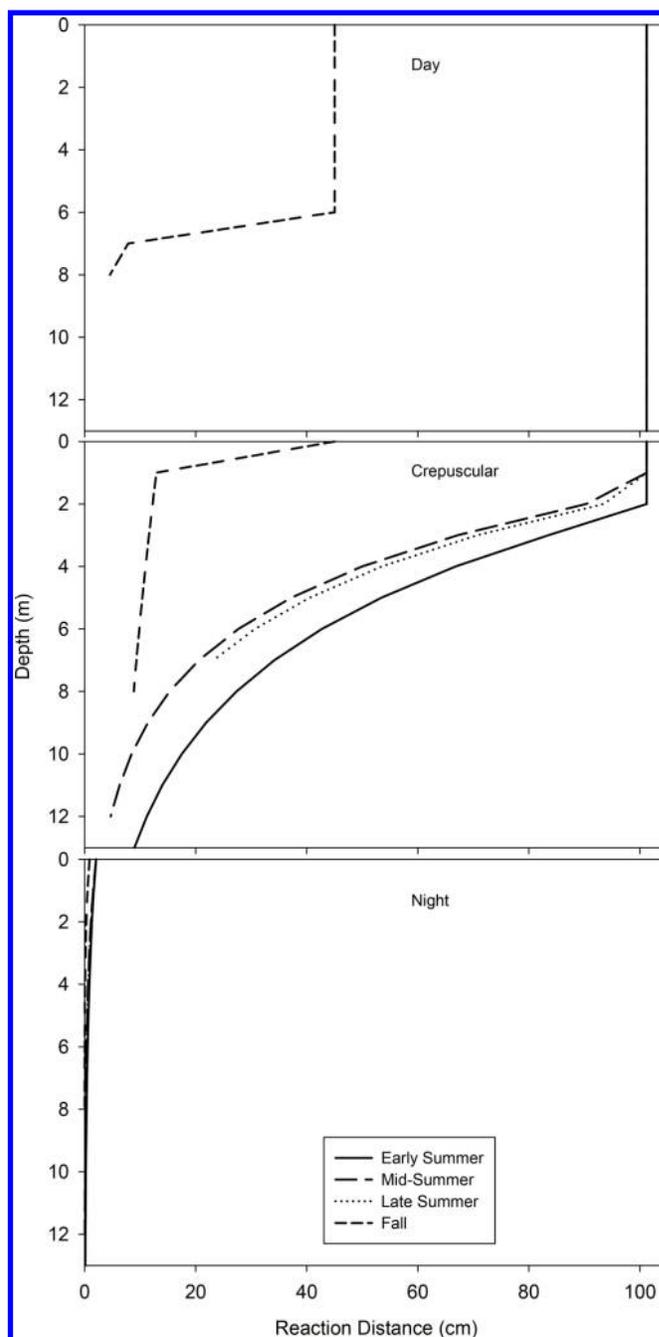
were most efficient during late summer (BioEff >1.0). Furthermore, these simulated, late summer predators were the only predators able to achieve positive growth at (0.25 g·day⁻¹). In contrast, early summer (BioEff = 0.31) and mid-summer (BioEff = 0.72) season simulations resulted in conditions whereby predators lost mass (–1.33 and –0.21 g·day⁻¹, respectively).

On the other hand, even at a capture success of 24%, lake trout during the fall were not able to achieve positive growth (BioEff = 0.07; –1.24 g·day⁻¹). In fact, positive growth could not be achieved even if these predators were allowed to consume all of the prey that they encountered (<1 prey fish·day⁻¹; BioEff = 0.30; –0.65 g·day⁻¹). However, during all other seasons, lake trout would reach

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Fig. 4. Predictions of cumulative hourly encounter rates (horizontal bars; prey·h⁻¹) for lake trout (*Salvelinus namaycush*) and average kokanee salmon (*Oncorhynchus nerka*) density (line; prey·1000 m⁻³) over diel periods during the four different reservoir states in Twin Pots Reservoir, Utah. All panels are scaled from 0.0 to 8.0 on the bottom *x* axis, with only fall consisting of a break from 0.1 to 3.0. Gray boxes at the bottom of each panel represent the bottom of the reservoir; the white area indicates inhabitable reservoir volume; during early summer, maximum depth was 13 m.
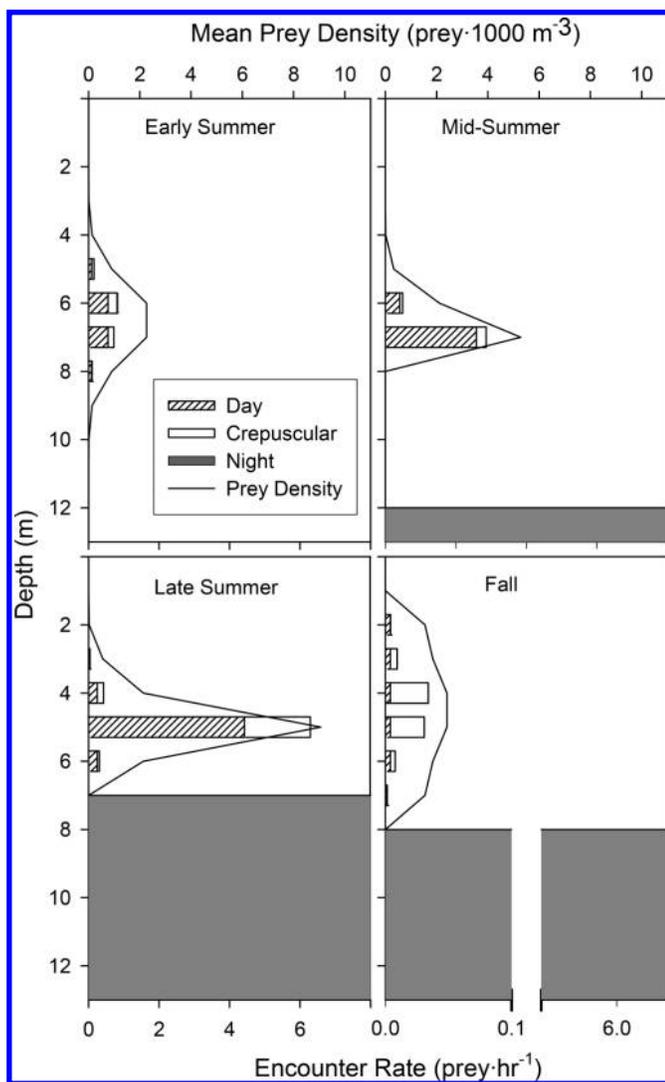
maximum consumption at a conservative capture success of less than 24%.

Typical versus high-water year

In years when Twin Pots Reservoir volume is more stable during fall, predators in our model simulations were much more successful relative to typical years of dynamic and turbid fall conditions. During a high-water year, reaction distances were similar to those of typical mid- and late summer conditions and more than double that of a turbid, low-water fall (Fig. 5). Although prey densities are greater at low water levels, encounter rates and, thus, consumption and growth rates are greater during a high-water fall (Fig. 5; Tables 2–3). Modeled encounter rates during stable, high-water years were 40× greater than those of turbid, fluctuating years (maximum of 1.2 vs. 0.03 prey·h⁻¹). Relative to other seasons, lake trout efficiency and growth was predicted to be lower during a fall season of high water levels; because the water column is not

stratified during fall, prey are more dispersed, and overall prey densities are lower during these times. Yet, the model predicted that predators in high-water years would encounter significantly more kokanee (9.2 vs. 0.4 fish·day⁻¹). As a result, these trout could achieve maximum BioEff between a capture success of 2% and 24% (15.2%, specifically) and, thus, potentially grow 0.72 g·day⁻¹.

Discussion

We used a multifaceted approach combining field measurements coupled with visual foraging and bioenergetic models to investigate how the performance and efficiency of predatory fish vary in reservoirs during typical, dramatically different seasonal water volumes. Our original hypothesis, that growth potential of sport fishes is greatest when water availability is greatest and reservoir volume fluctuates less dramatically, was confirmed. Modeled encounter rates were highest in late summer when kokanee densities were most concentrated and water was relatively clear. During fall, when depth-specific prey densities were relatively low and turbidity was highest, predator encounter rates were significantly lower. Furthermore, other physiological limitations (e.g., temperature) also affected predator–prey interactions. Based on these results, modeled lake trout, and likely other cold water piscivores, perform better in years when water levels fluctuate less dramatically across seasons.

In reservoirs where water levels fluctuate dramatically, turbidity is often the most important abiotic factor influencing predator efficiency and performance (Gregory 1993; Sweka and Hartman 2003), although other factors (e.g., temperature, reservoir volume) also limit predators. Highly turbid conditions reduced prey encounter rates. In this study, the most turbid conditions and, thus, least optimal foraging conditions occurred when temperatures were closest to optimal for predators, but predators could still not meet energetic demands. Some predators increase foraging effort and thus energy expenditure, as prey encounter rates decrease, potentially exacerbating the effects of low consumption rates under high turbidity conditions (Jönsson et al. 2012). During clearest water conditions, search volumes were greatest, and thus lake trout could most easily find prey, if present, consistent with previous studies (VanLandeghem et al. 2011).

The activity of many fishes varies over diel cycles, and depending on peak activity of predator and (or) prey, some variability of encounter rates was unsurprisingly not explained by the models used in this study (Helfman 1986; Boujard and Leatherland 1992). During the daytime, our model predicted maximum reaction distances to occur throughout the entire water column. Therefore, reaction distance was not a limiting factor if fish were actively feeding during the day. However, fish are often more active at dawn and dusk (Helfman 1981; Løkkeborg et al. 2000). Additionally, trout optic nerves increase underwater polarization of light during crepuscular times, improving visual acuity (Flamarique and Hawryshyn 1997). Nonetheless, for this study, we assumed that lake trout were most active during the day, slightly less active during crepuscular periods, and relatively dormant at night. In larger waterbodies such as Lake Superior, lake trout track their prey through diel vertical migrations to maximize fitness (Hrabik et al. 2006; Jensen et al. 2006). However, in the much smaller Twin Pots Reservoir, prey migrations were likely limited by overall habitat (e.g., maximum depth = 13 m) and abiotic conditions (e.g., dissolved oxygen); thus, schooling of kokanee was considered the most important means of predator avoidance for our analyses.

Distributions of both predator and prey are often influenced by preferred physiological conditions and habitats (Vanderploeg et al. 2009). Pelagic prey inhabit lower light levels, at greater depths, to avoid predators (Clark et al. 2003; Rick and Bakker 2010). Herein, mid- and late summer thermal regimes likely restricted habitat availability and thus limited the ability of prey to escape (Helland et al. 2007; Ludsin et al. 2009; Arend et al. 2011). As such, predator

Table 2. Estimated kokanee salmon (*Onchhorynchus nerka*) (fish·day⁻¹) and biomass (g) encountered by pelagic lake trout (*Salvelinus namaycush*) in Twin Pots Reservoir, Utah.

	Early summer	Mid-summer	Late summer	Fall (low water)	Fall (high water)
Total prey encountered[a] (fish·day⁻¹)	20.9	42.6	68.2	0.4	9.2
Day prey encountered (fish·day⁻¹)	19.3	41.5	61.8	0.2	6.9
Crepuscular prey encountered (fish·day⁻¹)	1.5	1.1	6.4	0.2	2.3
Night prey encountered (fish·day⁻¹)	0.0	0.0	0.0	0.0	0.0
Prey biomass encountered (g·day⁻¹)	64.1	130.7	209.3	1.3	28.4
2% capture success consumption (g·day⁻¹)	1.3	2.6	4.2[b]	0.0	0.57
24% capture success consumption (g·day⁻¹)	15.4[b]	31.4[b]	50.2[b]	0.3	6.81[b]

Note: Low (2%) and high (24%) estimates of consumption (g·day⁻¹) based on cumulative encounters.
[a]Simulated prey fish were 3.07 g.
[b]Values of consumption above the predicted maximum consumption threshold.

Table 3. Bioenergetic model inputs and outputs for consumption and growth by lake trout (*Salvelinus namaycush*) for seasonally distinct reservoir states in Twin Pots Reservoir, Utah.

|	Early summer	Mid-summer	Late summer	Fall (low water)	Fall (high water)
Days of simulation	160–170	222–232	253–263	283–293	283–293
Average thermal experience (°C)	9.5	13.0[a]	13.0[a]	11.5	10.5
BioEff of 2% capture success	0.31	0.72	1.0**	0.00	0.13
Growth potential of 2% capture success (g·day⁻¹)	−1.33	−0.21	**	−1.10	−1.93
BioEff of 24% capture success	1.0**	1.0**	1.0**	0.07 (0.30[b])	1.0**
Growth potential of 24% capture success (g·day⁻¹)	**	**	**	−1.24 (−0.65[c])	**
Consumption to achieve maximum BioEff (g·day¹)	4.24	3.30	3.30	4.38	4.32
Maximum growth potential (g·day⁻¹)	0.20	0.25	0.25	0.98	0.72
Maintenance consumption (g·day⁻¹)	3.8	2.78	2.78	2.46	4.16

Note: **, BioEff estimated to be maximum efficiency at 24% capture success, thus growth potential will be maximum as well.
[a]Assumed median temperature for predators to persist under thermal conditions.
[b]BioEff estimate for predator consuming all prey biomass encountered during turbid fall conditions.
[c]Potential growth estimate for predator consuming all prey biomass encountered during turbid fall conditions.

Fig. 5. (Left panel) Diel estimates of lake trout (*Salvelinus namaycush*) reaction distance (cm) during alternative states for fall in Twin Pots Reservoir. (Right panel) Predictions of cumulative hourly encounter rates (horizontal bars; prey·h⁻¹) for lake trout (*Salvelinus namaycush*) and average kokanee salmon (*Oncorhynchus nerka*) density (line; prey·1000 m⁻³) over diel periods during alternative fall reservoir states in Twin Pots Reservoir, Utah. Low-water conditions are significantly more turbid than high-water conditions. Gray boxes at the bottom of fall (low water) represent the bottom of the reservoir; the white area indicates available reservoir volume; during a high-water fall, maximum depth was 11 m.

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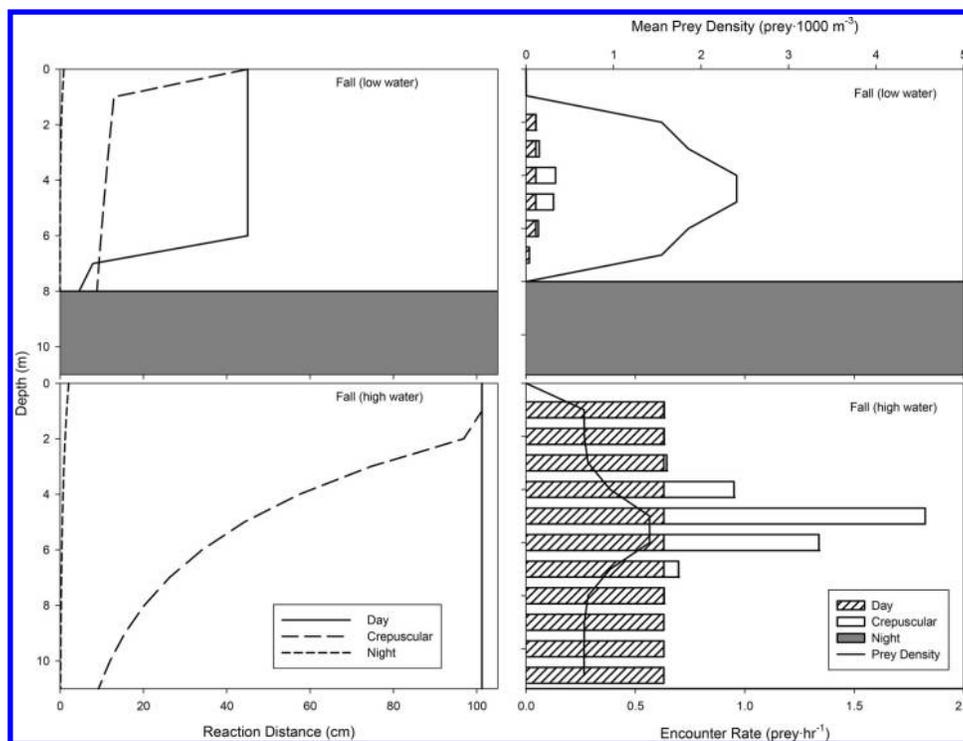
performance effectively increases, as represented by modeled encounter rates. However, piscivorous trout could experience decreased foraging success in late summer, contrary to our predicted outcomes (e.g., Hansen et al 2013a). Increased predator densities could have negated the ability of prey to escape to other habitats through schooling effects (Turesson and Brönmark 2007). Additionally, during a typical, low-water year in Twin Pots Reservoir, a lake trout's foraging efficiency is likely limited by turbidity in fall, and these predators are unable to take advantage of more suitable temperature and dissolved oxygen conditions. However, when turbidity is not a limiting factor, for a high-water year in Twin Pots Reservoir, lake trout are able to achieve the highest potential growth of all seasonal periods. This assumption is bolstered by empirical and anecdotal field observations of piscivorous trout exhibiting relatively high body condition in Twin Pots Reservoir during late summer and early fall.

This study improves upon our understanding of how fluctuating reservoir states and associated abiotic factors (e.g., turbidity) influence predator foraging efficiency. Our simulations are based on empirical observations of the physical states of the reservoir. However, improved field estimates of predator growth or measured consumption could improve our inference of bioenergetic scenarios. Nonetheless, fitting the model for estimated consumption and relying on relative, rather than absolute, comparisons of growth is a valid alternative, especially in a variable environment (Gaeta et al. 2012). In addition to other potential limitations, by selecting the smallest prey (50 mm), we could have underestimated the overall number of prey fish consumed. Based on the selected prey fish and length–mass relationship, a predator predicted to consume approximately 18 g of prey biomass could potentially consume one 150 mm prey or six 50 mm prey. Prey size affects the rate of digestion and foraging pattern in general and would influence real-time consumption capabilities (Legler et al. 2010). However, these differences in potential prey sizes would only be important during periods of low encounter rates (e.g., turbid, low-water fall), when a single encounter between big or small prey fish and a predator could significantly affect consumption, BioEff, and overall predator performance.

To compare reservoir physical states, we held pelagic prey fish abundance constant for each season. However, our results suggest that prey density can affect visual foraging, especially in less turbid conditions, when search volumes and thus encounter rates are greater. Furthermore, kokanee abundances and recruitment can vary annually as a result of predator–prey and environmental conditions (e.g., Beauchamp et al. 1997). Little is known about interannual prey density fluctuations in Twin Pots Reservoir, but connection to an upstream reservoir could supplement prey when water is flowing. Additionally, recruitment strength of year classes can be a function of hydrology. In East Canyon Reservoir, Utah, rainbow trout recruitment increases when higher water levels provide inshore cover and habitat (Tabor and Wurtsbaugh 1991). In this study, the hydroacoustic survey took place in mid-summer during a high-water year, which was immediately preceded by an extremely dry year. Thus, we estimated a relatively high density of small prey fish (50–150 mm). These prey densities could be much lower in a low-water year, depending on the availability of upstream inputs and (or) spawning habitats.

Our study simulated foraging efficiency and fish growth potential at four distinct reservoir states and has important implications for reservoir management. Decreased snowpack and periods of drought as a result of climate change may dictate future water use. Many western reservoirs already undergo dramatic seasonal fluctuations dependent on water availability, and smaller (<200 ha) reservoirs are increasingly vulnerable to rapid change. During a typical, low-water year in fall, reservoir height of Twin Pots Reservoir and similar reservoirs can increase by as much as 2 m·day⁻¹ when agricultural water use ends. These refill events can increase turbidity five-fold and greatly affect temperature and dissolved oxygen, which can stress fish populations. Second, foraging success of visual predators in

these reservoirs is highly susceptible to changes in water quality and level. For example, in Twin Pots Reservoir, predator encounter rates in late summer can be 50 times greater than those of a low-water fall. Alternatively, these late summer encounter rates are only approximately 2.5 times greater than those of a high-water fall. Third, interactions between water level, turbidity, and thermal regime and prey availability and reaction distance can structure how sport fish respond to seasonal and diel fluctuations. Our models predict that prized sport fish can gain (almost 1 g·day⁻¹) or lose (over 1 g·day⁻¹) significant body mass depending on how turbidity and prey densities influence prey encounter rates. Thus, water users need to understand the potential for adverse fish effects resulting from water level fluctuations. Communication between fisheries managers and these water users is important to efficiently achieve cost-effective goals of both groups.

For fisheries, managers can assess the consumptive pressure on prey and adapt either stocking plans or fishing regulations, or possibly even the timing and speed of reservoir drawdown and fill, accordingly. Furthermore, it is often pivotal that management actions adapt to individual reservoirs (Martin and Pope 2011). The same abiotic factors that vary seasonally can also vary spatially, and blanket strategies are less applicable for highly variable standing waters such as western reservoirs (Lottig et al. 2011; Sadro et al. 2012). The ability to integrate water demands and biotic response into management plans can benefit lakes and reservoirs both for anthropogenic use and for ecological integrity, either of which may be overlooked as a singular entity (Cowx and Aya 2011).

Acknowledgements

References

Adams, S.M., McLean, R.B., and Huffman, M.M. 1982. Structuring of a predator population through temperature-mediated effects on prey availability. Can. J. Fish. Aquat. Sci. **39**(8): 1175–1184. doi:10.1139/f82-155.

Arend, K.K., Beletsky, D., DePinto, J.V., Ludsin, S.A., Roberts, J.J., Rucinski, D.K., Scavia, D., Schwab, D.J., and Höök, T.O. 2011. Seasonal and interannual effects of hypoxia on fish habitat quality in central Lake Erie. Freshwater Biol. **56**(2): 366–383. doi:10.1111/j.1365-2427.2010.02504.x.

Baldwin, C.M., Beauchamp, D.A., and Van Tassell, J.J. 2000. Bioenergetic assessment of temporal food supply and consumption demand by salmonids in the Strawberry Reservoir food web. Trans. Am. Fish. Soc. **129**(2): 429–450. doi:10.1577/1548-8659(2000)129<0429:BAOTFS>2.0.CO;2.

Barnett, T.P., Adam, J.C., and Lettenmaier, D.P. 2005. Potential impacts of a warming climate on water availability in snow-dominated regions. Nature, **438**: 303–309. doi:10.1038/nature04141. PMID:16292301.

Beauchamp, D.A., Luecke, C., Wurtsbaugh, W.A., Gross, H.G., Budy, P.E., Spaulding, S., Dillenger, R., and Gubala, C.P. 1997. Hydroacoustic assessment of abundance and diel distribution of sockeye salmon and kokanee in the Sawtooth Valley lakes, Idaho. N. Am. J. Fish. Manage. **17**(2): 253–267. doi:10.1577/1548-8675(1997)017<0253:HAOAAD>2.3.CO;2.

Beauchamp, D.A., Baldwin, C.M., Vogel, J.L., and Gubala, C.P. 1999. Estimating diel, depth-specific foraging opportunities with a visual encounter rate model for pelagic piscivores. Can. J. Fish. Aquat. Sci. **56**(S1): 128–139. doi:10.1139/f99-217.

Berge, H.B. 2009. Effects of a temperature–oxygen squeeze on distribution, feeding, growth, and survival of kokanee (*Oncorhynchus nerka*) in Lake Sammamish, Washington. M.Sc. Thesis, School of Aquatic and Fishery Sciences, University of Washington, Seattle, Washington.

Biggs, R., Carpenter, S.R., and Brock, W.A. 2009. Turning back from the brink:

detecting an impending regime shift in time to avert it. Proc. Natl. Acad. Sci. **106**(3): 826–831. doi:10.1073/pnas.0811729106. PMID:19124774.

Boujard, T., and Leatherland, J.F. 1992. Circadian rhythms and feeding time in fishes. Environ. Biol. Fishes. **35**(2): 109–131. doi:10.1007/BF00002186.

Brett, J.R. 1971. Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). Am. Zool. **11**(1): 99–113. doi:10.1093/icb/11.1.99.

Budy, P., Thiede, G.P., Lobón-Cervia, L., Fernandez, G.G., McHugh, P., McIntosh, A., Vollestad, L.A., Becares, E., and Jellyman, P. 2013. Limitation and facilitation of one of the world's most invasive fish: an intercontinental comparison. Ecology, **94**(2): 356–367. doi:10.1890/12-0628.1. PMID:23691655.

Carlsson, P., and Caron, D.A. 2001. Seasonal variation of phosphorus limitation of bacterial growth in a small lake. Limnol. Oceanogr. **46**(1): 108–120. doi:10.4319/lo.2001.46.1.0108.

Carpenter, S.R., and Kitchell, J.F. (*Editors*). 1993. The trophic cascade in lakes. Cambridge University Press, New York.

Carpenter, S.R., Cole, J.J., Pace, M.L., Batt, R., Brock, W.A., Cline, T., Coloso, J., Hodgson, J.R., Kitchell, J.F., Seekell, D.A., et al. 2011*a*. Early warnings of regime shifts: a whole-ecosystem experiment. Science, **332**(6033): 1079–1082. doi:10.1126/science.1203672. PMID:21527677.

Carpenter, S.R., Stanley, E.H., and Vander Zanden, M.J. 2011*b*. State of the world's freshwater ecosystems: physical, chemical, and biological changes. Annu. Rev. Environ. Resour. **36**(1): 75–99. doi:10.1146/annurev-environ-021810-094524.

Cayan, D.R., Redmond, K.T., and Riddle, L.G. 1999. ENSO and hydrologic extremes in the western United States. J. Climate, **12**(9): 2881–2893. doi:10.1175/1520-0442(1999)012<2881:EAHEIT>2.0.CO;2.

Clark, K.L., Ruiz, G.M., and Hines, A.H. 2003. Diel variation in predator abundance, predation risk and prey distribution in shallow-water estuarine habitats. J. Exp. Mar. Biol. Ecol. **287**(1): 37–55. doi:10.1016/S0022-0981(02)00439-2.

Cooke, G.D., Welch, E.B., Peterson, S., and Nichols, S.A. 2005. Restoration and management of lakes and reservoirs. CRC Press, Boca Raton, Florida.

Cowx, I.G., and Aya, M.P. 2011. Paradigm shifts in fish conservation: moving to ecosystem services concept. J. Fish Biol. **79**(6): 1663–1680. doi:10.1111/j.1095-8649.2011.03144.x. PMID:22136245.

Environmental Systems Research Institute (ESRI). 2012. ArcGIS desktop: Release 10.1. Redlands, CA: Environmental Systems Research Institute, Redlands, California.

Feder, M.E., and Hofmann, G.E. 1999. Heat-shock proteins, molecular chaperones, and the stress response: evolutionary and ecological physiology. Annu. Rev. Physiol. **61**: 243–282. doi:10.1146/annurev.physiol.61.1.243. PMID:10099689.

Flamarique, I.N., and Hawryshyn, C.W. 1997. Is the use of underwater polarized light by fish restricted to crepuscular time periods? Vision Research, **37**(8): 975–989. doi:10.1016/S0042-6989(96)00236-2. PMID:9196717.

Gaeta, J.W., Read, J.S., Kitchell, J.F., and Carpenter, S.R. 2012. Eradication via destratification: whole-lake mixing to selectively remove rainbow smelt, a cold-water invasive species. Ecol. Appl. **22**(3): 817–827. doi:10.1890/11-1227.1. PMID:22645813.

Gaeta, J.W., Sass, G.G., and Carpenter, S.R. 2014. Drought-driven lake level decline: effects on coarse woody habitat and fish. Can. J. Fish. Aquat. Sci. **71**(2): 315–325. doi:10.1139/cjfas-2013-0451.

Garen, D.C. 1993. Revised surface-water supply index for western United States. J. Water Resour. Plann. Manage. **119**(4): 437–454. doi:10.1061/(ASCE)0733-9496(1993)119:4(437).

Gregory, R.S. 1993. Effect of turbidity on the predator avoidance behaviour of juvenile chinook salmon (*Oncorhynchus tshawytscha*). Can. J. Fish. Aquat. Sci. **50**(2): 241–246. doi:10.1139/f93-027.

Hansen, A.G., Beauchamp, D.A., and Baldwin, C.M. 2013*a*. Environmental constraints on piscivory: insights from linking ultrasonic telemetry to a visual foraging model for cutthroat trout. Trans. Am. Fish. Soc. **142**(1): 300–316. doi:10.1080/00028487.2012.732650.

Hansen, A.G., Beauchamp, D.A., and Schoen, E.R. 2013*b*. Visual prey detection responses of piscivorous trout and salmon: effects of light, turbidity, and prey size. Trans. Am. Fish. Soc. **142**(3): 854–867. doi:10.1080/00028487.2013.785978.

Hanson, P.C., Johnson, T.B., Schindler, D.E., and Kitchell, J.F. 1997. Fish Bioenergetics 3.0. University of Wisconsin Sea Grant, Madison, Wisconsin.

Helfman, G.S. 1981. Twilight activities and temporal structure in a freshwater fish community. Can. J. Fish. Aquat. Sci. **38**(11): 1405–1420. doi:10.1139/f81-187.

Helfman, G.S. 1986. Fish behavior by day, night, and twilight. *In* The behaviour of teleost fishes. *Edited by* T.J. Pitcher. Chapman and Hall, New York. pp. 366–387.

Helland, I.P., Freyhof, J., Kasprzak, P., and Mehner, T. 2007. Temperature sensitivity of vertical distributions of zooplankton and planktivorous fish in a stratified lake Oecologia, **151**(2): 322–330. doi:10.1007/s00442-006-0541-x.

Henderson, M.A., and Northcote, T.G. 1985. Visual prey detection and foraging in sympatric cutthroat trout (*Salmo clarki clarki*) and Dolly Varden (*Salvelinus malma*). Can. J. Fish. Aquat. Sci. **42**: 785–790. doi:10.1139/f85-100.

Hewett, S.W., and Johnson, B.L. 1992. Fish bioenergetics model 2: an update of a generalized bioenergetics model of fish growth for microcomputers. Sea Grant Institute, WIS-SG-92-250, Madison, Wisconsin.

Heyman, W.D., Ecochard, J.-L.B., and Biasi, F.B. 2007. Low-cost bathymetric mapping for tropical marine conservation—a focus on reef fish spawning aggregation sties. Marine Geodesy, **30**: 37–50. doi:10.1080/01490410701295996.

Hobbs, R.J., Arico, S., Aronson, J., Baron, J.S., Bridgewater, P., Cramer, V.A., Epstein, P.R., Ewel, J.J., Klink, C.A., Lugo, A.E., et al. 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. Global Ecol. Biogeogr. **15**(1): 1–7. doi:10.1111/j.1466-822X.2006.00212.x.

Horppila, J., Liljendahl-Nurminen, A., and Malinen, T. 2004. Effects of clay turbidity and light on the predator–prey interaction between smelts and chaoborids. Can. J. Fish. Aquat. Sci. **61**(10): 1862–1870. doi:10.1139/f04-123.

Hrabik, T.R., Jensen, O.P., Martell, S.J.D., Walters, C.J., and Kitchell, J.F. 2006. Diel vertical migration in Lake Superior pelagic community. I. Changes in vertical migration in response to varying predation risk. Can. J. Fish. Aquat. Sci. **63**(10): 2286–2295. doi:10.1139/f06-124.

Jensen, O.P., Hrabik, T.R., Martell, S.J.D., Walters, C.J., and Kitchell, J.F. 2006. Diel vertical migration in the Lake Superior pelagic community. II. Modeling trade-offs at an intermediate trophic level. Can. J. Fish. Aquat. Sci. **63**(10): 2296–2307. doi:10.1139/f06-125.

Johnson, B.M., and Martinez, P.J. 2012. Hydroclimate mediates effects of a keystone species in a coldwater reservoir. Lake. Reserv. Manage. **28**(1): 70–83. doi:10.1080/07438141.2012.658492.

Johnson, D.M., Behnke, R.J., Harpman, D.A., and Walsh, R.G. 1995. Economic benefits and costs of stocking catchable rainbow trout: a synthesis of economic analysis in Colorado. North Am. J. Fish. Manage. **15**(1): 26–32. doi:10.1577/1548-8675(1995)015<0026:EBACOS>2.3.CO;2.

Jönsson, M., Ranåker, L., Anders Nilsson, P., and Brönmark, C. 2012. Prey-type-dependent foraging of young-of-the-year fish in turbid and humic environments. Ecol. Freshwater Fish. **21**(3): 461–468. doi:10.1111/j.1600-0633.2012.00565.x.

Landres, P.B., Morgan, P., and Swanson, F.J. 1999. Overview of the use of natural variability concepts in managing ecological systems. Ecol. App. **9**(4): 1179–1188. doi:10.1890/1051-0761(1999)009[1179:OOTUON]2.0.CO;2.

Legler, N.D., Johnson, T.B., Heath, D.D., and Ludsin, S.A. 2010. Water temperature and prey size effects on the rate of digestion of larval and early juvenile fish. Trans. Am. Fish. Soc. **139**(3): 868–875. doi:10.1577/T09-212.1.

Lester, N.P., Bailey, P.E., and Hubert, W.A. 2009. Coldwater fish in small standing waters. *In* Standard methods for sampling North American freshwater fishes. *Edited by* S.A. Bonar, W.A. Hubert, and D.W. Willis. American Fisheries Society, Bethesda, Maryland. pp. 85–96.

Løkkeborg, S., Skajaa, K., and Fernö, A. 2000. Food-search strategy in ling (*Molva molva* L.): crepuscular activity and use of space. J. Exp. Mar. Biol. Ecol. **247**(2): 195–208. doi:10.1016/S0022-0981(00)00148-9. PMID:10742504.

Lottig, N.R., Stanley, E.H., Hanson, P.C., and Kratz, T.K. 2011. Comparison of regional stream and lake chemistry: differences, similarities, and potential drivers. Limnol. Oceanogr. **56**(5): 1551–1562. doi:10.4319/lo.2011.56.5.1551.

Ludsin, S.A., Zhang, X., Brandt, S.B., Roman, M.R., Boicourt, W.C., Mason, D.M., and Constantini, M. 2009. Hypoxia-avoidance by planktivorous fish in Chesapeake Bay: implications for food web interactions and fish recruitment. J. Exp. Mar. Biol. Ecol. **381**(S1): S121–S131. doi:10.1016/j.jembe.2009.07.016.

Luecke, C., Wengert, M.W., and Schneidervin, R.W. 1999. Comparing results of a spatially explicit growth model with changes in the length–weight relationship of lake trout (*Salvelinus namaycush*) in Flaming Gorge Reservoir. Can. J. Fish. Aquat. Sci. **56**(S1): 162–169. doi:10.1139/f99-208.

Lytle, D.A., and Poff, N.L. 2004. Adaptation to natural flow regimes. Trends Ecol. Evol. **19**(2): 94–100. doi:10.1016/j.tree.2003.10.002. PMID:16701235.

MacAvoy, S.E., Macko, S.A., and Garman, G.C. 2001. Isotopic turnover in aquatic predators: quantifying the exploitation of migratory prey. Can. J. Fish. Aquat. Sci. **58**(5): 923–932. doi:10.1139/f01-045.

Martin, D.R., and Pope, K.L. 2011. Luring anglers to enhance fisheries. J. Environ. Manage. **92**(5): 1409–1413. doi:10.1016/j.jenvman.2010.10.002. PMID:20965644.

Mazur, M.M., and Beauchamp, D.A. 2003. A comparison of visual prey detection among species of piscivorous salmonids: effects of light and low turbidities. Environ. Biol. Fish. **67**(4): 397–405. doi:10.1023/A:1025807711512.

Meyer, J.L., Sale, M.J., Mulholland, P.J., and Poff, N.L. 1999. Impacts of climate change on aquatic ecosystem functioning and health. J. Am. Water Resour. Assoc. **35**(6): 1373–1386. doi:10.1111/j.1752-1688.1999.tb04222.x.

Moss, J.L. 1985. Summer selection of thermal refuges by striped bass in Alabama reservoirs and tailwaters. Trans. Am. Fish. Soc. **114**(1): 77–83. doi:10.1577/1548-8659(1985)114<77:SSOTRB>2.0.CO;2.

Odhiambo, B.K., and Boss, S.K. 2004. Integrated echo sounder, GPS, and GIS for reservoir sedimentation studies: examples from two Arkansas lakes. J. Am. Water Resour. Assoc. **40**(4): 981–997. doi:10.1111/j.1752-1688.2004.tb01061.x.

Poff, N.L., Allan, J.D., Bain, M.B., Karr, J.R., Prestegaard, K.L., Richter, B.D., Sparks, R.E., and Stromberg, J.C. 1997. The natural flow regime. BioScience, **47**(11): 769–784. doi:10.2307/1313099.

Renwick, M.E. 2001. Valuing water in irrigated agriculture and reservoir fisheries: a multiple-use irrigation system in Sri Lanka. International Water Management Institute, Colombo, Sri Lanka.

Rick, I.P., and Bakker, T.C. 2010. Ultraviolet light influences habitat preferences in a fish under predation risk. Evol. Ecol. **24**(1): 25–37. doi:10.1007/s10682-008-9287-8.

Sadro, S., Nelson, C.E., and Melack, J.M. 2012. The influence of landscape position and catchment characteristics on aquatic biogeochemistry in high-elevation lake-chains. Ecosystems, **15**(3): 363–386. doi:10.1007/s10021-011-9515-x.

Sass, G.G., Carpenter, S.R., Gaeta, J.W., Kitchell, J.F., and Ahrenstorff, T.D. 2012. Whole-lake addition of coarse woody habitat: response of fish populations. Aquat. Sci. **74**(2): 255–266. doi:10.1007/s00027-011-0219-2.

Savitz, J., and Bardygula-Nonn, L. 1997. Behavioral interactions between coho (*Oncorhynchus kisutch*) and chinook salmon (*Oncorhynchus shawytscha*) and prey fish species. Ecol. Freshwater Fish, **6**(4): 190–195. doi:10.1111/j.1600-0633.1997.tb00162.x.

Schindler, D.E., and Scheuerell, M.D. 2002. Habitat coupling in lake ecosystems. Oikos, **98**(2): 177–189. doi:10.1034/j.1600-0706.2002.980201.x.

Stewart, D.J., Weininger, D., Rottiers, D.V., and Edsall, T.A. 1983. An energetics model for lake trout, *Salvelinus namaycush*: application to the Lake Michigan population. Can. J. Fish. Aquat. Sci. **40**(6): 681–698. doi:10.1139/f83-091.

Sweka, J.A., and Hartman, K.J. 2003. Reduction of reactive distance and foraging success in smallmouth bass, *Micropterus dolomieu*, exposed to elevated turbidity levels. Environ. Biol. Fish. **67**(4): 341–347. doi:10.1023/A:1025835031366.

Tabor, R.A., and Wurtsbaugh, W.A. 1991. Predation risk and the importance of cover for juvenile rainbow trout in lentic systems. Trans. Am. Fish. Soc. **120**(6): 728–738. doi:10.1577/1548-8659(1991)120<0728:PRATIO>2.3.CO;2.

Thimijan, R.W., and Heins, R.D. 1982. Photometric, radiometric, and quantum light units of measure: a review of procedures for interconversion. Hort. Sci. **18**(6): 818–822.

Turesson, H., and Brönmark, C. 2007. Predator–prey encounter rates in freshwater piscivores: effects of prey density and water transparency. Oecologia, **153**(2): 281–290. doi:10.1007/s00442-007-0728-9. PMID:17453254.

Vanderploeg, H.A., Ludsin, S.A., Ruberg, S.A., Höök, T.O., Pothoven, S.A., Brandt, S.B., Lang, G.A., Liebig, J.R., and Cavaletto, J.F. 2009. Hypoxia affects spatial distribution and overlap of pelagic fish, zooplankton, and phytoplankton in Lake Erie. J. Exp. Mar. Biol. Ecol. **381**(Suppl.): S92–S107. doi:10.1016/j.jembe.2009.07.027.

VanLandeghem, M.M., Carey, M.P., and Wahl, D.H. 2011. Turbidity-induced changes in emergent effects of multiple predators with different foraging strategies. Ecol. Fresh. Fish, **20**(2): 279–286. doi:10.1111/j.1600-0633.2011.00494.x.

Walters, C., Pauly, D., Christensen, V., and Kitchell, J.F. 2000. Representing density dependent consequences of life history strategies in aquatic ecosystems: EcoSim II. Ecosystems, **3**(1): 70–83. doi:10.1007/s100210000011.

Williamson, C.E., Saros, J.E., Vincent, W.F., and Smol, J.P. 2009. Lakes and reservoirs as sentinels, integrators and regulators of climate change. Limnol. Oceanogr. **54**(6.2): 2273–2282. doi:10.4319/lo.2009.54.6_part_2.2273.

Xenopoulos, M.A., Lodge, D.M., Alcamo, J., Märker, M., Schulze, K., and Van Vuuren, D.P. 2005. Scenarios of freshwater fish extinctions from climate change and water withdrawal. Global Change Biol. **11**(10): 1557–1564. doi:10.1111/j.1365-2486.2005.001008.x.

Yule, D.L., and Luecke, C. 1993. Lake trout consumption and recent changes in the fish assemblage of Flaming Gorge Reservoir. Trans. Am. Fish Soc. **122**(6): 1058–1069. doi:10.1577/1548-8659(1993)122<1058:LTCARC>2.3.CO;2.

Appendix A

Fig. A1. Map of study site, Twin Pots Reservoir, Utah.
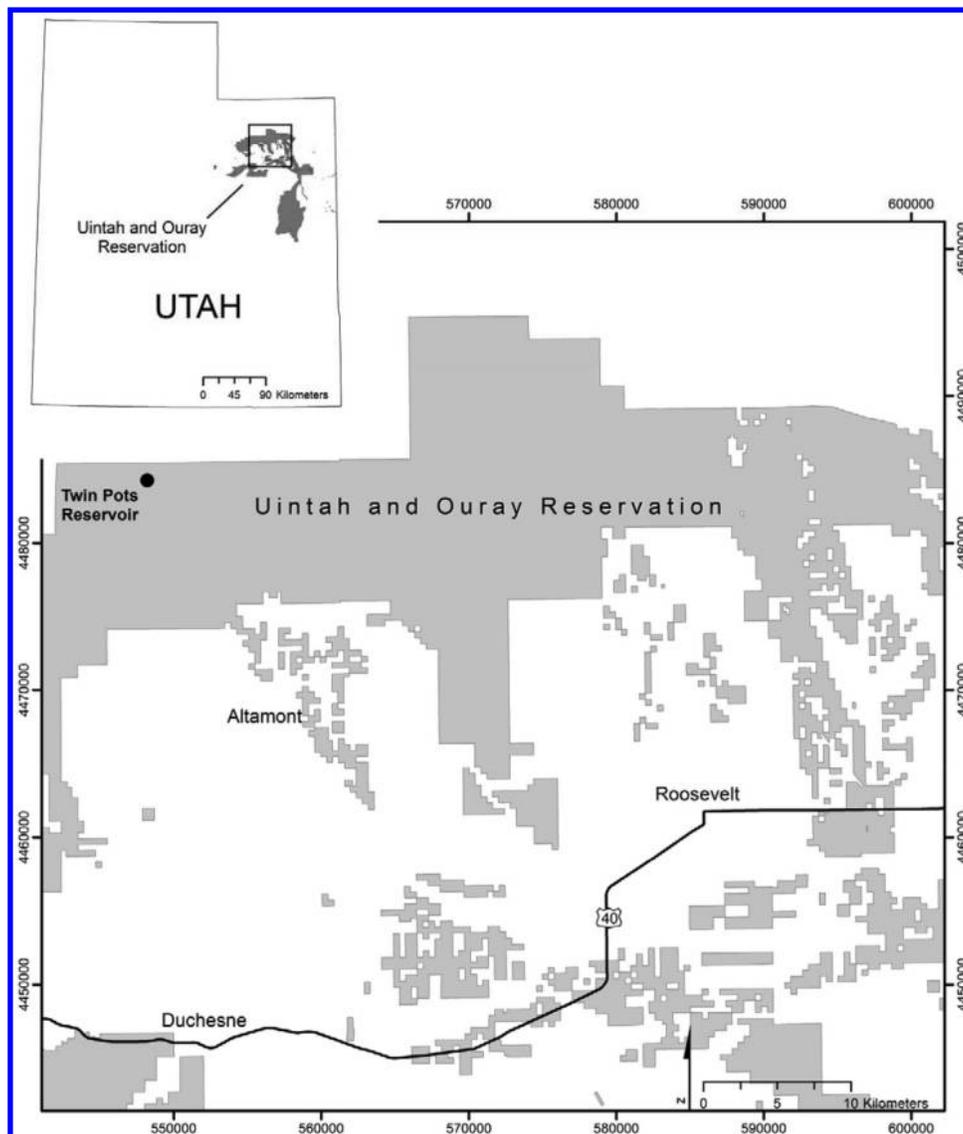
Fig. A2. Estimated vertical distribution of prey fish (50–150 mm total length) from hydroacoustics surveys at seasonal reservoir states during day, crepuscular, and night periods in Twin Pots Reservoir, Utah (horizontal bars). Dark gray boxes at the bottom of each panel represent the bottom of the reservoir; the white area indicates available reservoir volume; maximum depth was 13 m during early summer, 12 m during mid-summer, 7 m during late summer, and 8 m during fall.
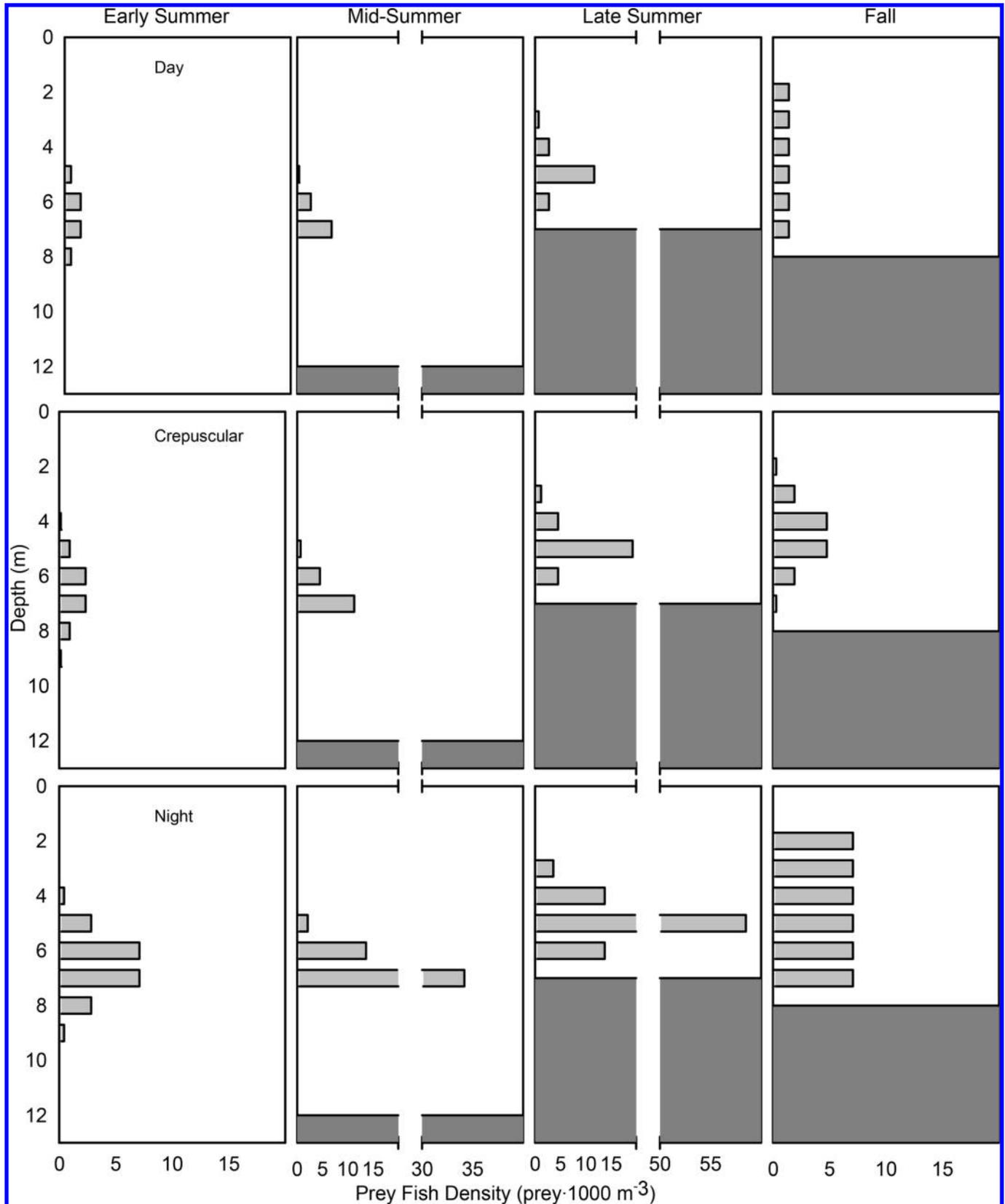
Fig. A3. Example echogram (Biosonics Visual Acquisition software, version 6.1) of a hydroacoustic transect during the 25–26 July 2011 survey. Most targets in 2–4 m depths are individual kokanee salmon (50–150 mm total length).