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ARTICLE

Earning their Stripes: The Potential of Tiger Trout and Other Salmonids as Biological Controls of Forage Fishes in a Western Reservoir

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Abstract

Maintaining a balance between predator and prey populations can be an ongoing challenge for fisheries managers, especially in managing artificial ecosystems such as reservoirs. In a high-elevation Utah reservoir, the unintentional introduction of the Utah Chub *Gila atraria* and its subsequent population expansion prompted managers to experimentally shift from exclusively stocking Rainbow Trout *Oncorhynchus mykiss* to also stocking tiger trout (female Brown Trout *Salmo trutta* × male Brook Trout *Salvelinus fontinalis*) and Bonneville Cutthroat Trout *O. clarkii utah* (hereafter, Cutthroat Trout) as potential biological control agents. We measured a combination of diet, growth, temperature, and abundance and used bioenergetic simulations to quantify predator demand versus prey supply. Utah Chub were the predominant prey type for tiger trout, contributing up to 80% of the diet depending on the season. Utah Chub represented up to 70% of the total diet consumed by Cutthroat Trout. Although Utah Chub dominated the fish biomass in the reservoir, we still estimated abundances of 238,000 tiger trout, 214,000 Cutthroat Trout, and 55,000 Rainbow Trout. Consequently, when expanded to the population level of each predator, tiger trout and Cutthroat Trout consumed large quantities of Utah Chub on an annual basis: tiger trout consumed 508,000 kg (2,660 g/predator) of the standing prey population, and Cutthroat Trout consumed an estimated 322,000 kg (1,820 g/predator). The estimated combined consumption by Cutthroat Trout and tiger trout exceeded the estimate of Utah Chub annual production. As such, our results suggest that the high rates of piscivory exhibited by Cutthroat Trout and tiger trout in artificial lentic ecosystems are likely sufficient to effectively reduce the overall abundance of forage fishes and to prevent forage fishes from dominating fish assemblages. Collectively, this research provides the first documented findings on tiger trout ecology and performance, which will aid managers in designing and implementing the best stocking strategy to optimize sport fish performance, control undesirable forage fish, and enhance and maintain angler satisfaction.

Biological agents are becoming increasingly common as a method for natural control of invasive species in an attempt to maintain native biodiversity worldwide (Freeman et al. 2010). Biological control—a potentially environmentally sound, effective means of reducing or mitigating nuisance species and their impacts through the use of

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natural enemies—depends upon parasites, pathogens, or predators to lower the population densities of the nuisance species (Debach 1964; Freeman et al. 2010; USDA 2013a). For example, sunfishes *Lepomis* spp. have been documented to regulate invasive rusty crayfish *Orconectes rusticus* in Wisconsin lakes (Roth et al. 2007; Tetzlaff et al. 2010), and European Eels *Anguilla anguilla* have similarly been successful at controlling invasive red swamp crayfish *Procambarus clarkii* in the Netherlands (Aquiloni et al. 2010; Musseau et al. 2015). Despite the prolific use of biological control agents, vertebrate species represent a small portion of all biological control targets (Saunders et al. 2010; USDA 2013b). However, the biomanipulation of fishes has become a common technique for preventing explosive prey bases from negatively affecting sport fish (Stewart et al. 1981; Hartman and Margraf 1993; Irwin et al. 2003). Many such techniques are employed within artificial systems, which commonly contain intentionally introduced and intensively managed species (Anderson and Neumann 1996).

Reservoir systems exhibit characteristics that are intermediate to lotic and lentic habitat (Wetzel 1990, 2001; Anderson and Neumann 1996). These artificial systems, where fish communities are often maintained through stocking, may demonstrate unpredictable food web interactions with decoupled predator and prey dynamics (Kitchell and Crowder 1986; Ruzycki et al. 2001). In addition, reservoirs are usually relatively young, such that members of the assemblage community may not have stabilized their interactions (Havel et al. 2005; Raborn et al. 2007) or the community may be unstable due to its simplicity (Stein et al. 1995). Unintentionally introduced species can be detrimental to intentionally introduced fishes through predation or competitive interactions for shared prey resources (Gardunio et al. 2011; Guy et al. 2011). However, even intentionally introduced species may not be successfully established (Kohler et al. 1986; Williamson and Fitter 1996; Bajer et al. 2015). Successful introductions, whether intentional or not, may initiate novel predator–prey interactions (Kitchell et al. 1997; Romare and Hansson 2003; Schoen et al. 2012), alter trophic structure (Reissig et al. 2006; Skov et al. 2010; Ellis et al. 2011), or increase the potential for competition (Tyus and Saunders 2000; Tronstad 2008; Winters and Budy 2015). Consequently, the unintentional introduction of undesirable fishes may disrupt linkages and alter the strength of interactions within reservoir food webs.

Piscivorous fishes are commonly introduced species; their intentional stocking is used as a management tool in an attempt to control undesired species (Courtenay and Kohler 1986; Irwin et al. 2003; Bunnell et al. 2006). A secondary goal of stocking piscivorous fish may be to enhance angling opportunities (Martinez et al. 2009). Nevertheless, top predators can potentially serve as powerful tools for invasive species management, wherein a carefully selected, upper-trophic-level

species theoretically uses the undesired organism as a primary food resource and reduces the population size (Ewel and Putz 2004; Hoddle 2004).

Whether a potential predator can control its prey base ultimately depends on prey supply (abundance and accessibility) and predator demand (production and biomass; Ney 1990). This link to prey availability, however, is not always apparent in manipulated, artificial assemblages (Vatland et al. 2008). Predator size relative to prey size limits a predator ability's to capture, handle, and consume prey (Hambright 1991; Magnhagen and Heibo 2001; Juanes et al. 2002). Similarly, the predator's gape size limits the potential size of prey captured (Truemper and Lauer 2005). As such, young fish demonstrating rapid growth rates may quickly exceed the gape of piscivores, thereby allowing them to become less vulnerable to predation and attain high survival rates (e.g., Gizzard Shad *Dorosoma cepedianum*; Noble 1981; Michaletz 2014). With few predators and abundant resources, the prey species may then dominate the assemblage (Stein et al. 1995). Therefore, an understanding of the mechanisms driving predator–prey relationships in coldwater impoundments can be challenging but is also critical for making informed management decisions (Johnson and Goettle 1999).

Bioenergetics-based modeling coupled with comprehensive field sampling provides a quantitative and predictive tool that managers can use to estimate current and future predator impacts on prey populations (Rice and Cochran 1984; Hanson et al. 1997). The approach, which is based on a balanced energy budget, uses physiological and allometric relationships driven by diet, thermal experience, and fish size to predict predator consumption, growth, or production of fish (Brandt and Hartman 1993; Beauchamp et al. 2007; Chipps and Wahl 2008). Bioenergetics modeling estimates the demand for the prey base, whereas comprehensive field work (e.g., hydroacoustic surveys) estimates the supply or availability of prey fish in the system. The results can be used to effectively evaluate complex interactions within reservoir food webs and the mechanisms that operate to structure these webs (Baldwin et al. 2000; Beauchamp and Van Tassell 2001; Irwin et al. 2003). The bioenergetics modeling approach has been effectively used to assess water quality constraints on fish growth (Budy et al. 2011); to evaluate management actions, such as slot limits (Luecke et al. 1994); to investigate species invasion success (Budy et al. 2013); and to estimate predation pressure (Peterson and Kitchell 2001; Ruzycki et al. 2001; Mesa et al. 2013).

Scofield Reservoir, Utah, is typical of many high-elevation reservoirs in the Intermountain West. A fast-reproducing non-game fish, the Utah Chub *Gila atraria*, was unintentionally introduced into the reservoir, and the population rapidly expanded starting in 2005. Utah Chub are native to the nearby Snake River and Lake Bonneville basins but are not native to the Colorado River drainage, where Scofield Reservoir is located. Managers expressed concern that the expanding

Utah Chub population would adversely affect the extremely popular blue-ribbon sport fishery for Rainbow Trout *Oncorhynchus mykiss*, as has been observed elsewhere (Hart and Birdsey 2008). Within the past decade, Bear Lake-strain Bonneville Cutthroat Trout *O. clarkii utah* (hereafter, Cutthroat Trout), Rainbow Trout, and tiger trout (female Brown Trout *Salmo trutta* × male Brook Trout *Salvelinus fontinalis*) have been stocked in relatively high numbers as an attempt to suppress the Utah Chub population. Accordingly, the Scofield Reservoir food web poses a unique opportunity to investigate the use of various salmonids as agents for the biological control of an undesired nongame fish population.

Our overall goal was to determine whether Utah Chub population abundance could be controlled by any one or a combination of three potential predatory trout species: Cutthroat Trout, Rainbow Trout, and tiger trout. Specifically, our objectives were to (1) estimate the abundance, biomass, and population growth of the principal prey fish, the Utah Chub, in Scofield Reservoir; (2) quantify predator consumptive demand relative to prey supply; and (3) assess the relative performance of the three popular sport fishes (Cutthroat Trout, Rainbow Trout, and tiger trout) as predators and in meeting the needs of anglers. To satisfy these objectives, we estimated CPUE and collected fish for measurements of growth and diet, conducted hydroacoustic surveys of fish density, and assembled this information into bioenergetics simulations of predator population consumption to be compared with prey abundance and production. In addition, we provide one of the first documented rigorous ecological studies of the tiger trout, which is a relatively new hybrid species.

METHODS

Study site.—Scofield Reservoir is a high-elevation (2,322-m) impoundment on the Price River in central Utah (Figure 1). The reservoir was impounded by Scofield Dam in 1926 and is predominantly used for irrigation water storage, with recreation and flood control as additional benefits (Bureau of Reclamation 2010). The reservoir has a capacity of 90,800,000 m³ (73,600 acre-feet) at full pool, a mean surface area of 1,139 ha, and a mean depth of 8 m (Bureau of Reclamation 2009). Scofield Reservoir is characterized as eutrophic, with “excessive” total phosphorous enrichment (Utah Department of Environmental Quality 2010). The phytoplankton community is dominated by blue-green algae—indicative of poorer water quality—with blooms typically occurring in summer (June–August). The reservoir stratifies thermally in summer, and hypolimnetic oxygen deficits historically lead to fish kills of varying degrees (Hart and Birdsey 2008). Zooplankton composition is typically dominated by cladocerans *Daphnia* spp. at densities of 0.09 *Daphnia*/L and at a biomass of 1.5 µg/L in the summer (our unpublished data).



FIGURE 1. Map of Scofield Reservoir, Utah, showing the eight locations where fish were sampled in 2011 and 2012.

Scofield Reservoir supports an extremely popular recreational fishery. Historically, approximately 600,000 age-1 Rainbow Trout (150–250 mm TL) were stocked annually. However, during nearly every year since 2005, the fish stocking program has been adjusted in response to the re-appearance of Utah Chub in gill nets (Utah Chub were found in the reservoir multiple times before 2005 but were removed by chemical treatment). The goal of trout stocking in Scofield Reservoir has been to reduce the Utah Chub population before an expansion of a magnitude similar to that observed in Strawberry Reservoir, Utah, where over 90% of the gill-net catch consisted of Utah Chub and Utah Suckers *Catostomus ardens* (Lentsch et al. 2001; Hart and Birdsey 2008). Tiger trout and Bear Lake-strain Bonneville Cutthroat Trout, as well as alternative sport fishes, have been stocked in Scofield Reservoir as potential biological controls for Utah Chub. To date, these newer populations of trout have demonstrated little to no natural reproduction and have been artificially maintained, with approximately 100,000 individuals (175 mm TL) of each species stocked yearly. The only other species present in the reservoir are the Redside Shiner *Richardsonius balteatus* and Mountain Sucker *Catostomus platyrhynchus*.

Predator abundance.—We sampled fishes seasonally in Scofield Reservoir during July 2011 through October 2012.

We delimited seasons as spring (April–May), summer (June–August), and autumn (September–October). We selected index sites to be representative of the reservoir's longitudinal axis from the upper riverine zone to the lower lacustrine zone (McMahon et al. 1996) while maintaining consistency with long-term Utah Division of Wildlife Resources (UDWR) monitoring in order to monopolize on previously collected data.

Gillnetting was used to collect data with which to evaluate the size structure, growth rate, body condition, and diets of salmonids in the reservoir. Two horizontal sinking gill nets were set at each of eight index sites within the reservoir (Figure 1). These experimental gill nets (1.8 m tall × 24 m long, with eight monofilament panels of 38-, 57-, 25-, 44-, 19-, 64-, 32-, and 51-mm bar mesh) were set in accordance with standard gill-net methods to capture a representative size distribution of all fish in the reservoir (Beauchamp et al. 2009; Lester et al. 2009). We placed gill nets in littoral areas offshore at depths predicted to have the greatest abundance of fish; the nets were set before dusk and pulled after dawn, spanning two crepuscular periods. We calculated CPUEs (fish/net-hour [mean ± 1.96 SE]) at each sample site for each trout species and for Utah Chub. Within each season, we summed catches from all gill nets and divided by the total effort in order to estimate the seasonal reservoirwide CPUE. Relative abundances of each species were expressed as a percentage of CPUE. We conducted ANOVA to compare CPUEs among salmonid species and among seasons. All statistical analyses were performed using the GLIMMIX procedure in SAS (SAS Institute 2009) with an a priori α of 0.05.

Predator diet composition.—We analyzed the diets of Cutthroat Trout, Rainbow Trout, and tiger trout captured in gill nets seasonally from July 2011 through October 2012. All organisms in the stomach contents were identified to the lowest possible taxonomic level (Brooks 1957; Edmonson 1959; Merritt and Cummins 1996). Stomach contents were grouped into prey fish (identified to species when possible), zooplankton, organic matter, aquatic invertebrates (classified to order, including Amphipoda, Coleoptera, Diptera, Ephemeroptera, Hemiptera, Isopoda, Mollusca, and Trichoptera), and terrestrial invertebrates (classified to order). Prey fish were counted and weighed (blot-dry wet weight to the nearest 0.001 g), and invertebrate prey belonging to each classification were weighed en masse. We measured intact prey fish to the nearest millimeter (backbone and SL). For model simulations (described below), we calculated diet composition as the proportion by wet weight and then presented diet data as seasonally aggregated percentages. We delimited seasons as spring (April–May), summer (June–August), and autumn (September–October). We applied these seasonal diet data to the bioenergetics simulations for the appropriate size-classes and interpolated changes in diet composition between seasonal inputs.

Predator growth.—Annual mean size at age was estimated from a combination of otolith aging data, analysis of length frequency modes, and mark–recapture data (from dye-marked fish). Whole otoliths were aged independently by at least two laboratory personnel who were experienced in otolith aging. Otoliths were viewed under a microscope, and age was estimated by counting the opaque bands (annuli) from the center to the anterior edge. We then used size-at-age data sets to estimate annual growth (g/year) from July 2011 to July 2012. The resulting growth estimates were used as size-specific growth inputs in the bioenergetics simulations.

Thermal history.—We estimated the thermal history of the modeled cohorts of trout from a combination of monthly vertical temperature profiles and remote temperature data loggers that were placed at depths of 3, 6, and 9 m and attached to a stationary buoy on the reservoir for a full year. Temperature was recorded at 1-h intervals from July 19 to September 7, 2011, and from April 23, 2012, to June 7, 2013. To obtain a representative simulation year, these data were combined with monthly temperature profiles taken by a temperature probe. Because the depth distribution of gill-net catches varied throughout the water column and because the reservoir is shallow, we used the average of data from the three temperature loggers as the representative thermal history. All sizes and species of salmonid were modeled with the same temperature regime. To identify temperature sensitivity of model-estimated consumption, we also ran a set of simulations using the species' thermal optimum for consumption (CTO) assigned for each day that temperature data from the reservoir were available. The CTO of a fish represents the optimum water temperature needed for maximum achieved consumption based on laboratory studies (Hartman and Hayward 2007). This scenario assumes that the trout will behaviorally thermoregulate when possible (Budy et al. 2013).

Prey biomass and production.—Hydroacoustic surveys were conducted in Scofield Reservoir to provide density and abundance information on fishes larger than 100 mm TL. Surveys took place during the new moon event when fish were most likely to be dispersed; we did this to reduce the likelihood of fish associating with the lake bottom, where they could not be detected by the acoustic transducer. We conducted nighttime cross-reservoir transects covering a representative area of the reservoir. During August 2011 (year 1), 12 acoustic transects were performed, with distances ranging from 436 to 2,279 m and with mean depths ranging from 4.0 to 10.5 m. During June 2013 (year 2), due to lower water levels, 11 acoustic transects were surveyed, with distances ranging from 417 to 2,250 m and with mean depths ranging from 4.4 to 7.6 m. Data were collected by using a Biosonics Model DE6000 scientific echosounder with a 420-kHz dual-beam transducer ($6^\circ \times 15^\circ$), which was towed on a fin at 1-m depth while recording data using Biosonics Visual Acquisition software. We sampled at a rate of 2 pings/s traveling at a boat speed of 1–2 m/s (2–5 km/h). The pulse width of the signal was 0.4 ms. We processed acoustic target and density data

by use of Biosonics Visual Analyzer software; single-fish targets with dual-beam target strengths ranging from -48 to -32 dB represented 100-mm and larger individuals (Dahm et al. 1985). Only echoes that met the single-target shape criteria used by the analysis software were selected to calculate target strengths and densities. We treated transects as replicates in the analysis to produce mean density (fish/m³ [mean \pm SE]), and we then extrapolated the density to lakewide abundance by using lake volume.

To verify and apportion the acoustic targets, we used gill-net catch information collected near the time of the acoustic surveys (August 2011; and UDWR gill-net catch from May 2013). We summarized gill-net catch for each species and size-class (100–150, 151–250, 251–350, and >350 mm TL) and determined the percentage of species by size-class to delineate the acoustic-derived abundance estimates. We estimated abundance for Utah Chub smaller than 100 mm (both larval and juvenile) by extrapolating from literature values of survival and fecundity for Utah Chub and Tui Chub *Siphateles bicolor* (Olson 1959; Bird 1975; Jackson et al. 2004). Hydroacoustic results from both years were employed in further analyses, as this facilitated a comparison of spring abundance versus late-summer abundance after the important summer growth period (i.e., intense feeding period) for trout.

Utah Chub production (P_{chub} ; kg/year) during the 2011–2012 simulation period was estimated for four size (age) classes (<100 , 100–150, 151–250, and 251–350 mm) using mean body size from each size-class and biomass from hydroacoustic estimates. Production was estimated as

$$P_{chub} = G \times B,$$

where G is the instantaneous rate of growth (natural logarithm of the ratio of final weight to initial weight), and B is the mean biomass (kg; Ney 1993).

Bioenergetics modeling.—The Wisconsin bioenergetics model (Hanson et al. 1997) was used to estimate individual consumption of Utah Chub prey ($\text{g}\cdot\text{g}^{-1}\cdot\text{year}^{-1}$) by each predatory trout in the reservoir. For Rainbow Trout, we used physiological parameters for steelhead (anadromous Rainbow Trout; Rand et al. 1993). For Cutthroat Trout, we used their closest published taxonomic surrogates (i.e., steelhead) for most parameters. We based the lower CTO and the upper thermal maximum for consumption (CTM) on models described by others (Dwyer and Kramer 1975; Beauchamp et al. 1995; Ruzycski et al. 2001). For tiger trout, the closest published taxonomic surrogate was the Brown Trout, which we modeled similarly with parameters from Dieterman et al. (2004; see also Whitlegde et al. 2010).

We ran models over a time period of 1 year, initiated on July 26 and continued through July 25 of the following year. We accounted for an ontogenetic shift in diet preferences based on fish size in model simulations; at approximately 350 mm, trout switch from a predominantly invertebrate diet

to becoming increasingly piscivorous. Age-3 and age-5 cohort growth of each species was used as representative of small (<350 mm) and large (≥ 350 mm) size-classes, respectively, so annual growth could be most accurately estimated given available data. Additionally, we accounted for seasonal variation in feeding habits, incorporating diet proportions seasonally throughout the year. Predator and prey energy densities were derived from the literature, from data on taxonomically close surrogates, or both (Winters 2014). The percentage of indigestible prey biomass was set at 10% for all invertebrate prey, 3.3% for prey fish (Stewart et al. 1983), and 25% for crayfish (Stein and Murphy 1976). We scaled individual consumption estimates to the population level (g of prey fish/year) by using abundance estimates from hydroacoustic surveys for each size-class of predator species. The cumulative uncertainty (variance) in overall population-level consumption estimates was estimated via the delta method (Bajer et al. 2004).

Predator performance.—We used bioenergetic efficiency ($BioEff$) as a scalar representation of the realized percentage of maximum possible consumption ($\text{g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$; 0–100%) for each of the size-class models based on fish growth observed in the field (Budy et al. 2013). The $BioEff$ value is a proxy for overall fish performance as a predator: a $BioEff$ near 100% indicates that a fish is feeding near its maximum possible consumption rate (based on temperature, diet, and body size), whereas a $BioEff$ value near 0% indicates that the fish is performing poorly, feeding at a rate much lower than theoretically possible.

In addition to determining the performance of trout as predators, we were also interested in trout performance in terms of overall factors that are important to anglers (e.g., plump, trophy-sized fish). We calculated the condition of all predators by using two indices, Fulton's condition factor (K_{TL}) and relative weight (W_r),

$$K_{TL} = \left(\frac{W}{L^3}\right) \times 100,000,$$

$$W_r = 100 \times \left(\frac{W}{W_S}\right),$$

where W is the weight (g) of the fish, L is the total length (mm) of the fish, and W_S is the standard weight of a fish of the same length. The K_{TL} index assumes that larger ratios reflect a healthier physiological state (Pope and Kruse 2007). Equations and values of W_S for lentic Cutthroat Trout and lentic Rainbow Trout were obtained from the literature (Simpkins and Hubert 1996; Kruse and Hubert 1997). We estimated parameters for lentic tiger trout by using (1) a length–weight regression of summer 2011 tiger trout data ($r^2 = 0.97$, $a = -6.2159$, $b = 3.4608$) and (2) literature values for lotic Brown Trout (Milewski and Brown 1994). A W_r of 100 is generally accepted as the national standard (Anderson

and Neumann 1996). We used ANOVA to compare K_{TL} among trout species and among seasons.

RESULTS

Predator Population Estimation

From July 2011 to October 2012, we captured and processed 699 Cutthroat Trout, 111 Rainbow Trout, 398 tiger trout, and 8,489 Utah Chub. We netted fish throughout the lake, with equal effort applied at each site (Figure 1). Utah Chub dominated the Scofield Reservoir fish community and were the most abundant species, regardless of season. We collected approximately 5 Utah Chub per gill-net-hour in 2012 (CPUE [mean \pm 1.96 SE] = 3.3 ± 0.9 chub/net-hour in spring, 6.8 ± 1.2 chub/net-hour in summer, and 5.2 ± 0.5 chub/net-hour in autumn); these catch rates were lower than previously recorded from UDWR sampling in 2008 and 2009.

Trout catch rates varied among seasons and among species; during 2012, trout were caught more frequently in summer (CPUE [mean \pm 1.96 SE] = 0.242 ± 0.09 trout/net-hour) than in spring (CPUE = 0.216 ± 0.11 trout/net-hour) or autumn (CPUE = 0.089 ± 0.04 trout/net-hour; ANOVA: $F = 34.39$, $df = 2, 14$, $P < 0.001$). We caught more Cutthroat Trout than tiger trout, and very few Rainbow Trout were captured. There were no significant differences in catch between Cutthroat Trout and tiger trout.

Hydroacoustic-based estimates of abundance were notably different among species; in August 2011, Cutthroat Trout made up 14% of the total population, with an estimated 215,000 fish (Figure 2). Tiger trout were caught in similar numbers to Cutthroat Trout: abundance was estimated at 238,000 tiger trout, making up 15% of the total estimated population. Rainbow Trout exhibited extremely low estimates of abundance (<3%), with the population appearing to consist of only a small number (55,000) of individuals. Abundance estimates were similar in June 2013, with the exception of an increase in the Cutthroat Trout population. Proportionally, the Cutthroat Trout and tiger trout populations were dominated by large fish (≥ 350 mm TL; 81% of Cutthroat Trout and 80% of tiger trout); however, the population of all sizes of Rainbow Trout remained low. Notably, species relative abundances have shifted considerably since the Utah Chub's establishment in Scofield Reservoir, as Rainbow Trout exhibited peak catch rates in 2005 (when Utah Chub were first discovered) and have since declined, comprising a small proportion of the total catch (Figure 3).

Predator Diet Composition, Growth, and Thermal History

Utah Chub were the predominant prey item for large (≥ 350 -mm TL) Cutthroat Trout and large tiger trout throughout the year (Figure 4). The percentage of fish in the diets of large Cutthroat Trout ranged from 35% in autumn 2011 to 69% in summer 2012. For large tiger trout, prey fish represented 19–79% of their total diet, depending on the season. Only

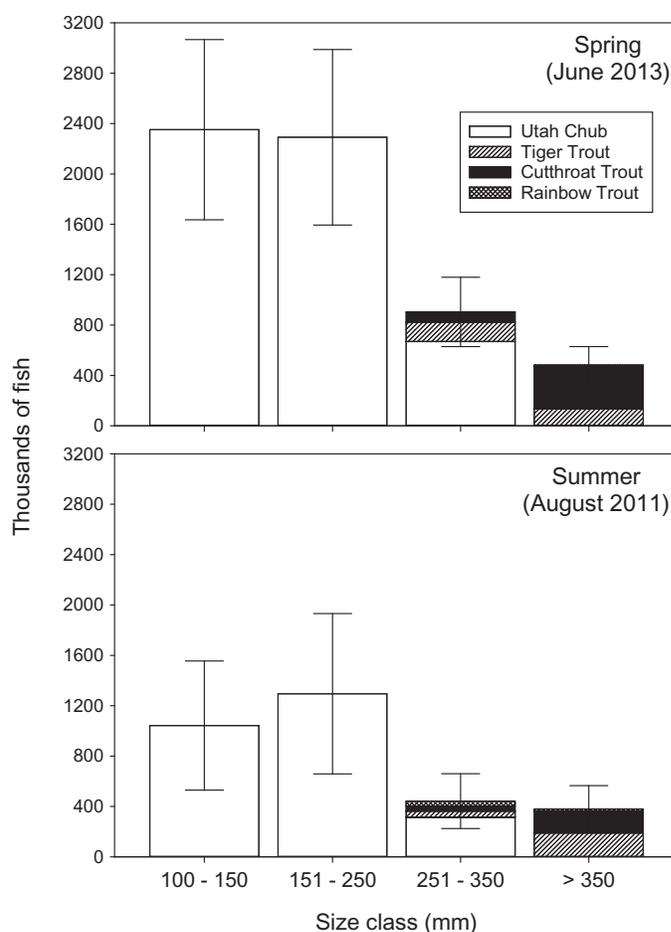


FIGURE 2. Abundance estimates (thousands of fish; \pm SE) for each size-class of Utah Chub and the three predatory trout species, as derived from hydroacoustic surveys conducted in Scofield Reservoir during spring (June 2013) and summer (August 2011).

one Redside Shiner and no trout were found in diets of the assessed trout species; thus, for simplicity, we assumed that all prey fish were Utah Chub. The relative importance of secondary food sources varied; large Cutthroat Trout relied heavily on Diptera and terrestrial invertebrates, whereas large tiger trout consumed significant portions of crayfish (likely northern crayfish *Orconectes virilis*). Aquatic invertebrates represented the largest diet proportion for small and large Rainbow Trout. Similarly, small Cutthroat Trout and small tiger trout relied heavily on aquatic invertebrates, terrestrial invertebrates, and crayfish (Winters and Budy 2015).

We determined annual growth estimates for a representative small size-class and large size-class of each trout species based on the most complete growth data available. For Cutthroat Trout, conservative estimates of starting and ending weight were used in bioenergetics simulations, as determined from length and weight changes in dye-marked cohorts (small Cutthroat Trout: 274–333 g; large Cutthroat Trout: 420–617 g). Rainbow Trout collected during both

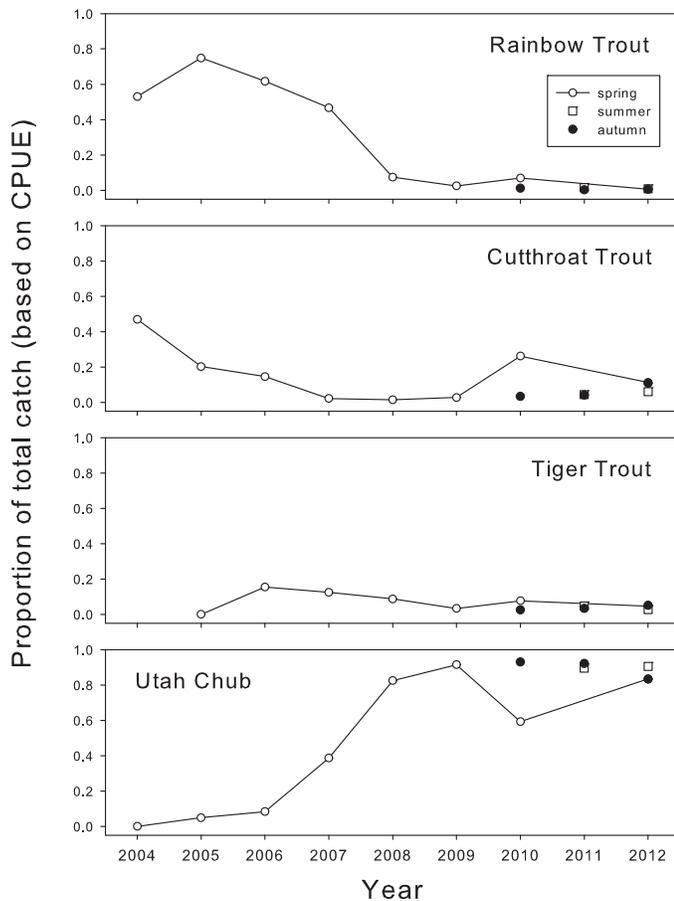


FIGURE 3. Proportion of total catch (based on CPUE) for each predatory trout species and for Utah Chub in Scofield Reservoir. Open circles represent data from yearly spring sampling conducted by the Utah Division of Wildlife Resources; additional summer and autumn points represent data collected for this study (metrics were calculated similarly).

2011 and 2012 ranged in age from 2 to 7 years as estimated via analysis of otoliths, with weight estimates based on size at age (small Rainbow Trout: 114–186 g; large Rainbow Trout: 495–614 g). There were no dye-marked cohorts of tiger trout in Scofield Reservoir; therefore, mean weight at size was determined from otolith size-at-age data only (small tiger trout: 134–327 g; large tiger trout: 761–1,901 g).

Maximum average daily temperature during the simulation period was 18.5°C. The CTO for Rainbow Trout was 20°C, which was higher than Rainbow Trout experienced in Scofield Reservoir. The CTO for tiger trout (17.5°C) was available in the reservoir during the summer months, and the CTO for Cutthroat Trout (14°C) was available throughout much of the study.

Prey Biomass and Production

The population abundance of Utah Chub (>100 mm TL; as estimated from hydroacoustic surveys) was 2,650,000 fish in August 2011. We estimated age-0 and age-1 Utah Chub

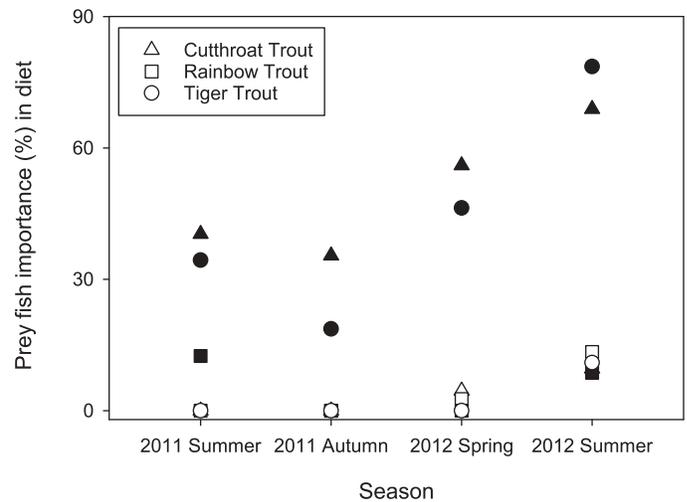


FIGURE 4. Prey fish importance (percentage by prey weight) in diets of Cutthroat Trout, Rainbow Trout, and tiger trout captured in Scofield Reservoir during each season. All fish found in the stomach contents were Utah Chub. Open symbols represent small trout, whereas shaded symbols represent large trout.

(those < 100 mm TL) as constituting an additional 9,027,000 fish in the population based on literature values of survival and eggs produced as back-calculated for the estimated adult population. Using biomass and mass gain by size-class, we estimated Utah Chub production at 226,000 kg/year (1,330,000 chub/year). There was nearly a doubling of small Utah Chub during June 2013 hydroacoustic surveys, soon after ice-off in the reservoir, leading to a much larger estimate of standing biomass (Figure 2).

Bioenergetics Simulations of Consumption

Of all the examined predator species, individual large tiger trout consumed the largest proportion of prey fish, primarily Utah Chub. The average large tiger trout consumed over 2,660 g of prey fish in a given year (63 chub/year; Table 1). The average large Cutthroat Trout consumed 1,820 g of Utah Chub annually (49 chub/year). The mean TL of Utah Chub that were consumed by Cutthroat Trout was 131 mm (37 g), and the mean TL of Utah Chub eaten by tiger trout was 139 mm (42 g). We used these prey sizes to scale the consumption estimates (by mass, g) to the number of Utah Chub. Rainbow Trout did not demonstrate significant piscivory; an individual large Rainbow Trout consumed only 400 g of Utah Chub in a year. The smaller sizes of trout (<350 mm TL) made only a minor contribution toward the overall consumption of Utah Chub prey.

When the estimated consumption by an individual predator was scaled to the overall reservoirwide population of each trout species, proportional contributions to total piscivory changed accordingly. The population of large Cutthroat Trout in the reservoir consumed over 315,000 ± 18,300 kg (mean ± variance) of Utah Chub (8.6 million chub) in a year, equivalent to about 38% of the overall reservoirwide consumption of Utah

TABLE 1. Estimates of annual Utah Chub consumption (g) by Cutthroat Trout, Rainbow Trout, and tiger trout at the individual predator level (g) and at the population level (kg). Consumption is presented for two representative size-classes of each predator for the 2011–2012 simulation year. Variance (calculated using the delta method) is reported at the population level for large trout only.

Size-class	Individual level		Population level			
	Consumption (g)	Number of Utah Chub consumed	Abundance	Consumption (kg)	Variance (kg)	Number of Utah Chub consumed
Cutthroat Trout						
Small	110	3	40,000	4,500		123,000
Large	1,820	49	175,000	318,000	18,000	8,600,000
Total	1,930	52	215,000	322,500		8,723,000
Rainbow Trout						
Small	90	3	40,000	3,600		117,000
Large	400	13	15,000	6,000	1,400	196,000
Total	490	16	55,000	9,600		313,000
Tiger trout						
Small	60	2	49,000	3,000		73,000
Large	2,660	63	190,000	505,000	312,000	12,016,000
Total	2,720	65	239,000	508,000		12,089,000

Chub (using the population estimate from the August 2011 hydroacoustic surveys, as this was during the bioenergetics simulation year). The highly piscivorous population of tiger trout contributed 60% of the overall consumption, consuming over $500,000 \pm 312,000$ kg of Utah Chub (12.0 million chub) per year. The Rainbow Trout population contributed less than 1% of the total piscivory in Scofield Reservoir. Scenarios where we assumed that the fish behaviorally thermoregulated and chose CTO when available did not strongly influence the estimated predators' consumption of Utah Chub; Cutthroat Trout consumption at CTO was less than 1% lower, and tiger trout consumption was less than 2% lower.

The combined consumption by Cutthroat Trout and tiger trout exceeded the annual production estimate of Utah Chub. Large Cutthroat Trout and large tiger trout alone consumed over 20 million chub, exceeding the combined estimate of 13 million Utah Chub as calculated based on abundance and annual production (Figure 5).

Predator Performance

Bioenergetics simulations indicated that *BioEff* values for all predator species were lower than 100%, suggesting that the fish were not feeding at their maximum possible predicted consumption rate. Cutthroat Trout fed at approximately 39% of maximum consumption, whereas Rainbow Trout fed more efficiently at 47% of their maximum consumption, and tiger trout were the most efficient, feeding at 56% of their maximum rate during the 2011–2012 simulation year. Additionally, Cutthroat Trout and tiger trout both exhibited lower *BioEff* with larger size.

The K_{TL} data additionally supported *BioEff* results. There were no significant differences in K_{TL} among seasons (ANOVA: $F = 0.89$, $df = 2, 14$, $P > 0.05$); however, there were notable condition differences among species (ANOVA: $F = 14.27$, $df = 2, 14$, $P < 0.001$). Cutthroat Trout exhibited the significantly lowest overall performance, with K_{TL} decreasing from 0.89 to 0.82 as seasons progressed. Overall performance of Rainbow Trout was substantially higher than that of Cutthroat Trout, but their K_{TL} also decreased seasonally from 0.97 to 0.90. Tiger trout performed overall best in the summer ($K_{TL} = 0.96$), with lower condition in the spring and autumn.

During summer 2012, all three species of trout exhibited W_r values that were significantly lower than standard performance (all t -tests: $P < 0.001$). Average W_r was 79 for both Cutthroat Trout and Rainbow Trout, where a W_r less than 80 is considered "severely thin" (Murphy et al. 1991). The average W_r for tiger trout was much higher (96) and representative of fish in relatively good condition. When standard values for lotic Brown Trout (Milewski and Brown 1994) were substituted into the tiger trout calculations, the average W_r decreased to 90, indicating that feeding conditions were suboptimal or that the fish were subject to competition.

DISCUSSION

In response to the rapid increase of the Utah Chub, an unwelcome invader, in Scofield Reservoir during recent years, we used a combination of field sampling, hydroacoustic surveys, and bioenergetics simulations for three top predators

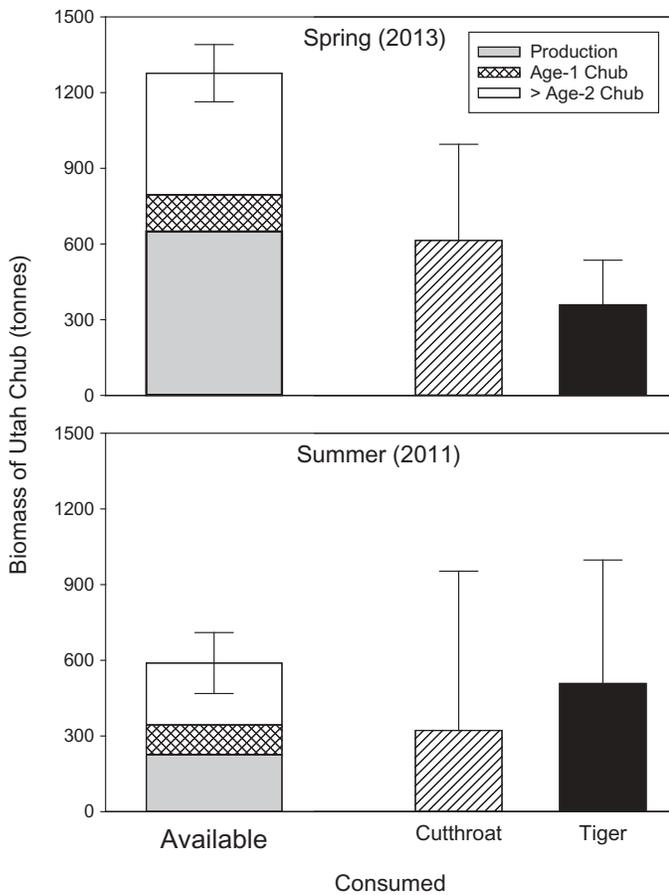


FIGURE 5. Comparison of Utah Chub abundance and annual production (“available”; $\pm 95\%$ confidence interval derived from hydroacoustic estimates of abundance) versus estimates of annual Utah Chub consumption by large Cutthroat Trout and tiger trout (“consumed”; \pm variance calculated using the delta method) in Scofield Reservoir based on spring (upper panel) and summer (lower panel) hydroacoustic surveys.

in the system to quantitatively assess the relative potential of these trout species to act as biological control agents. Comparison of Utah Chub consumption revealed striking differences among the three trout species, with important management implications. The population of large (≥ 350 -mm) tiger trout consumed the largest proportion of Utah Chub in Scofield Reservoir. Large tiger trout are voracious predators, collectively consuming an estimated 505,000 kg of Utah Chub in a single year. Furthermore, based on model simulations, large Cutthroat Trout relied heavily on Utah Chub as well, consuming almost 320,000 kg of Utah Chub annually at the population level. In contrast, Rainbow Trout did not consume a significant number of Utah Chub in Scofield Reservoir, and the surviving population of stocked Rainbow Trout was so small that their collective impact on Utah Chub was insignificant. Overall, comparisons between bioenergetic estimates of predator consumption versus Utah Chub production demonstrated that tiger trout and Cutthroat Trout both have

significant potential to act as effective agents of biological control on Utah Chub, whereas the strain of Rainbow Trout stocked into Scofield Reservoir currently contributes little to Utah Chub control or to realized angler satisfaction.

Utah Chub were caught in extremely high densities throughout our study period, confirming that the Utah Chub population has increased to very high levels that justify management concerns. Fish standing stock in Scofield Reservoir likely exceeds the standing stock commonly found in productive lakes in terms of Utah Chub biomass. Over the course of the study, hydroacoustic abundance estimates for the reservoir were 2.65–5.30 million Utah Chub larger than 100 mm TL and 9 million Utah Chub smaller than 100 mm, and Utah Chub production occurred at a rate of 1.3 million chub/year. However, it is important to note that our abundance and production estimates for Utah Chub are very likely to be conservative due to a few important assumptions used in this study: (1) acoustic surveys excluded targets within 1 m of the surface and at least 1 m off the lake bottom and were only able to clearly account for fish 100 mm and larger; and (2) the values for age-0 and age-1 Utah Chub were necessarily back-calculated based on literature estimates of fecundity and survival for Utah Chub and Tui Chub (Olson 1959; Bird 1975; Jackson et al. 2004). Nonetheless, our results are logical and consistent with expected values from similar prey-dominated systems. Eilers et al. (2011) estimated that up to 23 million Tui Chub were present in Diamond Lake, Oregon, before a prescribed rotenone treatment, with a density of “catchable” Tui Chub being equal to 0.09 fish/m³. Comparatively, we estimated Utah Chub densities of 0.04–0.13 fish/m³. The high production rates of Utah Chub in Scofield Reservoir are thus not surprising and are most likely attributable to high reproductive capability, favorable littoral habitat, and an abundant food supply (Neuhold 1957; Olson 1959; Sigler and Sigler 1996).

Despite these high densities of Utah Chub, our bioenergetics model predictions demonstrated that the large Cutthroat Trout population could consume more than half the standing prey biomass in Scofield Reservoir annually, highlighting this species’ potential to serve as an efficient biological control agent. The disparity between total consumption (21.1 million chub) and production (1.3 million chub) suggests that Cutthroat Trout exert strong predation pressure on Utah Chub. Bear Lake-strain Bonneville Cutthroat Trout, the strain stocked into Scofield Reservoir, are known to exhibit traits of top-level predators and attain large sizes when using fish as forage (Neilson and Lentsch 1988; Hepworth et al. 1999, 2009). In Lake Chelan, Washington, consumption of kokanee (lacustrine Sockeye Salmon *O. nerka*) by Lake Trout *Salvelinus namaycush* similarly exceeded kokanee production rates, leading to an almost 90% decline in the kokanee population over 5 years (Schoen et al. 2012). We estimate that an individual Cutthroat Trout in Scofield Reservoir can consume 1.8 kg of Utah Chub annually, similar to the annual consumption of Tui Chub (2.4–3.1 kg) by an individual large Lahontan Cutthroat Trout *O. clarkii henshawi* in Pyramid Lake, Nevada (Heredia 2014). Prey size is also an important factor determining

consumption (Scharf et al. 2000), and Cutthroat Trout in Scofield Reservoir were found to consume prey at and above their theoretical gape limit, as TLs of Utah Chub prey were up to 60% of predator TL (Winters 2014; Winters and Budy 2015). Therefore, although we underestimated one or more components of Utah Chub production (Jackson et al. 2004), our observations and those of others collectively support the argument that these piscivorous trout species can be used to effectively control Utah Chub in Scofield Reservoir if other environmental conditions remain the same.

Despite a paucity of literature on tiger trout ecology, tiger trout were similar to Cutthroat Trout in demonstrating the aggressive and piscivorous nature that was expected of this relatively new hybrid species. Tiger trout in Scofield Reservoir displayed strong predation impacts on Utah Chub prey, as well as relatively high catch rates, high condition metrics, and modest *BioEff* values. Furthermore, tiger trout have high proportional stock density (and relative stock density) values, indicating the species' importance to the Scofield Reservoir sport fishery (Winters 2014): the Utah state record tiger trout (currently 8.675 kg and 953 mm) has consistently been caught from Scofield Reservoir. Based on their popularity among anglers and their hypothesized biological control potential, tiger trout are currently being stocked in 40 bodies of water throughout Utah to potentially enhance fisheries and consume undesirable prey species (Utah Division of Wildlife Resources 2015). Furthermore, tiger trout have the added benefit that they are sterile hybrids and are unable to permanently expand beyond where they are stocked—an important conservation consideration for native species and ecosystems downstream (Zelasko et al. 2010).

Our study indicates that the Rainbow Trout, a ubiquitous and popular species stocked throughout the western USA and a potential top predator, does not contribute substantial predation pressure on Utah Chub in Scofield Reservoir. At least a dozen strains of Rainbow Trout are stocked worldwide, and they display a range of piscivory (Hudy and Berry 1983; Swales 2006). Rainbow Trout have demonstrated piscivory at sizes as small as 100 mm TL (Juncos et al. 2013) and at sizes greater than 250 mm TL (Beauchamp 1990) and are broadly documented to feed on fish prey at least seasonally (Galbraith 1967; Taylor and Gerking 1980; Juncos et al. 2011). For example, Haddix and Budy (2005) found that Rainbow Trout in Flaming Gorge Reservoir, Utah–Wyoming, performed poorly overall, consumed primarily aquatic invertebrates and zooplankton, and rarely demonstrated an ontogenetic shift to piscivory at larger sizes. In addition, the Rainbow Trout strain that is stocked into Scofield Reservoir likely originates from the Eagle Creek (California) strain, whose diet does not contain fish prey (Hubert et al. 1994; Wagner 1996). Consequently, it is unsurprising that these Rainbow Trout contributed little to the biological control of Utah Chub in Scofield Reservoir.

Poor overall performance of Rainbow Trout may also be due to competition for resources with other sport or nongame

species or to behavioral avoidance of other predatory species. In a laboratory experiment that was designed to supplement this study, Hafen and Budy (2015) demonstrated that Rainbow Trout initiated more aggressive interactions than either Cutthroat Trout or tiger trout; such behaviors may lead to reduced energy reserves and poor survival in natural environments. Rainbow Trout in Scofield Reservoir occupy an omnivorous trophic niche space, which is similar to the niche space of Utah Chub and trophically below the piscivorous niche space of Cutthroat Trout and tiger trout (Winters and Budy 2015). Thus, although Rainbow Trout are stocked at relatively large sizes and in large quantities into the reservoir, the presence of other top predators and competitors (including Utah Chub) in the system may influence the feeding and behavior of the Rainbow Trout, leading to their low apparent survival and possibly low realized growth potential in addition to their minimal biological control of Utah Chub.

In contrast to Rainbow Trout, the superior overall performance of Cutthroat Trout and tiger trout in Scofield Reservoir is likely largely due to their ontogenetic transition to a more piscivorous diet. Cutthroat Trout in the reservoir switch to a Utah Chub-based diet at around 300 mm TL. In contrast, Cutthroat Trout in a very unproductive reservoir (Bear Lake, Utah–Idaho) did not become piscivorous until 380 mm TL, and very high mortality of these adult age-classes was observed (Ruzycki et al. 2001). In Strawberry Reservoir, Utah, the diet of stocked Bear Lake-strain Cutthroat Trout was dominated by *Daphnia* prey, whereas fish prey only represented a small fraction of their diet (Baldwin et al. 2000). Additionally, piscivores may interact strongly with prey populations in one system while interacting very weakly, if at all, with the same prey species in other systems—an observation of interest in the context of a widely stocked, relatively new hybrid like tiger trout (Rudolf 2012). The superior overall performance of the tiger trout stocked in Scofield Reservoir also contradicts observations in at least one other Utah reservoir (data on tiger trout are still somewhat limited). Tiger trout that were stocked in Panguitch Lake, Utah, during 2006 demonstrated poor survival and were found in limited numbers during annual gill-net surveys, but prey may have been limiting due to a recent rotenone treatment (Hepworth et al. 2009). Those tiger trout were also annually stocked at a smaller size (75 mm) than the 150-mm TL individuals stocked into Scofield Reservoir. Similarly, tiger trout in eastern Washington lakes rarely became piscivorous, even in the presence of a dense Redside Shiner population (Miller 2010). In contrast, however, the superior performance of tiger trout in Scofield Reservoir was similar to that observed in High Savery Reservoir, Wyoming, where state record catches of tiger trout have become an annual occurrence (Carrico 2012). Although somewhat variable elsewhere, the strong overall performance we observed for tiger trout—both as predators

and in meeting angler desires—reflects their potential to provide biological control and to support a valuable sport fishery when conditions are suitable.

In our study, several different lines of evidence consistently demonstrated that piscivorous trout exerted a strong predatory effect on Utah Chub; however, there were some notable uncertainties associated with our bioenergetics estimates. Metabolic costs of activity, respiration, and thermal habitat parameters for Cutthroat Trout were borrowed from studies of steelhead, and parameters for tiger trout were borrowed from studies of the Brown Trout, one of the parent species of tiger trout (Ney 1990; Dieterman et al. 2004; Whitley et al. 2010). This choice is justified, as tiger trout have been generally accepted to behave similarly to Brown Trout, and no studies to date have quantified the consumption potential of this unique hybrid species. Nonetheless, borrowing parameters from other species could produce unreliable or biased results, especially when the physiology of the species varies. Sources of uncertainty can be amplified when growth rates are high, as in the present study (Bajer et al. 2004). These discrepancies may explain the estimated *BioEff* values and may have led to underestimation or overestimation of consumption (Ney 1993; Chipps and Wahl 2008; Hartman and Kitchell 2008). Although the borrowing of parameters from related species is a common practice (e.g., Beauchamp et al. 1995; Beauchamp and Van Tassel 2001; Ruzycki et al. 2001), more species-specific parameter estimates could improve bioenergetics predictions, specifically for the tiger trout.

Predator control of non-fish organisms as nuisance prey has been variable in effectiveness. Despite a common discussion of failure to biologically control target species (Williamson and Fitter 1996), Simberloff (2009) argued that many species have been successfully eradicated and other species have been maintained at low densities for long periods of time. Consequently, pessimism surrounding the potential to eradicate invasive species or manage them at very low densities may be unwarranted. The species-specific models presented herein were based on wild fish, natural prey, and ecologically realistic temperature ranges, which typically results in models with reasonable predictive capability (Mesa et al. 2013). Others have used a similar approach to predict consumption by Brook Trout (Hartman and Cox 2008), Bull Trout *Salvelinus confluentus* (Mesa et al. 2013), Chinook Salmon *O. tshawytscha* (Madenjian et al. 2004), hybrid sunfish (Green Sunfish *Lepomis cyanellus* × Bluegill *Lepomis macrochirus*; Whitley et al. 1998), and Burbot *Lota lota* (Paakkonen et al. 2003). Thus, we believe that our results represent a plausible reflection of the consumption occurring in Scofield Reservoir and indicate strong potential for Cutthroat Trout and tiger trout to act as effective biological control agents of undesired prey fish into the future.

Management Implications

The present findings contribute to our understanding of the potential for stocked fish predators to act as biological control

agents of unwelcome forage fishes. Our results suggest that the high rates of piscivory displayed by Cutthroat Trout and tiger trout in artificial lentic ecosystems are likely sufficient to effectively reduce the Utah Chub's overall abundance and potential to dominate fish assemblages if other environmental conditions do not change dramatically. Furthermore, since 2009, there has been a drastic reduction in Utah Chub catch rates, and the population no longer appears to be increasing. A simple cohort trend analysis of stocked trout over time—based on annual survival estimates of 87% for Cutthroat Trout and 52% for tiger trout—demonstrated that when Scofield Reservoir reached a threshold population level, the trout population began controlling Utah Chub (i.e., the Utah Chub population growth rate declined; Budy et al. 2014). In addition to preventing an increase in Utah Chub, we estimate that managers should maintain a minimum of 320,000 trout in the reservoir, ideally with a species composition that is skewed toward tiger trout over Cutthroat Trout. Based on this simple analysis, we predict that by 2021, very few large adult Utah Chub (i.e., those unsusceptible to predation) will remain in Scofield Reservoir, and we anticipate biological control.

Additionally, Scofield Reservoir tiger trout that are caught by anglers have been of state record status, an exciting aspect of this new fishery. Management regulations that protect large Cutthroat Trout and tiger trout and increase predator densities may provide the predation pressure that is necessary to further suppress overabundant Utah Chub populations, whereas Rainbow Trout have little potential to be responsive to management manipulations in this system. In other work, we demonstrated that Cutthroat Trout and tiger trout are capable of consuming Utah Chub up to 50% of their own size, whereas Rainbow Trout potentially share niche space with Utah Chub (Winters and Budy 2015). A shift from the stocking of Rainbow Trout to stocking tiger trout and Cutthroat Trout may be warranted, especially if Utah Chub reduction is the overall management goal. In addition, herein we have provided some of the first recorded quantitative findings on tiger trout ecology and performance. Careful scrutiny of the current system as well as management goals and objectives should be taken into consideration when determining management actions for other reservoir systems.

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