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Ecosystem ecology meets adaptive management: food web response to a controlled flood on the Colorado River, Glen Canyon

Wyatt F. Cross,[1,2,7] Colden V. Baxter,[3] Kevin C. Donner,[3] Emma J. Rosi-Marshall,[4] Theodore A. Kennedy,[5]
Robert O. Hall, Jr.,[2] Holly A. Wellard Kelly,[4] and R. Scott Rogers[6]

[1]*Department of Ecology, 310 Lewis Hall, Montana State University, Bozeman, Montana 59717 USA*
[2]*Department of Zoology and Physiology, University of Wyoming, Laramie, Wyoming 82071 USA*
[3]*Department of Biology, Idaho State University, Pocatello, Idaho 83209 USA*
[4]*Cary Institute of Ecosystem Studies, Millbrook, New York 12545 USA*
[5]*U.S. Geological Survey, Southwest Biological Science Center, Flagstaff, Arizona 86001 USA*
[6]*Arizona Game and Fish Department, Flagstaff, Arizona 86001 USA*

Abstract. Large dams have been constructed on rivers to meet human demands for water, electricity, navigation, and recreation. As a consequence, flow and temperature regimes have been altered, strongly affecting river food webs and ecosystem processes. Experimental high-flow dam releases, i.e., controlled floods, have been implemented on the Colorado River, USA, in an effort to reestablish pulsed flood events, redistribute sediments, improve conditions for native fishes, and increase understanding of how dam operations affect physical and biological processes. We quantified secondary production and organic matter flows in the food web below Glen Canyon dam for two years prior and one year after an experimental controlled flood in March 2008. Invertebrate biomass and secondary production declined significantly following the flood (total biomass, 55% decline; total production, 56% decline), with most of the decline driven by reductions in two nonnative invertebrate taxa, *Potamopyrgus antipodarum* and *Gammarus lacustris*. Diatoms dominated the trophic basis of invertebrate production before and after the controlled flood, and the largest organic matter flows were from diatoms to the three most productive invertebrate taxa (*P. antipodarum*, *G. lacustris*, and Tubificida). In contrast to invertebrates, production of rainbow trout (*Oncorhynchus mykiss*) increased substantially (194%) following the flood, despite the large decline in total secondary production of the invertebrate assemblage. This counterintuitive result is reconciled by a post-flood increase in production and drift concentrations of select invertebrate prey (i.e., Chironomidae and Simuliidae) that supported a large proportion of trout production but had relatively low secondary production. In addition, interaction strengths, measured as species impact values, were strongest between rainbow trout and these two taxa before and after the flood, demonstrating that the dominant consumer–resource interactions were not necessarily congruent with the dominant organic matter flows. Our study illustrates the value of detailed food web analysis for elucidating pathways by which dam management may alter production and strengths of species interactions in river food webs. We suggest that controlled floods may increase production of nonnative rainbow trout, and this information can be used to help guide future dam management decisions.

Key words: dam; high-flow experiment; organic matter flows; regulated river; secondary production; species interactions; trophic basis of production.

Introduction

Human alteration of ecosystems is a global phenomenon with serious consequences for biological diversity, energy and material cycling, climate, and human well-being (Vitousek et al. 1997, Chapin et al. 2000). Changes to physical characteristics of landscapes can create novel biological assemblages that tolerate or even thrive in altered physical conditions (With 2002, Johnson et al. 2008). Such changes can affect ecosystem-level processes because species composition and consumer–resource interactions govern flows of energy and materials (Carpenter et al. 1985, Jones and Lawton 1995, Schmitz 2010). Highly altered ecosystems, therefore, may serve as endpoints for examining how changes in assemblage structure influence function, and detailed study of these ecosystems can help develop key management and restoration strategies (Hobbs and Huenneke 1992, Stanford et al. 1996).

River regulation (via dam construction) represents a pervasive alteration of the landscape, and has led to unprecedented changes in river flow regime, temperature regime, and sediment delivery worldwide (Nilsson et al. 2005, Poff et al. 2007, Olden and Naiman 2010).

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[7] E-mail: wyatt.cross@montana.edu

Regulation of large rivers can cause substantial ecological discontinuities that facilitate introduction and establishment of invasive species (Bunn and Arthington 2002, Johnson et al. 2008), which can modulate flows of energy and materials. Although many studies have documented structural changes to river assemblages below dams (e.g., Englund and Malmqvist 1996, Stevens et al. 1997, Vinson 2001), few have constructed detailed flow food webs for these heavily altered ecosystems. Characterization of energetic and material flows in food webs is much more informative than structural information (i.e., abundance, biomass, diversity) because flows can be used to test hypotheses related to consumer–resource interaction strengths, the potential for food limitation, and the importance of animals in whole-ecosystem material cycling (Hall et al. 2003, Cross et al. 2007, Benke and Huryn 2010). Moreover, flow-based food webs can identify key pathways of materials in ecosystems (Hall et al. 2000) and can provide a mechanistic framework to inform adaptive management decisions regarding changes in flow regime, species introductions, and temperature mitigation (Kennedy and Gloss 2005). Despite the high potential of this approach, it has not yet been applied to adaptive management (sensu Holling 1978, Walters 2002) of river ecosystems.

Water managers and policy makers increasingly recognize that human needs can be balanced with maintained ecological integrity of freshwater ecosystems (Baron et al. 2002, Postel and Richter 2003, Richter et al. 2003). Many management decisions for regulated rivers are now geared towards restoring the "natural" river ecosystem with regard to physical characteristics, while still maintaining water availability for a variety of human uses (Arthington and Pusey 2003, Allan and Castillo 2007). For example, controlled floods aim to restore geomorphic processes as well as key components of the natural disturbance regime that are necessary for many aquatic organisms (Poff et al. 1997, Patten et al. 2001, Robinson and Uehlinger 2008). These controlled floods represent ecosystem-level experiments that can advance our understanding of the ecosystem, thereby informing future management decisions in an adaptive management framework (Walters 2002, Poff et al. 2003). However, these floods are most useful for adaptive management if detailed process-based research is conducted before, during, and after the experimental event (Souchon et al. 2008).

The Glen Canyon Adaptive Management Program implemented three controlled floods on the Colorado River, USA, in March 1996, November 2004, and March 2008. These experimental floods were geared towards partially restoring the natural disturbance regime and redistributing tributary-derived fine sediment to build sandbars for recreational use (Patten et al. 2001). In addition, these floods aimed to restore backwater habitat for downstream native fishes (e.g., humpback chub, *Gila cypha*), while maintaining a productive, nonnative rainbow trout (*Oncorhynchus mykiss*) fishery in the 25-km tailwater reach below Glen Canyon Dam. Previous research examining the influence of these floods on the Colorado River food web has focused predominantly on assemblage structural attributes, reporting changes in abundance and biomass of dominant taxa over relatively short time scales (Shannon et al. 2001, Valdez et al. 2001). While these studies are extremely useful for short-term assessment of river assemblage responses to experimental floods, process-based studies of food web interactions and ecosystem processes are needed to help inform future adaptive management decisions.

Here we present a three-year analysis of secondary production and flow food webs in the tailwater reach of the Colorado River below Glen Canyon Dam. Our primary objective was to build detailed flow food webs (sensu Benke and Wallace 1997, Hall et al. 2000) to characterize and understand the response of the river food web to a 60-h controlled flood in March 2008. Our approach allowed us to (1) elucidate dominant pathways of material flow in the food web, (2) assess the potential for food limitation of predatory rainbow trout, and (3) quantify variation in consumer–resource interaction strengths. We show that trout production increased following the flood, despite a large reduction in total invertebrate production. This counterintuitive result is reconciled by flow food web analysis that demonstrates increased availability and consumption of highly palatable prey items following the flood. In particular, prey items that benefitted from the flood were taxa that most likely limit rainbow trout production and for which trout exhibit the highest interaction strengths. Our results underscore the value of detailed food web analysis for supporting decision-making in an adaptive management framework and provide quantitative information that can be used in predictive modeling of future water release scenarios on the Colorado River.

Methods

Study site

The Colorado River watershed includes a large area ($\sim$629 000 km^2) of the western United States and drains portions of seven states on its path toward the Gulf of California. Six major dams regulate flow in the lower Colorado River basin, and the timing and magnitude of discharge is now largely determined by fluctuating demand for irrigation water and electricity (Topping et al. 2003). Since completion of Glen Canyon dam in 1963, river flow, temperature, and sediment delivery in the Colorado River have been altered (Gloss et al. 2005), leading to significant changes in the river ecosystem and establishment of many nonnative invertebrate taxa (Blinn and Cole 1991, Stevens et al. 1997). In 1995, New Zealand mudsnails (*Potamopyrgus antipodarum*) were discovered below Glen Canyon Dam and have since become a dominant component of the invertebrate assemblage (Cross et al. 2010).

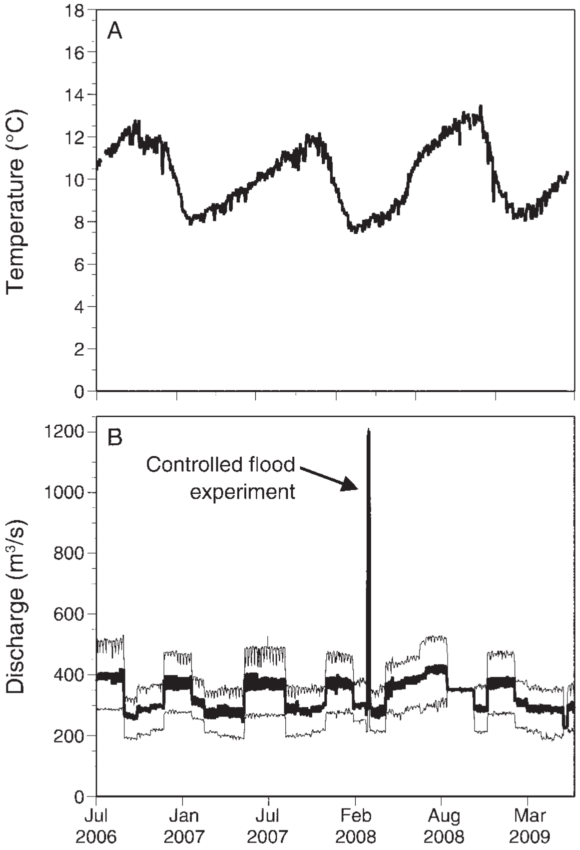

FIG. 1. (A) Mean daily water temperature and (B) daily discharge (mean in thick black line, with minimum and maximum shown with thin black lines) in the Colorado River, Glen Canyon, Arizona, USA, between July 2006 and June 2009. Panel B shows the timing of the controlled flood.

We studied the 25-km segment of the Colorado River directly downstream of Glen Canyon Dam near Page, Arizona. River discharge originates from the hypolimnion of Lake Powell, and water temperature at the downstream end of the reach (Lees Ferry) is relatively cold throughout the year (mean daily temperature was 10.1°C during July 2006–June 2009; Fig. 1A) with low diel fluctuation (0.5°–1°C). There are no perennial tributaries in this segment and, consequently, the water is clear for all but a few days of the year. River width and thalweg depth average ~120 m and 7 m, respectively, at a discharge of 325 m^3/s (Grams et al. 2007; P. E. Grams, *unpublished data*). Discharge varies widely on a diurnal, seasonal, and annual basis to meet shifting demands for hydroelectric power and water delivery (Topping et al. 2003). Downstream of Glen Canyon, in Grand Canyon National Park, river characteristics change markedly because of gradual river warming and seasonal inputs of tributary sediment and organic matter (Carothers and Brown 1991).

River substrata in Glen Canyon consist of variably sized talus, cobble–gravel bars, cliff faces, and sandy depositional zones. Filamentous algae (predominantly *Cladophora glomerata*) dominate river biofilms throughout most of the year (Angradi and Kubly 1993), and sloughing and transport peak in the spring (Shannon et al. 1996; T. A. Kennedy, *unpublished data*). Fish species richness in Glen Canyon is low (predominantly rainbow trout, brown trout, and common carp), and nonnative rainbow trout constitute >95% of abundance and biomass (McKinney et al. 2001, Gloss and Coggins 2005).

Between 5 and 9 March 2008, a controlled flood experiment was conducted below Glen Canyon Dam (Fig. 1B). This experimental flood lasted ~60 hours, with a maximum discharge of ~1200 m^3/s. The magnitude of this controlled flood, as well as previous experimental floods, was only ~50% of the average annual pre-dam flood (Topping et al. 2003).

Invertebrate abundance, biomass, and production

We quantitatively sampled dominant benthic habitats for invertebrates each month between July 2006 and June 2009. Habitat classes included cobble/gravel bars, talus/cliff faces, and fine-grained depositional zones (hereafter referred to as cobble/gravel, talus/cliff, and depositional, respectively). The number of samples collected from habitats was roughly proportional to their areal contribution based on habitat surveys ($n = 5$ for cobble/gravel and talus/cliff, and $n = 10$ for depositional; see *Habitat area estimation* below). We sampled cobble/gravel habitat with a Hess sampler (0.085 m^2, 250-μm mesh size) to a depth of ~10 cm, and depositional zones with a standard Ponar dredge sampler (0.052 m^2) deployed from a motor boat. Talus/cliff habitat was sampled with a custom suction device (battery-powered submersible bilge pump connected to pool hosing, a Nitex bag and dolphin bucket [250-μm mesh]). Each suction sample consisted of 30 sequential intakes, totaling a sample area of 0.066 m^2. We sampled during minimum daily discharge (usually between 06:00 and 09:00 h) to ensure that samples were collected from the permanently wetted zone (Blinn et al. 1995).

We preserved samples in the field (70% EtOH) and brought them to the laboratory for subsequent processing. Each sample was rinsed onto nested sieves (pore sizes 1 mm and 250 μm), and material retained on each sieve was elutriated to separate organic from inorganic material. All invertebrates were removed from the large fraction (>1 mm) at 10× magnification, counted, and total body lengths measured (nearest 0.5 mm) on the first 30 individuals encountered of each taxon. Prohibitively large samples were subsampled using a device modeled after the Folsom Plankton Splitter (Wildco, Buffalo, New York, USA). Organic material in the smaller fraction (i.e., <1 mm and >250 μm) was placed in a known volume of water, suspended in a modified Imhoff cone (Wards Natural Science, Rochester, New York, USA) with forced air, and subsampled (by volume) with a 60-mL plastic syringe. Invertebrates in subsamples were removed at 15× magnification, counted, and measured to the nearest 0.5 mm (first 30 encountered of each taxon). Individuals counted but not measured were assumed to have the same size distribution as those that were directly measured on that date. Biomass of each taxon was calculated for each habitat on each date using either length–mass relationships developed for Glen Canyon or literature-based relationships (Benke et al. 1999, Cross et al. 2010; USGS Grand Canyon Monitoring and Research Center, *unpublished data*).

We estimated annual secondary production (ash free dry mass; g $\text{AFDM}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) of invertebrate taxa using methods most appropriate for each taxon (Benke 1993, Benke and Huryn 2006). The instantaneous growth method was used to quantify production of New Zealand mudsnails (*P. antipodarum*) and *Gammarus lacustris* by applying empirically derived size-specific growth rates (g; d^{-1}) from Glen Canyon: for *P. antipodarum,* $g = -0.006 \times$ shell length in millimeters $+ 0.029$; for *G. lacustris,* $g = -0.016 \times \ln$(body length measured in millimeters) $+ 0.042$ (Cross et al. 2010). We also used the instantaneous growth method to estimate production of dominant Oligochaeta taxa using either literature-based size-specific growth rates (Lumbricidae; Barne and Striganova 2005) or application of a constant daily growth rate (0.0095 d^{-1}) derived from initial and final body size (3 mm and 23 mm, respectively) and a maturation time of 7.5 months (Tubificidae; Poddubnaya 1980; estimate based on moderate density and temperature). For Chironomidae, we used the size- and temperature-specific equation of Huryn (1990). This equation, based on a different geographic region, may lead to a small error in our production estimates. However, large variability in biomass across samples and sampling dates should far outweigh variation driven by potential differences in individual growth rates. For other taxa with overlapping and/or indistinguishable cohorts, we used the size–frequency method corrected with our best estimate of cohort production intervals (CPIs) based on size frequency data (Turbellaria, Simuliidae, Physidae; Hamilton 1969, Benke 1979, Benke and Huryn 2006). For the few remaining taxa (Acari, Ceratopogonidae, Cladocera, Copepoda, Sphaeridae, Ostracoda, Nematoda), we multiplied mean annual biomass values by appropriate production : biomass (P:B) ratios (Table 1). Error in our production estimates based on the size frequency method or P:B ratios (i.e., all taxa except *P. antipodarum*, *G. lacustris*, Oligochaeta, and Chironomidae) would have little effect on our results as these taxa only represented 4% of assemblage-wide mean habitat-weighted biomass.

We used bootstrap analysis to generate 95% confidence intervals for mean annual abundance, biomass, and production according to Benke and Huryn (2006). Briefly, size-specific abundance data from replicate samples in each habitat on each date were resampled with replacement 1000 times to generate vectors of mean size-specific abundance and biomass. For those taxa in which we applied the instantaneous growth method, each of the biomass estimates was multiplied by size-specific growth rates and the time interval between sampling dates to generate 1000 estimates of interval production. These estimates were summed across sampling intervals to generate a vector of annual production. For production estimates that used the size frequency method, two sources of variation were included in bootstrapped estimates: (1) resampled abundance data and (2) randomly selected CPIs within a restricted range based on size frequency data (e.g., between 335 and 365 days; selected from a normal distribution). Vectors of annual abundance, biomass, and production were generated for each taxon in each habitat. Habitat-weighted vectors (1000 values) were generated by multiplying values in each habitat-specific vector by the relative proportion of that habitat per average square meter. These values were summed across habitats to generate habitat-weighted vectors. Means and the 2.5% and 97.5% quantiles were calculated from habitat-weighted vectors.

Habitat area estimation

We quantified the area of dominant habitat types in Glen Canyon at 48 linear transects (approximately every 0.3 km to 0.5 km) between 9.7 km and 24 km below Glen Canyon Dam with a motorized boat and an underwater video sled (see Cross et al. 2010 for details). At each transect, linear habitat proportions were estimated visually using timed videos, total ferry time (in minutes), and total river width (in meters). Major habitat categories used for our analysis corresponded to the three major habitats sampled for invertebrates and comprised 52% depositional, 27% cobble/gravel, and 21% talus/cliff.

Rainbow trout abundance, biomass, and secondary production

Abundance of rainbow trout was estimated in Glen Canyon on three to four dates per year between 2006 and 2009. On each date, 34–36 reaches were surveyed with single-pass boat electro-fishing, half of which were fixed monitoring locations and the other half were randomly distributed among representative habitats (as described in McKinney et al. 1999). The number of fish captured during these monitoring surveys was used to generate population estimates for the entire Glen Canyon segment. A capture probability (0.095) was estimated by comparing data from two previous years (2000 and 2004) during which both monitoring and whole population estimates via mark–recapture were conducted (Arizona Game and Fish Department, *unpublished data*). River conditions (e.g., clarity, conductivity) during this earlier period were similar to the years of our study. We assumed a constant capture probability among sample dates, and our main source of error was associated with

TABLE 1. Abundance (N), biomass (B), production (P), and production : biomass ratios (P:B) of invertebrates and rainbow trout (*Oncorhynchus mykiss*) in the Colorado River, Glen Canyon, USA.

	Abundance (number/m^2)		Biomass (mg AFDM/m^2)		Production (mg AFDM·m^{-2}·yr^{-1})		
Taxon	N	CI	B	CI	P	CI	$P:B$
Year 1 (July 2006–June 2007)							
P. antipodarum	144 257	(106 946–191 497)	4366	(3353–5525)	13 259^{a}	(10 238–16 677)	3.0
Gammarus lacustris	3562	(2753–4430)	1186	(861–1574)	7010^{a}	(5398–9000)	5.9
Tubificida (a)	41 728	(33 913–51 997)	1262	(1040–1498)	4287^{a}	(3543–5068)	3.4
Turbellaria	1501	(1255–1775)	150	(115–195)	754^{a}	(577–983)	5.0
Physidae	352	(215–527)	146	(104–193)	1077^{a}	(676–1625)	7.4
Lumbricidae	284	(215–368)	331	(237–436)	706^{a}	(526–905)	2.1
Chironomidae	5801	(4404–7381)	85	(65–109)	559^{a}	(433–690)	6.6
Ostracoda	1889	(1405–2374)	54	(37–75)	274^{a}	(183–377)	5.0
Nematoda	922	(754–1111)	12	(9–14)	116^{a}	(95–142)	10.0
Sphaeridae	204	(66–421)	23	(8–44)	116	(41–219)	5.0
Simuliidae	33	(7–66)	8	(3–13)	49^{a}	(21–83)	6.1
Cladocera	1676	(1162–2234)	4	(3–5)	37	(26–50)	10.0
Copepoda	3822	(2719–4981)	4	(3–5)	36	(26–47)	10.0
Tubificida (b)	83	(52–118)	7	(4–11)	57	(28–109)	8.1
Ceratopogonidae	3	(<1–7)	<1		0.8	(0.0–2.0)	3.21
Acari	54	(18–108)	<1		1^{a}	(0.2–2)	5.0
Total invertebrates	206 431	(167 650–255 012)	7649	(6533–8894)	28 339^{a}	(24 448–32 246)	3.7
Oncorhynchus mykiss	0.013	(0.011–0.015)	596	(510–692)	183^{a}	(157–210)	0.3
Year 2 (July 2007–June 2008)							
P. antipodarum	58 834	(44 834–73 509)	4280	(3044–6014)	10 664^{a}	(6800–17 042)	2.5
Gammarus lacustris	3754	(2957–4601)	1384	(1062–1732)	8685^{a}	(6536–10 995)	6.3
Tubificida (a)	19 996	(16 649–23 569)	808	(674–964)	2859^{b}	(2322–3477)	3.5
Turbellaria	748	(582–938)	77	(58–98)	382^{b}	(287–489)	5.0
Physidae	311	(142–539)	128	(48–241)	494^{b}	(373–627)	3.9
Lumbricidae	2190	(1110–3461)	2254	(1149–3787)	5469^{b}	(2543–9401)	2.4
Chironomidae	6268	(5353–7167)	152	(111–201)	657^{a}	(548–757)	4.3
Ostracoda	734	(564–903)	14	(11–18)	70^{b}	(53–90)	5.0
Nematoda	939	(673–1248)	13	(9–17)	127^{a}	(92–167)	10.0
Sphaeridae	40	(4–83)	6	(<1–12)	29	(2–58)	5.0
Simuliidae	311	(153–484)	70	(25–121)	348^{b}	(141–604)	5.0
Cladocera	2455	(896–4637)	5	(2–9)	46	(17–85)	10.0
Copepoda	4109	(2783–5515)	3	(2–4)	29	(19–40)	10.0
Tubificida (b)	27	(15–40)	3	(2–5)	27	(12–46)	9.0
Ceratopogonidae	2	(0–5.8)	<1		0.1	(0.0–0.3)	6.0
Acari	2	(<1–5)	<1		0.1^{a}	(0.0–0.3)	5.0
Total invertebrates	101 276	(86 508–117 367)	9132	(7266–11 366)	29 886^{a}	(23 896–37 372)	3.3
Oncorhynchus mykiss	0.014	(0.012–0.016)	515	(417–635)	140^{a}	(117–166)	0.3
Year 3 (July 2008–June 2009)							
P. antipodarum	19 008	(15 123–23 579)	863	(692–1045)	1998^{b}	(1644–2389)	2.3
Gammarus lacustris	1475	(1158–1851)	588	(455–762)	2647^{b}	(2091–3346)	4.5
Tubificida (a)	34 289	(29 243–40 099)	1168	(990–1375)	3933^{ab}	(3312–4665)	3.4
Turbellaria	711	(587–838)	116	(86–150)	577^{ab}	(428–748)	5.0
Physidae	173	(134–213)	91	(69–116)	500^{b}	(388–626)	5.5
Lumbricidae	216	(123–357)	376	(253–505)	634^{a}	(428–859)	1.7
Chironomidae	8373	(6960–9882)	252	(190–330)	937^{b}	(808–1072)	3.7
Ostracoda	446	(357–560)	6	(5–7)	31^{c}	(26–36)	5.0
Nematoda	1737	(1490–2015)	21	(18–25)	215^{b}	(184–249)	10.0
Sphaeridae	122	(83–164)	12	(9–17)	62	(43–85)	5.0
Simuliidae	912	(576–1337)	222	(124–350)	1177^{c}	(672–1824)	5.3
Cladocera	3359	(2227–4614)	5	(4–7)	53	(36–73)	10.0
Copepoda	6987	(5405–8725)	4	(3–5)	37	(29–46)	10.0
Tubificida (b)	152	(102–216)	23	(16–32)	86	(53–124)	3.7
Ceratopogonidae	1	(<1–2)	<1		<1	(0.0–0.0)	11.2
Acari	5	(1–9)	<1		<1	(0.0–0.0)^{b}	5.0
Total invertebrates	78 153	(70 884–86 015)	3749	(3386–4153)	12 876^{b}	(11 700–14 185)	3.4
Oncorhynchus mykiss	0.056	(0.048–0.064)	847	(742–960)	467^{b}	(406–532)	0.6

Notes: Numbers in parentheses are bootstrap percentile 95% confidence intervals. Different lowercase superscript letters indicate significant differences in production among years for each taxon (nonoverlapping confidence intervals). Ash free dry mass is abbreviated as AFDM.

variation in abundance among sampled reaches. Size-specific biomass was calculated for each reach on each date using a fork length–mass relationship developed in Glen Canyon (R. S. Rogers, *unpublished data*). On each sampling date, a subsample of trout (n = 8–24) representing a range of size classes was sacrificed, and their gut contents were removed and preserved in 95% ethanol (see *Gut content analysis* below).

Secondary production of rainbow trout was estimated with the instantaneous growth rate method (Benke 1993, Benke and Huryn 2006). Size-specific growth rates were derived from length-at-age data from Glen Canyon (R. S. Rogers, *unpublished data*). Bootstrap analysis (as described above for invertebrates in *Invertebrate abundance, biomass, and production*) was used to generate bootstrap percentile 95% confidence intervals for annual values. In brief, the size-specific abundance data from replicate samples on each date were resampled with replacement 1000 times to generate vectors of mean size-specific abundance and biomass. Each of these biomass estimates was multiplied by size-specific growth rates and the time interval between sampling dates to generate estimates of interval production, which were summed across intervals to generate vectors of annual production. Annual secondary production (g $\mathrm{AFDM{\cdot}m^{-2}{\cdot}yr^{-1}}$) was estimated on a per square meter basis.

Gut content analysis

To quantify the proportion of dominant food resources consumed by invertebrates, we used standard gut content analysis (Benke and Wallace 1980, Hall et al. 2000). Invertebrates were collected seasonally from multiple sites in Glen Canyon between June 2006 and January 2009 and immediately preserved in Kahle's solution (Stehr 1987). We quantified the proportions of food types in the diets of *G. lacustris*, *P. antipodarum*, Lumbricidae, Tubificidae, Simuliidae, and non-Tanypodinae Chironomidae. These taxa represented between 88% and 96% of total annual production. Dissected gut contents were sonicated, filtered onto gridded Metricel membrane filters (25 mm diameter, 0.45 μm pore size; Pall Corporation, Ann Arbor, Michigan, USA), and mounted on slides using Type B immersion oil and nail polish sealant. For preparation of each slide, we used gut contents from one to four individuals of each taxon. During each sampling date, two to four slides for each taxon were analyzed. Approximately 50 food particles from each slide were identified along random transects and their area measured using a phase-contrast compound microscope (100×, and 400× to confirm difficult identifications) equipped with a digital camera and image analysis software (ImagePro Plus, Media Cybernetics, Bethesda, Maryland, USA). Particles were categorized as either: diatoms, filamentous algae, amorphous detritus, leaf material, fungi, macrophytes, or animal material. For each slide we calculated the proportion of each food item in the gut by dividing the area of each category by the total area of the 50 particles measured. For trophic basis of production calculations (see next section), we applied average values from multiple slides.

We examined diet composition of rainbow trout on 11 dates between 2006 and 2009 (total $n = 164$). For each individual, we removed the foregut contents and manually separated the dominant food categories (i.e., filamentous algae/epiphytes, terrestrial plant material, terrestrial invertebrates, and aquatic invertebrates). We further separated aquatic invertebrates into groups at the same level of taxonomic resolution as benthic invertebrate samples. For each individual, diet categories were oven-dried at 60°C for 24 h and weighed. Final dietary proportions were based on the proportion that each food item contributed to total dry mass. Diet proportions were averaged across all individuals analyzed in a given season. Diets of age zero fish ($n = 40$) were examined and analyzed separately from age-1+ fish.

Trophic basis of production and flow food webs

We quantified annual organic matter flows through the food web using the trophic basis of production method which estimates (1) contributions of different food resources to animal production and (2) rates of resource consumption that support measured rates of animal production (Benke and Wallace 1980). For each taxon, seasonal proportions of food types consumed during a given year were averaged to obtain annual average proportions. The relative fraction of annual production attributed to each food type (F_i) was calculated as

$$F_i = (G_i \times \mathrm{AE}_i \times \mathrm{NPE}) \tag{1}$$

where G_i is the proportion of food type i in a consumer's gut, AE_i is the assimilation efficiency of food type i, and NPE is the net production efficiency. The actual amount of consumer j's production attributed to each food type (PF_{ij} measured in g $\mathrm{AFDM{\cdot}m^{-2}{\cdot}yr^{-1}}$) was calculated as

$$\mathrm{PF}_{ij} = \frac{F_i}{\sum_{i=1}^{n} F_i} \times P_j \tag{2}$$

where P_j = annual secondary production (g $\mathrm{AFDM{\cdot}m^{-2}{\cdot}yr^{-1}}$) of consumer j. Lastly, annual flows from each food type i to consumer j (FC_{ij} measured in g $\mathrm{AFDM{\cdot}m^{-2}{\cdot}yr^{-1}}$) were calculated as

$$\mathrm{FC}_{ij} = \frac{\mathrm{PF}_{ij}}{\mathrm{AE}_i \times \mathrm{NPE}}. \tag{3}$$

We used the following assimilation efficiencies for invertebrate consumers: diatoms 0.3, amorphous detritus 0.1, leaf litter 0.1, filamentous algae 0.3, macrophytes 0.1, fungi 0.7, and animal material 0.7 (Bärlocher and Kendrick 1975, Benke and Wallace 1980, 1997). Assimilation efficiencies used for rainbow trout were: most aquatic invertebrates 0.75, Physidae 0.15, *P. antipodarum* 0.09 (Vinson and Baker 2008), terrestrial invertebrates 0.7, terrestrial plant material 0.05, filamentous algae/epiphytes 0.1 (see Leibfried 1988, Angradi 1994). Error in annual estimates of organic matter flows was quantified by resampling secondary production (randomly selected between the maximum and minimum values assuming a uniform distribution) and NPE values (randomly selected between 0.2 and 0.3 for age-0 and age-1 rainbow trout and between 0.075 and 0.15 for larger age 2–7 rainbow trout; held constant at 0.5 for invertebrates; Benke and Wallace 1980) to generate 1000 estimates of annual flows.

Although there are multiple approaches for estimating production and consumption by fishes (e.g., bioenergetics models; Kitchell et al. 1977, Hanson et al. 1997), we opted to use the instantaneous growth method and trophic basis of production approach because we had detailed information on size-specific growth rates from Glen Canyon and we wished to avoid uncertainties associated with applying bioenergetic model parameters from other ecosystems and taxa to Glen Canyon. Nonetheless, our annual estimates of production and consumption agreed with those based on the Wisconsin bioenergetics model (Hanson et al. 1997).

To examine the strength of interactions between trout predators and their prey, we calculated "species impact" (SI) values for each year of the study following Wootton (1997). SI values were calculated as

$$\mathrm{SI} = \frac{\mathrm{FC}_{ij}}{B_i} \qquad (4)$$

where FC_{ij} is the mean annual flow (g $\mathrm{AFDM \cdot m^{-2} \cdot yr^{-1}}$) of a given prey item to a predator, and B_i is the mean annual habitat-weighted biomass of that prey item (g $\mathrm{AFDM/m^2}$). The units of this metric are ($\mathrm{yr^{-1}}$), and can thus be directly compared with annual biomass turnover rates of prey (i.e., P : B ratios).

We visually compared bootstrap percentile 95% confidence intervals to examine differences among years in secondary production, trophic basis of production, organic matter flows, and species impact values. Means with nonoverlapping confidence intervals were interpreted as significantly different.

Invertebrate drift concentration

To examine patterns of concentration and composition of invertebrates in the drift before and after the controlled flood, we measured daytime rates of invertebrate drift at Lees Ferry monthly between October 2007 and October 2009 following McKinney et al. (1999). We used a plankton net with a 50-cm opening, 0.25-mm mesh, and 1:5 ratio of opening diameter to net length (to minimize back-pressure and clogging) outfitted with a flow-meter (General Oceanics, Miami, Florida, USA). Depth-integrated samples were collected from the thalweg by slowly raising and lowering the weighted net (45 kg sounding mass) using a hand-powered winch. Triplicate samples were collected at five evenly spaced intervals between 07:00 and 19:00 h, preserved in the field, and processed as above for benthic invertebrates. The volume of water filtered, which was used to determine concentrations of organisms in drift, was typically 10–80 $\mathrm{m^3}$. Bootstrap analysis was used to generate 95% confidence intervals for concentrations of drifting invertebrates.

RESULTS

Physical characteristics

Mean daily water temperature in Glen Canyon varied between 7.5°C and 13.5°C during the three-year study, with maximum and minimum temperatures occurring in November and February, respectively (Fig. 1A). Mean daily discharge varied between 225 $\mathrm{m^3/s}$ and 433 $\mathrm{m^3/s}$, except during the controlled flood when discharge was held at ~1200 $\mathrm{m^3/s}$ for 60 hours (Fig. 1B). In general, mean daily discharge was higher in summer and winter than autumn and spring, and there was considerable daily and hourly variation (Fig. 1B).

Biomass and secondary production

Total invertebrate secondary production declined following the flood. Annual habitat-weighted invertebrate production was similar (overlapping 95% CIs) and relatively high in years one and two of the study, averaging 28.3 g $\mathrm{AFDM \cdot m^{-2} \cdot yr^{-1}}$ and 29.9 g $\mathrm{AFDM \cdot m^{-2} \cdot yr^{-1}}$, respectively (Table 1). In contrast, total invertebrate production was significantly reduced in year three (12.9 g $\mathrm{AFDM \cdot m^{-2} \cdot yr^{-1}}$; Table 1) following the controlled flood.

The two-fold reduction in year three production was largely driven by declines in *P. antipodarum* (84% lower in year three relative to years one and two) and *G. lacustris* (66% lower in year three relative to years one and two; Table 1, Fig. 2), although there was substantial interannual variability in production of other taxa. The invertebrate assemblage was relatively species-poor and unevenly distributed with regard to secondary production, particularly during the first two years of study (Table 1, Fig. 2). For example, four taxa (*P. antipodarum*, *G. lacustris*, Tubificida (a), and Lumbricidae) represented between 89% and 93% of invertebrate production in years one and two (Table 1). Following the flood, production was more evenly distributed among taxa, but the four aforementioned taxa still represented 71% of total invertebrate production (Table 1, Fig. 2). Despite reduced whole-assemblage production following the flood, a few taxa significantly increased their production in year three relative to years one and two (i.e., Chironomidae, Simuliidae, Nematoda; Table 1, Fig. 2).

Annual patterns in invertebrate biomass closely followed production (Table 1), but mean monthly habitat-weighted biomass varied greatly (Fig. 3). Biomass peaked in autumn and early winter of each year. In months prior to the controlled flood (March 2008), *P. antipodarum* dominated invertebrate biomass (average of 51% of total biomass; Fig. 3), but their contribution declined substantially in months following the flood (19% of total biomass). Similarly, biomass of *G. lacustris* was reduced by the flood, but their relative contribution to total biomass did not change (~12–14%; Fig. 3; see Appendix A for habitat-specific biomass and error estimates).

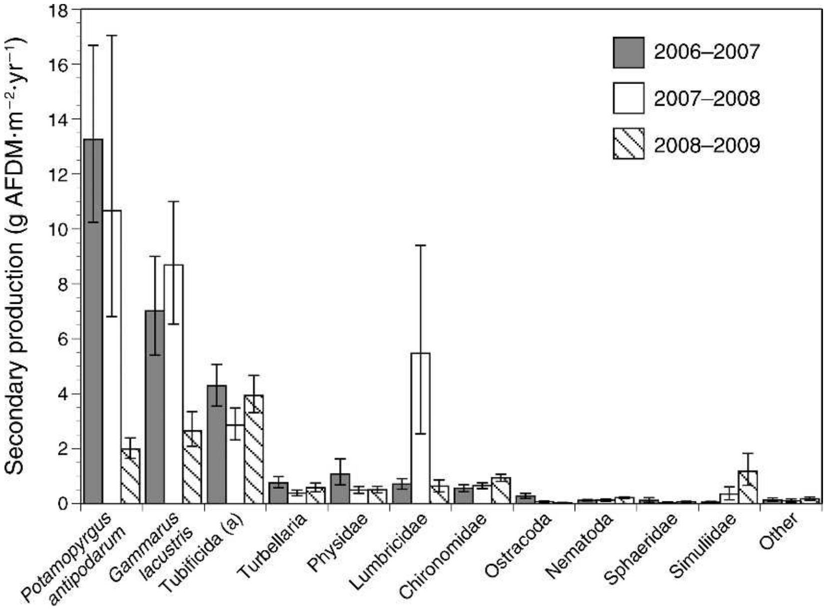

FIG. 2. Annual habitat-weighted invertebrate secondary production (ash free dry mass; g AFDM·m^{-2}·yr^{-1}) was dominated by relatively few taxa and was considerably higher in 2006–2007 and 2007–2008 relative to 2008–2009. Error bars represent bootstrap percentile 95% confidence intervals. The "Other" category includes Cladocera, Copepoda, Tubificida (b), Ceratopogonidae, and Acari.

Trout production increased after the flood. Annual production of rainbow trout averaged 0.18 and 0.14 g AFDM·m^{-2}·yr^{-1} in years one and two of the study (Table 1). In year three, following the flood, rainbow trout production increased significantly (+194%; to 0.47 g AFDM·m^{-2}·yr^{-1}) despite the reduced production of the invertebrate assemblage. Increased survival, abundance, and instantaneous growth rates of age-0 and age-1 fish drove this increase in production following the controlled flood (Korman et al. 2011; see Appendix B for size frequency histograms over time).

Flow food webs and trophic basis of production

At the base of the food web, the dominant flows were from diatoms and amorphous detritus to the three most productive taxa: *P. antipodarum*, *G. lacustris*, and Tubificida (black arrows in Fig. 4). Consumption by these three taxa alone represented 89%, 79%, and 72% of total organic matter flows to invertebrates in years one, two, and three, respectively. Overall patterns of consumption were similar in years one and two, but flows to Lumbricidae increased significantly in year two (Fig. 4B). Following the flood (2008–2009), total flows of organic matter to invertebrates declined significantly (i.e., year three flows were 39% of years one and two; Fig. 4C), but flows to a few taxa increased (e.g., Chironomidae and Simuliidae; Appendix C), reflecting increases in their secondary production.

Organic matter flows to rainbow trout were relatively diverse and included a variety of aquatic and terrestrial invertebrate taxa, as well as filamentous algae and leaf litter (gray arrows in Fig. 4). The highest magnitude flow in all years was of filamentous algae (predominantly *Cladophora glomerata*), representing between 30% and 40% of total consumption by trout. Annual consumption by rainbow trout was similar in years one and two (year one, 3.6 g AFDM·m^{-2}·yr^{-1} [95% CI: 2.5–5.3]; year two, 2.1 g AFDM·m^{-2}·yr^{-1} [1.5–2.9]), but increased by ~80% following the flood (year three, 5.1 g AFDM·m^{-2}·yr^{-1} [4.0–6.4]). Trout ate more Chironomidae, Simuliidae, and *G. lacustris*, following the flood, yet there were significant interannual differences for most prey types (Appendix D). In general, patterns of consumption by invertebrates and rainbow trout were represented by few large- and many small-magnitude flows (Fig. 4; Appendices C and D).

Invertebrate production was predominantly supported by those items that were consumed the most (Fig. 5A). For example, diatoms fueled between 68% and 76% of invertebrate production, while amorphous detritus supported an additional 14–21% (Fig. 5A). Proportional contributions of basal resources to invertebrate production varied significantly among years (see Appendix E), but these differences were relatively small in magnitude ($\leq$10%).

Relatively few invertebrate taxa supported rainbow trout production, and this pattern did not parallel consumption (i.e., Fig. 4) of prey (Fig. 5B). The largest contributors to trout production were *G. lacustris*, Simuliidae, and Chironomidae (Fig. 5B). Two of these taxa (i.e., Simuliidae and Chrionomidae) supported between 43% and 50% of trout production, but only comprised a small percentage of total invertebrate secondary production (i.e., 2–3% before the flood and

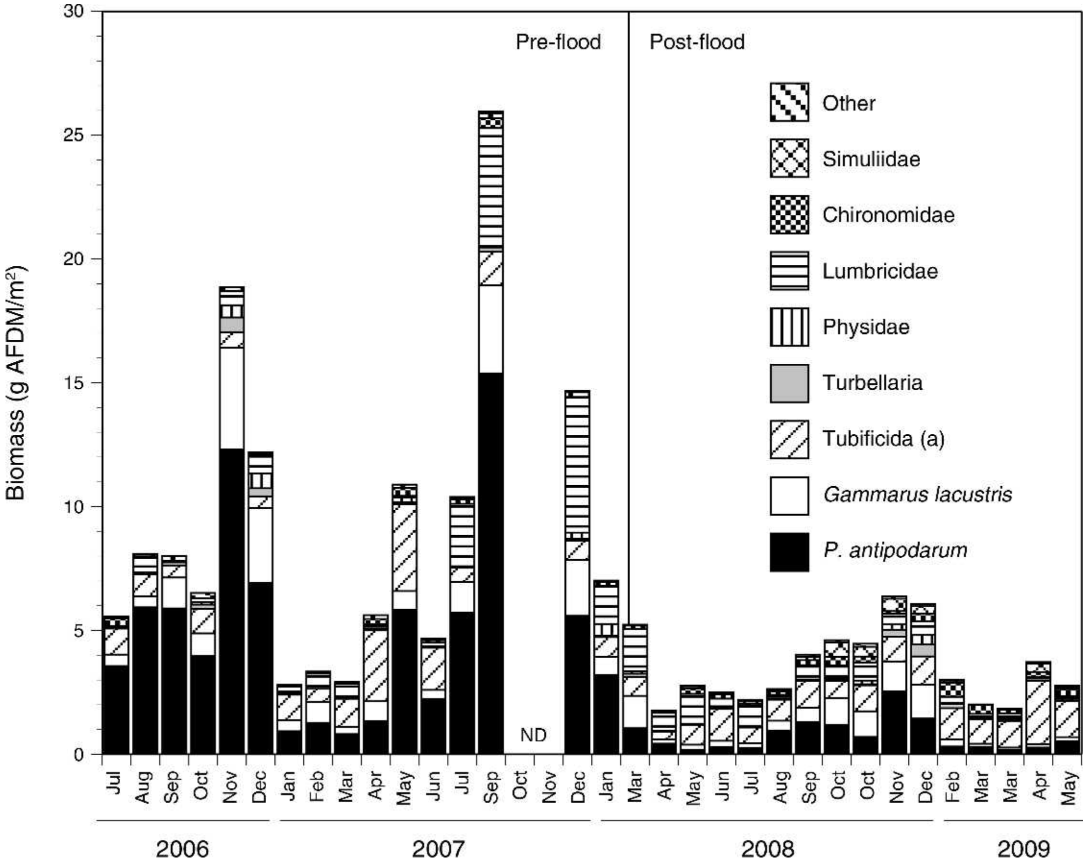

FIG. 3. Mean monthly habitat-weighted invertebrate biomass (g AFDM/m^2) was dominated by *P. antipodarum* and *G. lacustris*, declined following the controlled flood, and was generally highest during autumn months. ND indicates no habitat-weighted data due to missing depositional samples in October and November 2007. The "Other" category includes Cladocera, Copepoda, Tubificida (b), Ceratopogonidae, Acari, Ostracoda, and Nematoda. The vertical line represents the timing of the controlled flood. Missing months indicate that no samples were taken; duplicate months indicate that samples were taken twice during that month (usually the beginning and end).

16% after the flood). Although trout consumed large amounts of filamentous algae, this food item was unimportant in fueling trout production (Figs. 4 and 5) because its assimilation efficiency is low relative to invertebrates. Proportional contributions of food resources to rainbow trout production differed significantly among years (Appendix E). Most notably, the contribution of Simuliidae increased in each successive year, while the proportional contribution of Chironomidae declined (Fig. 5B; Appendix E).

The potential for food limitation of rainbow trout appeared to be low before and after the flood based on ecosystem-wide estimates of invertebrate production and trout demand (Fig. 6). Total invertebrate production far exceeded annual demands of rainbow trout in all years, resulting in large annual surpluses of invertebrate prey regardless of whether *P. antipodarum* (a taxon with very high production, but limited consumption and assimilation by trout) were included (Fig. 6). In contrast, detailed comparisons of taxon-specific production and trout demand revealed potential for food limitation during all three years, with strongest potential during year 1 (Table 2). In particular, annual consumption of Simuliidae overlapped with estimates of Simuliidae production during all three years of the study. In addition, consumption of Chironomidae did not differ from Chironomidae production during years one and three (Table 2).

Species impact

Species impact values (yr^{-1}), calculated as flows (g AFDM·m^{-2}·yr^{-1}) to rainbow trout divided by mean annual biomass of prey (g AFDM/m^2; Wootton 1997), revealed that trout interacted most strongly with a small subset of the invertebrate assemblage, and this impact varied among years (Fig. 7). Species impact values overlapped with or were higher than mean annual P : B values of Chironomidae and Simuliidae, demonstrating that trout consumption keeps up with (and is comparable to) biomass turnover of these prey. Species impact values were much lower for other dominant prey, and consistently fell below the average prey P : B values (Fig. 7).

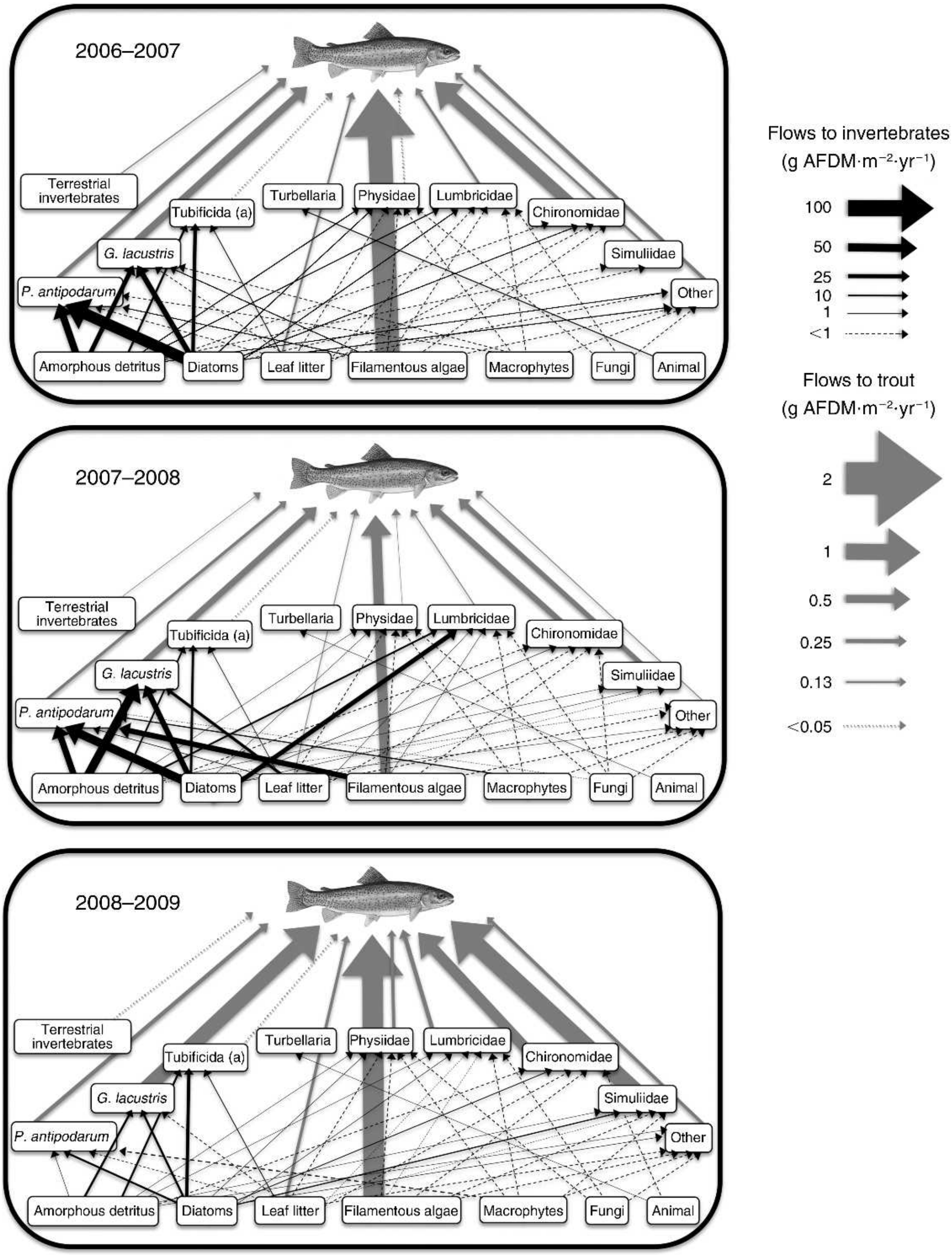

FIG. 4. Annual organic matter flows (i.e., consumption in g AFDM·m^{-2}·yr^{-1}) in the Glen Canyon food web in (A) 2006–2007, (B) 2007–2008, and (C) 2008–2009. Arrow widths represent the magnitude of flows from resources to consumers (see key; note different scale for flows to invertebrates and flows to rainbow trout). Black arrows are flows from basal resources to invertebrate taxa; gray arrows are flows from resources to rainbow trout. Flows from basal resources to the "Other" invertebrate category include flows to Ostracoda, Nematoda, Sphaeridae, Cladocera, Copepoda, Tubificida (b), Ceratopogonidae, and Acari. Flows from the "Other" category to rainbow trout include flows of unidentified aquatic and terrestrial invertebrates. The rainbow trout image is used courtesy of the U.S. Fish and Wildlife Service.

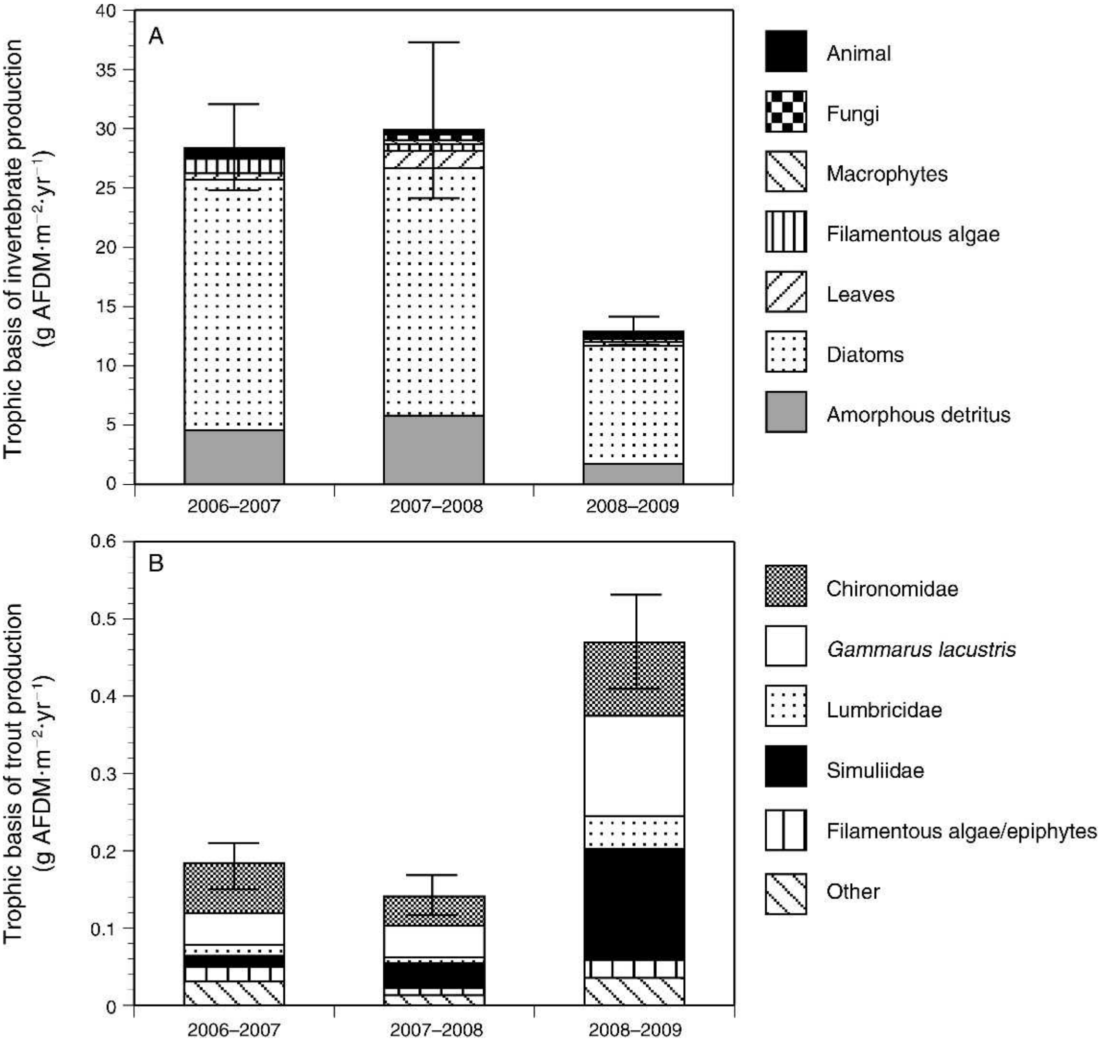

FIG. 5. (A) Invertebrate production was predominantly supported by diatoms. (B) Rainbow trout production was predominantly supported by Chironomidae, *G. lacustris*, and Simuliidae. Stacked areas show the absolute amount of secondary production (g AFDM·m^{-2}·yr^{-1}) supported by each food resource. Error bars represent bootstrap percentile 95% confidence intervals of annual habitat-weighted secondary production. The "Other" category in the lower panel includes Physidae, *P. antipodarum*, Tubificida, terrestrial invertebrates, terrestrial plant material, and unidentifiable aquatic and terrestrial invertebrates.

Drift

Concentrations of invertebrate drift increased in months following the controlled flood (Table 3). A direct comparison of the October to March time period revealed a 148% mean increase in drift concentrations following the flood. This result was even more pronounced (i.e., 188% increase) when *P. antipodarum* was removed from the analysis (Table 3). Large increases in drift were also apparent when comparing the entire pre- and post-flood time series (i.e., total drift biomass, 75% increase; without *P. antipodarum*, 193% increase; Table 3). Importantly, Chironomidae (up to 400% increase) and Simuliidae (~800% increase; T. A. Kennedy, *unpublished data*) largely drove increased drift concentrations, and these two taxa had the highest interaction strengths with trout.

DISCUSSION

Rainbow trout increased their production following the controlled flood, despite a large decline in production of the invertebrate assemblage. This counterintuitive result was reconciled by a significant increase in production of invertebrate taxa most important to rainbow trout, as well as an increase in the occurrence of these prey in the drift following the flood that was sustained for at least 18 months. In particular, drift concentrations increased dramatically for the two invertebrate taxa that had the highest rainbow trout species impact values. We suggest that conditions after the flood were much more favorable for age-0 trout than years prior, and that flood-induced changes in food availability and accessibility drove the positive trout response. Interestingly, the controlled flood effectively

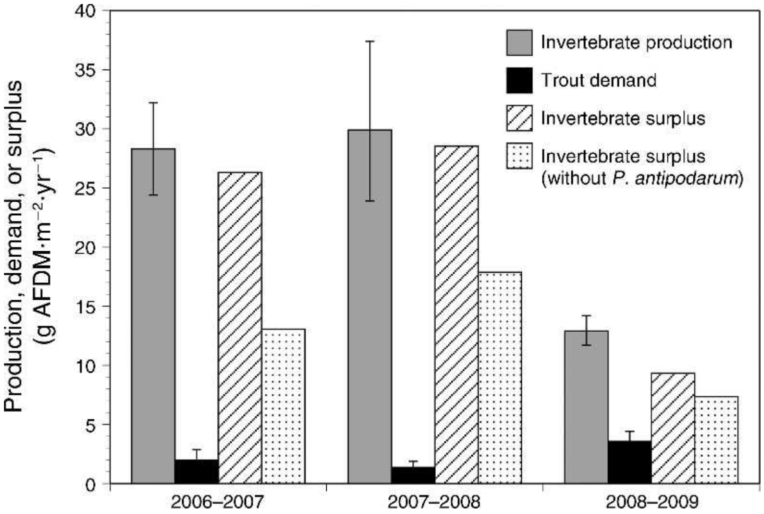

FIG. 6. Rainbow trout demand was much lower than total habitat-weighted invertebrate production during all three years of the study, with large apparent surpluses of invertebrate prey. All units are g AFDM$\cdot$m$^{-2}\cdot$yr^{-1}. Error bars represent bootstrap percentile 95% confidence intervals. See text for description of why these coarse total budgets may be misleading.

reduced production of the invasive New Zealand mudsnail. This taxon represents a "trophic dead end" in Glen Canyon because it has high production and uses considerable energy at the base of the food web, but does not support a substantial amount of production at higher trophic positions. We suggest that controlled floods may benefit nonnative rainbow trout and reduce populations of dominant nonnative invertebrates (i.e., New Zealand mudsnails).

Flow food webs and insights for river management

Ecologists increasingly recognize the importance of production-based approaches for understanding food web interactions and ecosystem dynamics (Woodward et al. 2005, Wootton and Emmerson 2005, Benke and Huryn 2010). In streams, early research in this area was motivated by the "Allen paradox" (Allen 1951, Waters 1988), in which benthic invertebrate production appeared to be too low to support the energetic demands of fish predators. Huryn (1998), using a production budget approach in a New Zealand stream, demonstrated that annual energetic demand (i.e., consumption) of nonnative trout was statistically indistinguishable from the annual supply of invertebrate prey (i.e., secondary production), highlighting strong potential effects of trout on stream food webs.

We used a similar approach in our study, but additionally estimated taxon-specific flows of prey resources to rainbow trout by incorporating trout gut content information (sensu Hall et al. 2000). This exercise provided insights that would not have been possible with an aggregated total budget approach. For example, our annual energetic budgets (Fig. 6) suggested that food limitation was unlikely throughout the study because invertebrate production far exceeded the energetic demands of trout. However, some invertebrate taxa were either rarely consumed by trout or contributed little to their production (e.g., Tubificida and *P. antipodarum*). Trout consumed nearly all of the annual production of few key taxa (e.g., Chironomidae and Simuliidae; Table 2), and these were the taxa that supported the near majority of trout production throughout the study (43–50%). Moreover, production of these two key taxa and their contribution to drift increased substantially following the flood. These results align with Rader's (1997) analysis that ranked Chironomidae and Simuliidae among taxa that had the highest propensity to drift and occurred most frequently in the diets of trout. Our results also agree with prior research in Glen Canyon suggesting a high potential for food limitation of rainbow trout (e.g., McKinney and Speas 2001). Thus, insights from our detailed food web analysis, together with patterns observed in the literature, suggest a chain of causal linkages among the experimental flood, increased production and drift of key taxa available to drift-feeding salmonids, and a two-fold increase in trout production despite a decline in total production of invertebrates. Two important points emerge from these results: (1) total benthic secondary production does not necessarily reflect production that is available to drift feeding salmonids, and (2) aggregated production budgets (as in Fig. 6) may be misleading with regard to ecosystem-level assessments of food limitation.

Food web linkages with the highest species impact values were not the largest from an energy flow perspective. For example, flows of Chironomidae and Simuliidae were relatively small in comparison to other prey items before the flood. Nonetheless, these linkages represented the strongest interaction strengths (Fig. 7),

TABLE 2. Secondary production of dominant invertebrate taxa consumed by rainbow trout and annual consumption by rainbow trout (i.e., demand).

	2006–2007		2007–2008	
Taxon	Production ($\mathrm{g\ AFDM \cdot m^{-2} \cdot yr^{-1}}$)	Demand ($\mathrm{g\ AFDM \cdot m^{-2} \cdot yr^{-1}}$)	Production ($\mathrm{g\ AFDM \cdot m^{-2} \cdot yr^{-1}}$)	Demand ($\mathrm{g\ AFDM \cdot m^{-2} \cdot yr^{-1}}$)
Chironomidae	0.56 (0.43–0.69)	0.73 (0.50–1.05)†	0.66 (0.55–0.76)	0.36 (0.26–0.50)
G. lacustris	7.01 (5.40–9.00)	0.44 (0.31–0.63)	8.69 (6.54–11.00)	0.38 (0.28–0.52)
Lumbricidae	0.71 (0.53–0.91)	0.16 (0.11–0.22)	5.47 (2.54–9.40)	0.06 (0.04–0.07)
Physidae	1.08 (0.68–1.63)	0.006 (0.004–0.008)	0.49 (0.37–0.63)	0.03 (0.02–0.04)
P. antipodarum	13.3 (10.3–16.7)	0.26 (0.18–0.37)	10.66 (6.80–17.04)	0.18 (0.13–0.24)
Simuliidae	0.05 (0.02–0.08)	0.15 (0.10–0.21)†	0.35 (0.14–0.60)	0.31 (0.22–0.42)†
Tubificida (a)	4.29 (3.54–5.07)	0.04 (0.03–0.06)	2.86 (2.32–3.48)	0.008 (0.006–0.011)

† Trout demand overlaps with or exceeds the 95% confidence intervals of invertebrate prey production.

and increased production of these taxa following the flood reduced constraints on trout production. In contrast, although energy flows of *G. lacustris* to trout were relatively large, the interaction strength was consistently weak, and flood-induced reductions in *G. lacustris* did not negatively affect trout production. Thus, by using an observational approach to assess interaction strengths (Wootton 1997), we were effectively able to predict the most important linkages that drive the response of rainbow trout to controlled floods. These results are consistent with theoretical (McCann et al. 1998) and empirical (e.g., Paine 1992) research demonstrating that (1) food webs generally consist of few strong and many weak links and (2) changes in abundance of strongly interacting species are likely to affect food web productivity and stability.

We can only speculate as to why production of Chironomidae and Simuliidae increased following the controlled flood. Our leading hypothesis is that flood-induced scouring of the benthos led to increased habitat quality for these taxa. In particular, Simuliidae often prefer "clean" epilithon for attachment, and our observations suggest that epilithon was scoured in mobile river habitats (i.e., cobble/gravel and depositional; T. A. Kennedy, *unpublished data*). In addition, benthic scouring may have led to early successional stages of epilithic algae that are typically of high nutritional value and rapid growth (e.g., Fisher et al. 1982). Additional research is warranted to determine mechanisms causing increased production of these key invertebrate taxa.

River regulation and experimental floods

Controlled floods have been implemented in a few rivers (e.g., Molles et al. 1998, Patten et al. 2001, Scheurer and Molinari 2003) as an attempt to restore or mimic some degree of natural flow variability to the ecosystem. In rare cases, these floods have been conducted frequently enough to fundamentally alter community structure and ecosystem processes. For example, an unprecedented seven-year series of experimental floods on the Spöl River in Switzerland shifted the invertebrate assemblage towards small-bodied and short-lived taxa (Robinson et al. 2003, Robinson and Uehlinger 2008). In addition, these floods reduced cover of attached moss, altered biomass and species composition of diatoms, and reduced primary production and ecosystem respiration (Uehlinger et al. 2003, Mannes et al. 2008). Interestingly, these changes increased the quality of fish habitat and the number of brown trout (*Salmo trutta*) redds during the time period of the experimental floods (Ortlepp and Mürle 2003). Although the setting and size of the Colorado River below Glen Canyon dam is quite different than the Spöl River, our results were parallel and suggest some degree of generality in the direction of food web response following restorative controlled floods.

The large increase (194%) in rainbow trout production following the flood was driven by increased survival and growth rates of age-0 trout (Korman et al. 2011; Appendix B). Because the flood occurred during the average time of peak spawning (about 6 March, based on 2003–2009; Korman et al. 2011), there was significant potential for reduced survival and weak cohort strength in 2008. Nonetheless, rainbow trout survival rates following the flood were much higher than predicted based on the number of observed viable spawning redds (Korman et al. 2011). In particular, individuals that hatched over a month following the flood (i.e., after 15 April) had extremely high survival rates and had instantaneous growth rates that were among the highest on record for Glen Canyon (Korman et al. 2011). Together, these changes resulted in extremely high abundance of juvenile rainbow trout in 2008, and continued high recruitment and abundance in 2009, a full year following the flood (Appendix B). We suggest that conditions after the flood were much more favorable for age-0 trout than years prior, and that flood-induced changes in food availability and accessibility played a key role.

The seasonal timing of controlled floods (i.e., spring vs. autumn) may influence the magnitude of ecological response and the recovery rates of ecosystem processes following the flood. Of the three controlled floods conducted on the Colorado River, two were in spring (March–April 1996 and 2008) and one was in autumn (November 2004). These time periods represent strongly contrasting conditions, particularly with regard to

TABLE 2. Extended.

2008–2009	
Production (g AFDM·m^{-2}·yr^{-1})	Demand (g AFDM·m^{-2}·yr^{-1})
0.94 (0.81–1.07)	0.68 (0.55–0.84) †
2.65 (2.09–3.35)	0.93 (0.75–1.15)
0.63 (0.43–0.86)	0.26 (0.20–0.32)
0.50 (0.39–0.63)	0.20 (0.16–0.27)
2.00 (1.64–2.39)	0.25 (0.20–0.31)
1.18 (0.67–1.82)	1.11 (0.88–1.41)†
3.93 (3.31.–4.67)	0.002 (0.002–0.003)

light, temperature, and invertebrate biomass. During spring, temperature is low and invertebrate biomass is generally at the annual minimum (Figs. 1 and 3). This season also precedes months of peak solar insolation (Yard et al. 2005), and late spring coincides with high rates of primary production and downstream algal transport (Shannon et al. 1996). Thus, conditions following spring floods should promote rapid recovery of biological processes (i.e., within weeks). In contrast, November has relatively high water temperatures and invertebrate biomass, but precedes winter months of minimal insolation, low temperatures, and reduced gross primary productivity (R. O. Hall, Jr., *unpublished data*). Therefore, recovery of biological processes from autumn floods should be protracted relative to spring floods.

The low number of controlled floods on the Colorado River below Glen Canyon Dam ($n = 3$) precludes strong inference about biological recovery relative to flood timing. It is intriguing that rainbow trout recruitment and survival was high after both the 1996 and 2008 spring floods (Gloss and Coggins 2005; Korman et al. 2011), yet rainbow trout did not respond positively to the controlled flood conducted in autumn 2004 (Makinster et al. 2010). Unfortunately, parallel data on invertebrate biomass or production surrounding the autumn 2004 flood are not available, and thus, seasonal variation in trout response cannot be attributed to differences in invertebrate assemblage response. While past research associated with the spring 1996 flood showed a rapid recovery of algal and invertebrate biomass in Glen Canyon (i.e., within about three months; Blinn et al. 1999, Valdez et al. 1999, Shannon et al. 2001), our study showed little sign of invertebrate biomass recovery and a large reduction in annual invertebrate production. These differences in response among two floods conducted in the same season (spring) may be related to significant changes in assemblage structure over time; invasive *P. antipodarum* dominated invertebrate biomass and production in our study, but was at very low abundance in 1996 (Cross et al. 2010). These data suggest that the timing of floods may be a key factor influencing rainbow trout response, but

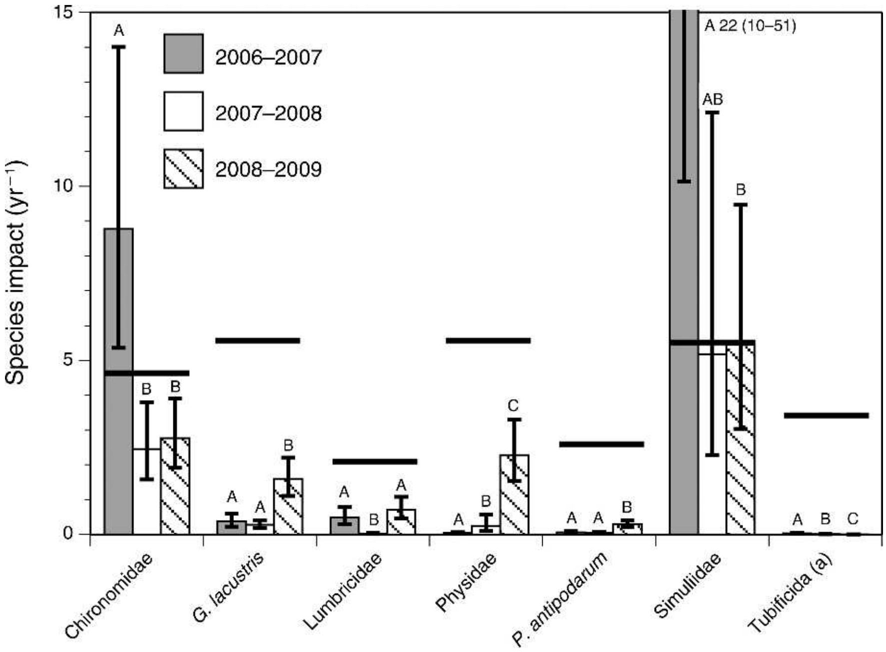

FIG. 7. Rainbow trout had large species impacts (yr^{-1}; Wootton 1997) on Chironomidae and Simuliidae, as evidenced by values equal to or greater than prey annual production : biomass ratios (yr^{-1}; bold horizontal bars). Error bars represent bootstrap percentile 95% confidence intervals. Different letters among bars within a given prey item represent significant differences among years (nonoverlapping 95% confidence intervals). Note that the species impact for Simuliidae in 2006–2007 is not shown entirely. Horizontal bars represent the mean annual production : biomass values (yr^{-1}) of prey items.

TABLE 3. Average concentration of invertebrates in daytime drift (mg AFDM/m^3) before and after the March 2008 controlled flood.

Period	Total invertebrate drift biomass (mg AFDM/m^3)	Total invertebrate drift biomass without *P. antipodarum* (mg AFDM/m^3)
Pre-flood (Oct 07–Mar 08)	0.09 (0.07–0.12)[a]	0.06 (0.05–0.07)[a]
Post-flood (Oct 08–Mar 09)	0.23 (0.21–0.26)[b]	0.23 (0.20–0.26)[b]
Post-flood (Apr 08–Oct 09)	0.163 (0.127–0.208)[b]	0.16 (0.13–0.21)[b]

Notes: Drift collections started in October 2007; thus, our pre-flood record only spans October 2007–March 2008. We present average drift for two different post-flood time periods: October 2008–March 2009 (which matches the seasonality of our pre-flood data set) and April 2008–October 2009, which represents our entire post-flood data set. Numbers in parentheses are bootstrap percentile 95% confidence intervals. Lowercase superscript letters indicate significant differences in drift concentrations among time periods (nonoverlapping confidence intervals).

effects of flood timing on invertebrate recovery and production are equivocal because data are currently lacking. Because the timing of controlled floods is a point of considerable discussion and interest among stakeholders, varying the timing of controlled floods is a logical choice for future experimentation. Considering the highly altered physical and biological status of the Colorado River in Grand Canyon, matching the timing of experimental floods to stated management goals may be more critical than matching their timing to the historic natural flood regime (i.e., snowmelt during spring–early summer).

Management implications

Flood-induced changes to the food web in the Glen Canyon tailwater should not be viewed in isolation. Shifts in production and food web dynamics in Glen Canyon can alter communities and ecosystem processes downstream in Grand Canyon National Park. Consideration of these upstream–downstream linkages is critical because the river ecosystem changes longitudinally and management goals along this continuum may differ or even conflict (Susskind et al. 2010).

Native fishes such as humpback chub and flannelmouth sucker (*Catostomus latipinnus*) comprise a substantial component of the downstream fish assemblage (Gloss and Coggins 2005, Coggins and Walters 2009, Makinster et al. 2010). Humpback chub, in particular, are protected under the Endangered Species Act and there is concern that competition with (and predation by) nonnative fishes, such as rainbow trout, threatens their persistence (Gloss and Coggins 2005; Yard et al. 2011). These concerns motivated a massive 3.5-year effort (2003–2006) to remove nonnative trout from the downstream area of river that corresponds to the highest densities of humpback chub (i.e., near the mouth of a tributary, the Little Colorado River; Coggins et al. 2011). This removal effort was very successful; trout numbers were reduced to <10% of pre-removal levels, and recent data suggest that adult humpback chub abundance has been increasing since around 2002 (Coggins and Walters 2009). Unfortunately, changes in river temperature during this same time period somewhat confound a mechanistic explanation (Vernieu et al. 2005). That is, increases in humpback chub since 2002 could be due to decreases in nonnative rainbow trout, increases in water temperatures that allow for higher humpback chub growth and survival rates, or a combination of the two (Coggins et al. 2011).

Nonetheless, recent evidence suggests that rainbow trout populations are increasing again in lower segments of Grand Canyon, and it is likely that this increase is being driven by downstream migration of individuals that emerged in Glen Canyon following the flood (Makinster et al. 2010). Although a positive rainbow trout response to the flood in Glen Canyon may benefit the recreational sport fishery in this segment, consequent increases in abundance of trout downstream may reduce populations of native fishes. To make matters more complex, there is a perception that controlled floods may benefit downstream native fishes by redistributing sediment, rebuilding sandbars, and increasing backwater habitat (U.S. Bureau of Reclamation 2007). Thus, there is a great deal of uncertainty regarding whether controlled floods will positively or negatively influence native fishes downstream and this uncertainty represents a key question for future research.

Controlled floods on the Colorado River have been broadly designed to "assist in conservation of endangered species, provide benefits to sediment conservation, increase scientific understanding, and collect data for use in determining future dam operations" (U.S. Bureau of Reclamation 2007, also see Patten et al. 2001). Our study was limited to the 25-km tailwater section in Glen Canyon and cannot provide information regarding effects on downstream endangered species (e.g., humpback chub) or sediment dynamics. However, our study clearly illustrates the value of quantitative food web analysis for quantifying how dam operations ripple through food webs to influence rainbow trout predators. In Glen Canyon, floods can benefit rainbow trout by increasing productivity and drift of the invertebrate taxa that support a large proportion of trout production. Floods in Glen Canyon effectively reduce biomass and production of undesirable New Zealand mud snails that dominate flows of energy at the base of the food web and represent a trophic dead end. However, future research is needed to address two key questions: (1)

What are the net effects of controlled floods on species of concern in downstream river segments (humpback chub), and (2) what are the effects of varied timing and magnitude of controlled floods on the Colorado River ecosystem?

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APPENDIX A

Size-binned histograms of rainbow trout density and relative proportions in the Glen Canyon reach of the Colorado River, Arizona, USA, on nine dates between June 2006 and April 2009 (*Ecological Archives* A021-092-A1).

APPENDIX B

Mean organic matter flows (i.e., consumption) of invertebrate taxa to rainbow trout during the three years of study (*Ecological Archives* A021-092-A2).

APPENDIX C

Mean proportional contribution of different food resources to invertebrate and rainbow trout production during the three years of study (*Ecological Archives* A021-092-A3).

SUPPLEMENT

Data from invertebrate foods webs in Glen Canyon, Colorado River, USA (*Ecological Archives* A021-092-S1).