RELATIONSHIPS AMONG BASAL ENERGY AVAILABILITY, NONNATIVE PREDATOR SUCCESS, AND NATIVE FISH DECLINES IN THE UPPER GILA RIVER BASIN, NM, USA.

by

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Abstract

Nonnative species represent a major threat to the continued persistence of native fishes globally, especially in the Colorado River Basin of western North America, where there are now more nonnative than native fishes. In the upper Gila River, a tributary of the Colorado, numerous nonnative fishes have established populations, and predation by these nonnatives has been linked to extirpation of native fishes under low-flow conditions at some locations. Historically, the upper Gila lacked a top piscivore, and it is unclear what mechanisms have allowed the establishment of nonnative piscivores and resultant extension in food chain length. To investigate the phenomenon of increased food chain length through nonnative introductions we explored the influence of autochthonous energy availability on nonnative predator abundance, food chain length, and abundance of other trophic levels. Predictions were that increased basal energy availability would lead to increased nonnative predator abundance and thus increased food chain length, based upon predictions from food web theory. Annual production and biomass of four trophic levels measured across six longitudinally-positioned sites were calculated between June 2008 and June 2009 to test these predictions. In addition, energy demand of trophic levels relative to energy supply was compared across sites using a quantitative food web approach, to evaluate energy limitation across trophic levels. Primary production was found to vary considerably across the upper Gila (1,677-16,276 kcal m^{-2} yr^{-1}), but production and biomass of other trophic levels was not related to this gradient as predicted. In addition, food chain length demonstrated a marginally-significant negative relationship with primary production (R^2=0.42, d.f.=5, p=0.16), which was in contrast with predicted responses. These results suggest that energy availability does not appear to be a limiting factor to the production or

biomass of consumers. The influence of other mechanisms on food chain length in the upper Gila River, in particular disturbance frequency and intensity, deserve further investigation.

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INTRODUCTION

Nonnative Species

The introduction of nonnative species represent a major threat to freshwater ecosystems globally (Malmqvist and Rundle 2002; Dudgeon et al. 2006). Threats created by nonnatives through interactions with native biota include predation, competition, hybridization, disease transmission, and habitat modification (Gozlan et al. 2010 and references therein). Additionally, nonnative species may interact synergistically with one another to influence native organisms, creating an "invasional meltdown" in the recipient ecosystem (Simberloff and Von Holle 1999). Synergistic interactions between nonnative species and anthropogenic modifications (including climate change) of aquatic habitats can also create dire consequences for native fauna, threatening stability, diversity, and continued ecosystem functioning (Johnson et al. 2008; Rahel and Olden 2008). Predictions indicate that the number of nonnative introductions worldwide will continue to increase in the coming decades, creating further strain on already stressed native communities (Levine and D'Antonio 2003).

Similar to global patterns, the Colorado River Basin of western North America has experienced introductions of numerous nonnative species. Over 90 species of fish have been introduced into the basin, with about 1/2 of those species having established reproducing populations (Rinne and Minckley 1991; Rinne and Janisch 1995; Olden and Poff 2005). These introductions have contributed to the current decline of native fishes, with 25 of the 31 native and mostly endemic species of the basin experiencing multiple degrees of imperilment, from range reduction to extinction (Minckley 1991; Fagan et al. 2005; Olden and Poff 2005). Invasion of taxa other than fish, including the American bullfrog (*Rana catesbeiana*), red swamp crayfish (*Procambarus clarkii*), and northern crayfish (*Orconectes virilis*) have also occurred,

bringing their own suite of negative consequences and contributing to native declines (Clarkson and DeVos 1986; Johnson 1986; Mueller et al. 2006). Determining the degree to which nonnative species are directly responsible for native declines in the Colorado Basin has proven problematic owing to the confounding effects of flow modification and habitat alteration, which are pervasive throughout the basin (Poff et al. 1997; Propst et al. 2008).

Although flow alterations are extensive in the Colorado River Basin, streams with only modest modifications do remain, creating an opportunity to study the effects of nonnatives in the absence of anthropogenic changes in flow. The upper Gila River of southwestern New Mexico provided just such an opportunity. A 19-year study by Propst et al. (2008) across the upper Gila reported that naturally occurring periods of low flow tended to benefit nonnative fishes, whereas native fishes increased in abundance during periods of higher flow. During periods of low flow, nonnatives could extirpate native fishes. In addition to temporal variability related to flow, spatial variability in the abundance of nonnatives was also observed, leading to spatially variable extirpations of native fishes. While flow accounted for the temporal variability of nonnatives, no mechanism was proposed to account for the spatial variability of nonnative occurrence and native extirpation.

A major factor hypothesized for the lack of native persistence at some sites in the upper Gila was predation pressure created via nonnative fishes. Historically, the upper Gila lacked a top piscivore, except for potentially the headwater chub (*Gila nigra*) and the Colorado pikeminnow (*Ptycocheilus lucius*) (Sublette et al. 1990). Using both diet and stable isotope data, Pilger et al. (2010) demonstrated that many of the nonnative fishes in the upper Gila were piscivorous, functionally extending community food chain length. This phenomenon begs the question of what mechanisms are responsible for variation in food chain length, and by

extension, the spatial variation in abundance of nonnative predators across the upper Gila River Basin?

Food Chain Length

The literature is replete with theorized mechanisms responsible for variation in food chain length across ecosystems (Rosenzweig 1971; Fretwell 1977; Pimm and Lawton 1977; Pimm 1982; Briand and Cohen 1987; Cohen and Newman 1991; Hairston and Hairston 1993; Marks et al. 2000). One potential mechanism that has received both a great deal of attention and scrutiny is the idea that energy availability is the master variable controlling food chain length (Hairston et al. 1960; Fretwell 1977; Oksanen et al. 1981; Oksanen and Oksanen 2000). This mechanism predicts that increased primary productivity leads to an increase in food chain length. Reasoning behind the predicted influence of primary production on trophic structure is the inefficiency with which energy is transferred between trophic levels, which is generally 10-20% (Lindeman 1942; Fretwell 1977). Applying these concepts to the upper Gila, we would thus expect increases in biomass of nonnative predators with increased primary production. Furthermore, this theory would suggest that native fishes of the upper Gila, which predominantly occupy the 3rd trophic level (Pilger et al. 2010), would demonstrate no population response with increases in primary production, because their populations would be regulated by nonnative predators (Fretwell 1977). Continuing down the food chain, the abundance of herbivorous species (mainly macroinvertebrates) is expected to increase with increases in primary productivity, while the abundance of primary producers remains constant, thus exhibiting the classic "stair-stepped pattern of biomass accrual across productivity gradients" (Oksanen et al. 1981). This pattern also states that the 2nd and 4th trophic levels will be energy limited, while the 1st and 3rd trophic levels will be predator limited, combining both bottom-up and top-down

interactions in food web structure (Fretwell 1977). Underlying assumptions of these predictions include: equilibrial communities that do not receive allochtonous energy inputs, consumer populations which closely track their resources, no omnivory, consumers that do not interfere with one another, and relatively high transfer efficiencies (15%) between trophic levels (Fretwell 1977; Oksanen et al. 1981; Marks et al. 2000). Deviations from these assumptions, which is likely occurring for some of these assumptions in the upper Gila River (allochtonous inputs, omnivory), and incorporation of more complex dynamics (allochtonous energy inputs, interference competition, imperfect tracking of resources by consumers) result in theoretical predictions that the abundance of both native and nonnative fish populations would increase with increases in primary production (Mittelbach et al. 1988; Arditi and Ginzburg 1989; Oksanen 1995).

For primary productivity gradients to be responsible for variation in the abundance of nonnative predators across the upper Gila, energy limitation is required as the primary determinant of food chain length. This is not an unreasonable assumption, because numerous empirical studies have documented energy limitation to consumers in lotic ecosystems (Fisher and Gray 1983; Waters 1988; Huryn 1996). In Sycamore Creek, AZ, the consumption by herbivorous macroinvertebrates, which were functionally the top trophic level in the system, exceeded gross primary production, thus suggesting energy limitation and confirming theoretical predictions (Fretwell 1977; Fisher and Gray 1983). Arguably the most famous example of energy limitation in a lotic ecosystem is that of the Allen Paradox in Horokiwi Stream, New Zealand (Allen 1951; Huryn 1996). The original formulation of the Allen Paradox stated that standing stock biomass of macroinvertebrates was not sufficient to sustain predatory brown trout (*Salmo trutta*) populations, and thus energy supply did not match energy demand (Allen 1951).

However, refinement of this study to include macroinvertebrate production instead of biomass, meiofauna and hyporheic prey resources, piscivory (including cannibalism), and input of terrestrial insects, resulted in a balanced budget of energy demand and energy supply, and thus a resolution to the apparent paradox (Huryn 1996). Regardless, the balance of this energy budget suggested that all available resources were required for sustenance of trout populations. Abundance of nonnative fishes across the upper Gila could be limited in a similar fashion, with those locations which had the greatest abundance of nonnative predators in Propst et al. (2008) predicted to have the highest primary production.

For the variation in abundance of nonnative predators across the upper Gila to be resultant from primary production, spatial variation in primary production is required. General predictions of spatial variability of primary production are that increases should occur from low order (Strahler order 1-4) to middle order (Strahler order 5-7) locations, as a result of decreased canopy cover and increased temperatures (i.e. River Continuum Concept of Vannote et al. 1980). Because the upper Gila ranges from Strahler order (1-6), these mechanisms could be anticipated to operate. Downstream increases in primary productivity in the upper Gila could further be surmised by nutrients gradients resulting from anthropogenic and natural physical processes (Acuna and Dahm 2007), and the change from canyon bound to open valley reaches. Therefore, abundance of nonnative predators should be expected to increase in a downstream fashion as a result of increased primary production.

The aforementioned arguments rely upon the linear increase of both food chain length and even-numbered trophic levels (in a 4 level food chain) with increases in primary production for their foundation, but other patterns have been observed. Relationship between food chain length and energy availability can also be negative due to an increase in abundance of inedible

prey, or unimodal as a result of intraguild predation (Abrams 1993; Arim et al. 2007). Furthermore, mechanisms other than energy availability have been proffered to explain variation in food chain length (Post 2002). A hierarchy of alternative mechanisms presented by Post (2002) proclaimed that history of community organization is the overriding factor controlling food chain length. If physical barriers prevent predator colonization, or sufficient evolutionary time has not passed for in situ predator evolution, then food chain length will be limited to those trophic levels which can colonize or evolve (Post 2002). After history of community organization energy availability is the next factor predicted to be an important determinant of food chain length. Beyond these two levels, other factors predicted to influence food chain length in order of descending importance include: predator-prey interactions/size ratios, disturbance, and ecosystem size or colonization/stability. Acknowledgment of the concomitant operation of these mechanisms is required for proper understanding of variation of nonnative abundance across the upper Gila.

Nonnative Predatory Effects

Irrespective of the underlying mechanism relating energy availability to food chain length, nonnative predators have invaded across the upper Gila in varying abundances, and are influencing native biota (Propst et al. 2008; Pilger et al. 2010). The question now becomes what quantitative effect are nonnative predators having, and what is the environmental context (in terms of productivity regime) under which they are able to eliminate native populations? Several studies have sought to address the quantitative effects of nonnative predators. Johnson et al. (2008) used bioenergetics models to show that smallmouth bass (*Micropterus dolomieu*) and northern pike (*Esox lucius*), two nonnative predators found in the Yampa River of Colorado, could consume a substantial amount of fish prey when prey densities were low, and even greater

amounts when prey densities were high. This study did not account for the fraction of fish prey consumed relative to availability, making it difficult to determine overall effect on native fishes. Huryn (1998) constructed quantitative food webs in Stony Creek and Sutton Stream of New Zealand to evaluate the predatory effects of nonnative brown trout (*Salmo trutta*) compared with native river galaxias (*Galaxias eldoni*). High consumption values of brown trout on herbivorous macroinvertebrates created a trophic cascade in Sutton Stream, greatly increasing primary production relative to Stony Creek where only river galaxias were present. These studies have provided valuable contributions towards understanding of nonnative predator effects, but accounting for the spatial and temporal variation of these effects and the environmental context under which they operate has yet to be accomplished. Environmental context of coexistence between natives and nonnatives has related to flows (Propst et al. 2008), but it has yet to be investigated under the context of productivity regime.

Under the framework of food web theory and environmental context of native/nonnative interactions, we seek to evaluate the overarching questions of what influence does productivity have on food chain length/nonnative abundance across the upper Gila, and what quantitative effects are nonnative predators having on native prey? This will be accomplished using a quantitative food web approach. Specifically, we will focus on four main questions with associated predictions.

Questions and Predictions

1. Does production and biomass in four trophic levels vary along a longitudinal gradient across the upper Gila?

-Primary production is predicted increase downstream along the continuum of the upper Gila (Vannote et al. 1980), thus the production and biomass of the 2nd and 4th trophic

levels are expected to increase moving downstream, while the biomass of 1st trophic level and biomass and production of the 3rd trophic level shows no response with increased primary production.

2. Is the energy supply of supporting trophic levels sufficient to meet the energy demand of native and nonnative fishes across the upper Gila?

-2nd and 4th (nonnative predators) trophic levels will be energy limited, with energy limitation greatest at upstream locations as a result of lower predicted primary production.

3. Is the number of trophic levels associated with energy availability?

-Increasing energy availability will lead to an increase in the number of trophic levels as a result of decreased energy limitation.

4. Is the dominance of native fishes relative to nonnative predators influenced by autochthonous energy availability?

-Increasing primary productivity will lead to lower dominance of native fishes as a result of increased abundance and predation pressure of nonnatives.

STUDY AREA

This study was conducted across six longitudinally-positioned sites in the upper Gila River Basin of southwestern New Mexico (Figure 1). Three of these sites (West Fork, Middle Fork, and Riverside) correspond in location to long-term monitoring sites described in Propst et al. (2008) and Pilger et al. (2010). The three most-upstream sites, West Fork (33°13'45"N, 108°15'46"W), Middle Fork (33°13'33"N, 108°14'34"W), and Grapevine (33°10'41"N, 108°12'33"W) occur in the Mogollon Mountains of the Gila National Forest and Gila Wilderness

Area, which is dominated by pine (*Pinus* spp.) and juniper (*Juniperus* spp.), with sycamore (*Platanus* spp.), cottonwood (*Populus* spp.), and willow (*Salix* spp.) also present near the riparian area. Sites are within protected federal lands and receive relatively little anthropogenic disturbance (Propst et al. 2008). A long canyon and a sharp drop in elevation (1695m-1410m) separate Grapevine and the next mainstem site, Gila Farm (33°02'17"N, 108°32'01"W), where the mountainous terrain shifts to a lowland valley. Gila Farm is located on a Nature Conservancy preserve and is bordered to the north by federal land, and also has low anthropogenic disturbance. In between Gila Farm and the next mainstem site, Riverside (32°56'11"N, 108°36'12"), human population densities increase, two small agricultural diversions are present, and there is an increase in both farming and ranching. The riparian zone of Riverside is owned by The Nature Conservancy and consists of a pasture recovering from over-grazing with few trees present, as well as remnant pieces of asphalt from old US Highway 180. Similar anthropogenic alterations that characterize the watershed of Riverside continue towards the most downstream study site, Bird Area (32°50'49"N, 108°35'38"), which is located at the northern edge of the Big Burro Mountain range on another section of the Gila National Forest. The riparian zone of Bird Area is more developed than at Riverside and consists of a mix of cottonwood (*Populus* spp.), willow (*Salix* spp.), and sycamore (*Platanus* spp.) species.

Numerous gradients occur in the physical and chemical characteristic in the Gila River as it flows between West Fork and Middle Fork tributaries to Bird Area. In general, mean temperature, discharge at baseflow, nitrate (NO_3^-), and depth increase downstream (Table 1). This longitudinal variation likely has direct affects on the abundances of aquatic organisms, as well as indirect effects through mediation of energy availability. One of the most crucial physical properties of the upper Gila Basin occurs in the form of intra- and inter-annual variability in

discharge. Within the course of a year the greatest discharge generally occurs during the winter months (December –March) as a result of snowmelt and greater precipitation as well as during the late summer monsoonal season (late July-September), with low flows occurring in June and early July (Propst et al. 2008). Among-year variation in flows results from the El Niño Southern Oscillation (ENSO), with higher flow characteristic of El Niño years (Molles and Dahm 1990).

Sampling reaches at the six sites were chosen to include two or three riffle-pool complexes, and were assumed to be long enough to capture meaningful reach-scale variation. At West Fork and Middle Fork, three contiguous riffle-pool complexes were selected with total reach lengths of 198m and 193m, respectively. At the other sites two contiguous riffle-pool complexes were selected, with total reach lengths of 276m, 191m, 245m, and 300m, respectively. Riffle-pool complexes were always selected so that the reaches terminated in a downstream pool. Sampling was conducted during June, August, and October of 2008, as well as February and June 2009 to quantify standing stock biomass and productivity of different trophic levels. For all trophic levels, the metric used to quantify energy availability was annual production (kcal m^{-2} yr^{-1}) and mean annual biomass (kcal m^{-2}).

METHODS

Quantification of Primary Producers

To estimate standing stock biomass of primary producers we measured chlorophyll *a* concentration (Sartory and Grobbelarr 1984; Steinman et al. 2006). We acknowledge that this method only accounts for algae and Cyanobacteria and ignores other potentially important primary producers such as macrophytes and bryophytes, but these taxa are relatively rare in the Gila except during prolonged periods of low flow (J. Whitney, pers. obs.). During each sampling trip chlorophyll *a* samples were collected from each site by randomly selecting three rocks along

six transects. At tributary sites one transect occurred per macrohabitat (riffle or pool), whereas mainstem sites had two transects in the larger of the two riffle and pool macrohabitats and one transect in the smaller of the two. Samples were stored frozen for 1-2 weeks after collection and then using ethanol extraction and spectrophotometry chlorophyll *a* concentrations were estimated (Steinmann et al. 2006). Sample period values were averaged across the year to obtain an annual estimate of chlorophyll *a* concentration from each site. See Appendix A for detailed methods of chlorophyll *a* analysis.

In addition to algal biomass, metabolism estimates of gross primary production and community respiration were calculated from diel oxygen curves using the one-station method (Bott 1996) corrected for the reaeration flux from the surface-renewal model (SRM) (Owens 1964; Bott 1996). Metabolism measurements occurred at each of the six sites during June, August, and October of 2008, as well as June 2009. Metabolism estimates were not conducted in February 2009, and were not possible at the three most-downstream sites (Gila Farm, Riverside, and Bird Area) during August 2008 as a result of high monsoonal flows. At each site Yellow Springs Incorporated (YSI) model 600XLM sondes placed in the well-mixed thalweg recorded dissolved oxygen (DO) concentration and temperature every 10 minutes for 24 hours. The mass-transfer coefficient $f_{(20°C)}$ of the SRM was estimated by measuring depth (cm) and velocity (cm/s) every 0.5-1.0m along 10 evenly-spaced transects at each site during June 2008. Discharge during other sampling periods was similar to the discharge during which SRM estimates were calculated, so it was assumed that reaeration values were similar among these sampling periods. The mass transfer coefficient $f_{(20°C)}$ was converted to a reaeration coefficient *k* via division by mean depth and was also temperature corrected using the equation of Elmore and West (1961). Dissolved oxygen curves corrected for reaeration were used to calculate daily gross primary

productivity (GPP) and community respiration (CR_{24}) following the algorithm of Bott (2006) in units of g O_2 m^{-2} day^{-1}. Autotrophic respiration was calculated by multiplying GPP by 0.5 (Dodds and Cole 2007), with heterotrophic respiration calculated by subtracting autotrophic respiration from total respiration. An arithmetic mean and associated standard error of the four (or three for the three most downstream sites) estimates of GPP and CR_{24} were calculated and multiplied by 365 to obtain annual estimates. Standard errors were converted to 95%CI's through multiplication by 1.96. GPP and CR_{24} were converted to kcal m^{-2} yr^{-1} (kcal= (g O_2 x 0.83 x 0.375) x 11.4) (Bott 2006) to facilitate comparison with production calculated for other trophic levels.

Macroinvertebrate Production and Biomass

To address our questions regarding the variability of macroinvertebrate consumer populations and their relationship with native and nonnative fish quantitative sampling was conducted at each of the six sites. Fifteen replicate samples were collected from each site during each sampling period, with sampling method dictated by effective habitat type (sensu Resh 1979; Smock et al. 1985). In pool macrohabitats, six replicate samples were taken, with three taken per pool in mainstem sites and two taken per pool in tributary sites. For each sample a 0.018 m^2 stovepipe core was inserted approximately 10 cm into the stream bed and substratum inside the core was removed. Six replicate samples were taken in riffle macrohabitats, with three per riffle at mainstem sites and two per riffle at tributary sites. Riffle samples were collected using a 0.093 m^2 Surber sampler, with disruption of substrates in the sampling area occurring until all macroinvertebrates had been removed from all rocks and substrates (approximately 5 minutes). Three large woody debris (LWD) samples were collected from each site. Woody debris was selected so that it occurred at a depth that was continuously submersed and also well-attached so

that it could not be easily washed away, thus making it suitable for macroinvertebrate colonization. For each LWD sample, a bucket was placed around the piece of wood so that any macroinvertebrates that were dislodged during cutting would be washed into the bucket. A small hand-saw was then used to separate the attached wood, with the wood then being scrubbed in the bucket to remove any attached macroinvertebrates. Surface area of LWD samples was determined by measuring the circumference and total length of the piece of scrubbed wood and then multiplying those values. This assumes that the wood's shape approximated that of a cylinder. All samples were elutriated through a 250 µm sieve and preserved in 10% formalin until processing in the laboratory.

Laboratory processing of samples began with separation of macroinvertebrates that were >1mm from organic debris and sediment within the sample. All separated macroinvertebrates >1mm were enumerated under a 0.8-10x dissecting microscope, identified to family for Insect taxa or to Class for non-insect taxa using Merritt et al. (2008) and Thorp and Covich (2001), and their length measured to the nearest 1mm (case width for caddisfly larvae of the family Helicopsychidae). Macroinvertebrates were also categorized as either primary consumers (collector-gatherer, filtering-collector, scraper, and shredder) or secondary consumers (predator) based on information in Merritt et al. (2008) and Thorp and Covich (2001), in addition to ^{13}C and ^{15}N isotope data collected by Pilger et al. (2010) (Table 2). The rest of the sample which contained invertebrates that were <1mm was split (1/2 to 1/16 of original sample) using a splitting wheel and invertebrates were then enumerated. Invertebrates <1mm were identified to family or order for insect taxa and to class for non-insect taxa, and categorized into a trophic level (primary or secondary consumer). Numbers of individuals per sample were divided by sampling area to determine density.

Annual secondary production and mean annual biomass was estimated for each macroinvertebrate taxa using a combination of the size-frequency method corrected for the cohort production interval (CPI) for abundant taxa and the P/B ratio for rare taxa (Table 2). The equations of Krueger and Martin (1980) were used to estimate the weighted annual mean and variance of density, as well as size-frequency production with associated 95%CI's. See Appendix A for detailed description of macroinvertebrate production methods.

Fish, Crayfish, and Bullfrog Tadpole Production and Biomass

Fish, crayfish (*Orconectes virilis*), and tadpole (*Rana catesbeiana*) production, density, and biomass values were estimated to evaluate spatial variation in production, energy demand, and energy availability of native fishes and nonnative organisms. Populations within sample sites were estimated in June, August, and October of 2008 and June 2009. Populations estimated at the 3 downstream sites (Gila Farm, Riverside, and Bird Area) during August 2008 were excluded from analyses since high discharge prevented reliable population estimates. Fish population estimates were based on a capture-mark-recapture technique (Seber 1982; Hayes et al. 2007) using a combination of seining and electrofishing equipment. Electrofishing (Smith-Root Model LR-24 backpack electroshocker) was conducted in an upstream fashion to sample all major pool habitats (rocky shores, root wads, debris dams) where seining was not possible, with seining (4.6 m x 1.2 m seine with 3.2 mm mesh) done moving downstream in all other pool habitats (open water, mid-channel). A combination of electrofishing and kick-seining was done in riffle habitats. For all individuals >50mm captured, total lengths were measured and then either an upper or lower caudal fin clip was given to mark the individual. Attempts to use blocknets (2.54 cm mesh) to enclose large fishes were only successful during low flows. For small fishes at this time or all fishes at other times we likely violated the assumption of a closed

population. To account for potential effects of this violation and evaluate the extent of fish movement over the study period individuals collected in up- and downstream habitats were given differential marks. Lower fin clips were given to those individuals captured in the middle and downstream macrohabitats of the study reach, whereas individuals from the upstream macrohabitats received upper caudal clips. Individuals were released into their respective macrohabitats and the recapture was conducted approximately 14-24 hours after the initial mark using identical capture methods. Number recaptured in different habitats relative to those recaptured in the same habitat as marked gave us an indication of movements within the study reach. Population estimates and associated variances were calculated following the equations of the Chapman estimator (Seber 1982; Hayes et al. 2007). Density was calculated by dividing population estimates by total reach area (m^2).

During June, August, and October 2008, weights were taken from a subsample of individuals of each species marked, representing the range of sizes encountered. Using $\log_{10}$ transformed length (independent variable) and weight (dependent variable) data, linear regression was used to estimate the slope and y-intercept of the equation relating length and weight. Using these estimated parameters for each species weights were calculated for all individuals captured during the course of the study.

Annual secondary production and mean annual biomass was estimated for each species encountered across sites using a combination of the size-frequency method corrected for the cohort production interval (CPI) for abundant taxa and the P/B ratio for rare taxa in a similar manner as macroinvertebrate methods (Table 3). The equations of Garman and Waters (1983) were used to estimate the weighted annual mean and variance of density and individual weight,

as well as size-frequency production with associated 95%CI's. See Appendix A for detailed production and mean annual biomass methods.

Consumption

To estimate the energetic demand of fishes across the upper Gila we calculated consumption following the approach of Benke and Wallace (1980). With this method, three main pieces of data are required: quantitative data on consumer gut contents, the ecological efficiencies of food consumed, and the production of consumer taxa (Benke and Huryn 2006). Quantitative data on gut contents of fish species in the upper Gila was acquired from Pilger et al. (2010), who examined specimens collected between 2007-2009 across six sites in the upper Gila Basin (3 of those sites corresponded to sites in the present study: West Fork, Middle Fork, and Riverside). They identified gut contents to the lowest practical taxonomic level and then assigned to one of five categories: detritus, algae, herbivorous invertebrate, predaceous invertebrate, or fish. Mean percent gut content of the different food categories were calculated for each fish species and, coupled with ^{15}N signatures, were used to assign fish to a trophic level (primary, secondary, or tertiary consumer) (Table 4). Assimilation efficiencies (the proportion of food ingested that is assimilated) for all consumer species of these different food categories were estimated as followed: detritus = 0.10, algae = 0.30, all other animal categories = 0.70 (Benke and Huryn 2006). These estimates represent coarse approximations of actual assimilation efficiencies, which vary from consumer to consumer; however, these estimates represent the relative changes in assimilation efficiency with differing food qualities, with poorer quality food having lower assimilation efficiencies. Net production efficiency (the proportion of food assimilated that goes towards production) was estimated at 0.5 for all species and all food categories. Using these values, gross production efficiency (the proportion of ingested food that

goes towards production) thus ranged from 0.05-0.35. Combining consumer production data (methods described previously) with quantitative gut contents and ecological efficiencies, the total amount of each food category consumed (kcal m^{-2} yr^{-1}) by fish was calculated and compared with production of the supporting trophic level.

Data Analysis

To test longitudinal variation in production and biomass of four trophic levels in the upper Gila Basin we compared 95% confidence intervals of production and biomass across sites. Production and biomass of primary and secondary consumers were summed both within and across macroinvertebrate and fish taxa to generate a community-wide measure of those trophic levels. This was not necessary for primary producers, since the methods used to calculate primary production and autotrophic biomass are inherently community-wide measures (Benke 1993). No summation across disparate taxa was required for tertiary consumers either, since only fish represented this highest trophic level (Table 4). If no overlap in 95%CIs among sites existed within a trophic level, those sites were determined to have significantly different productivities or biomasses. To determine if production and biomass of trophic levels met theoretical expectations, those values were regressed against gross primary production using least-squares linear regression in the program R version 2.8.1 (R Development Core Team 2008).

Spatial variability in the ability of production to meet the energetic demand created via native and nonnative fish consumption was also evaluated by overlap in 95%CIs. Gross primary production, herbivorous invertebrate production, and secondary consumer production (predaceous invertebrates + fish) was compared to fish consumption of algae, herbivorous invertebrates, and secondary consumers (predaceous invertebrates + fish) at each site,

respectively. Total fish production was included in secondary consumer production for comparison with fish consumption, although not all of these fish are secondary consumers. However, this should not overly bias results, since the only fish that are primary or tertiary consumers are large bodied, low-density adults which are not available for consumption (Pilger et al. 2010). The majority of fishes in the Gila River are secondary consumers (Pilger et al. 2010). Overlap of the 95%CI of production of a trophic level with the total consumption value of that trophic level by fishes represented potential energy limitation.

To determine if a relationship between food chain length and primary production exists, we calculated proportional consumption of secondary consumers (fish + predaceous invertebrates) by predatory fish, a metric of food chain length (Arim et al. 2007). This value was then regressed against gross primary production. An increase in the proportion of secondary consumers in the diet of predators represents an increase in food chain length (Arim et al. 2007).

We also used linear regression to assess whether the dominance of native fishes over nonnative predators is influenced by primary production. Dominance was calculated as the ratio of native fish production to nonnative predator production, with larger values equaling greater dominance of native fishes over nonnative predators. This ratio was regressed against gross primary production. To determine whether native and nonnative populations are demonstrating responses to one another or if they are responding to similar environmental gradients, total nonnative production (crayfish + tadpoles + fish) was regressed against native fish production.

RESULTS

Spatial Variation in the Production and Biomass of Trophic Levels

Mean annual gross primary production (GPP) varied over an order of magnitude (1,677-16,276 kcal m^{-2} yr^{-1}) across our six study sites in the upper Gila River Basin. As a result of unequal variances in GPP, $\log_{10}$ transformations were done prior to all analyses. Consistent with our predictions, a general downstream increase was seen in values of GPP, with Riverside and Bird Area having significantly greater GPP than West Fork and Gila Farm based on non-overlapping 95%CIs (Figure 2). Middle Fork also had significantly greater GPP than WF, but was not statistically different from Gila Farm. Grapevine was not significantly different from any site. Community respiration demonstrated a significant positive relationship with GPP (R^2=0.69, d.f.=5, p=0.04) and was always much greater than GPP across all sites, thus making all sites net heterotrophic (Figure 2). Community respiration ranged from a minimum of 8,294 kcal m^{-2} yr^{-1} at Gila Farm to a maximum of 29,621 kcal m^{-2} yr^{-1} at Riverside (Figure 2). In contrast to our predictions, algal biomass tracked the downstream increase of GPP, demonstrating a significant positive relationship (R^2=0.72, d.f.=5, p=0.03) (Figure 3). However, the magnitude of differences between the highest and the lowest site was much less than was present in GPP (0.08-0.34 g chl *a* m^{-2}). All sites except Grapevine had a significantly greater chlorophyll *a* concentration when compared with West Fork, with no other sites exhibiting significant differences (Figure 4).

Variability of primary consumer production was much lower when compared with values of GPP, although an approximately a 5-fold difference occurred between the most and least productive sites (Figure 5). In contrast with our predictions primary consumer production demonstrated no significant relationship with increases in GPP (R^2=0.11, d.f.=5, p=0.52) (Figure 6). Riverside and Bird Area had significantly greater productivities than Middle Fork and Grapevine, with no other sites exhibiting significant differences (Figure 5). Macroinvertebrates

comprised the largest percentage of primary consumer production across sites, responsible for 96-99% of production (Table 5). The taxa responsible for this production varied across sites, but Baetidae, Chironomidae, Leptohyphidae, Hydropsychidae, and Simuliidae were usually the most productive primary consumer taxa (Appendix B). In terms of native vs. nonnative fish production, native fishes comprised 99-100% of total fish primary consumer production across sites, although these values were still small relative to macroinvertebrates. Also in opposition to predictions, biomass values did not increase downstream with increases in GPP (R^2=0.05, d.f.=5, p=0.68) (Figure 3), with the only significant difference in biomass among sites existing between two of the most productive sites, Riverside and Bird Area (Figure 4).

Secondary consumer production demonstrated the predicted response of no relationship with increases in GPP (R^2=0.11, d.f.=5, p=0.54) (Figure 6). West Fork, Middle Fork, and Grapevine all had significantly greater secondary consumer production when compared with Gila Farm, with West Fork also having significantly greater production than Bird Area (Figure 5). The range of secondary consumer production was much lower than those encountered in primary producer and consumer production, with only 18 kcal m^{-2} yr^{-1} separating the most productive from the least productive sites. Also in contrast with primary consumer production, vertebrate taxa were generally responsible for the greatest percentage of secondary consumer production, accounting for 41-74% (Table 5). Some of the most productive secondary consumer taxa across sites included *Catostomus insignis*, *Agosia chrysogaster*, and *Meda fulgida* (Appendix B). Similar to the production of fish primary consumers, native fishes were responsible for 99-100% of fish secondary consumer production across sites. Biomass values were also in accord with prediction, demonstrating no relationship with increased GPP (R^2=0.05, d.f.=5, p=0.67) (Figure 3). West Fork and Middle Fork had significantly greater biomass than all

other sites, with Grapevine also possessing significantly greater biomass than Gila Farm (Figure 4).

The production of tertiary consumers also did not match our predictions, and demonstrated a marginally significant negative response with increases in GPP (R^2=0.46, d.f.=5, p=0.14) (Figure 6). West Fork had significantly greater tertiary consumer production compared with all other sites (Figure 5). Middle Fork and Gila Farm had significantly greater production than Grapevine, with Riverside and Bird Area having significantly lower tertiary consumer production than all other sites. Values ranged from 0.21 at Bird Area to 4.32 kcal m^{-2} yr^{-1} at West Fork. Vertebrate taxa were responsible for 100% of tertiary production, with *Gila nigra* being the only native tertiary consumer. In contrast to the relative productivities of native vs. nonnative primary and secondary consumer fishes, nonnative fishes made up the largest proportion of tertiary consumer production, which was 99-100% at all sites except Middle Fork, where production of the native *Gila nigra* results in only 49% production of nonnative tertiary consumer fishes. Tertiary consumer biomass showed similar trends, having a significantly negative relationship with GPP (R^2=0.78, d.f.=5, p=0.02) (Figure 3). West Fork and Gila Farm had significantly greater biomass values than all other sites, with Middle Fork and Grapevine also having significantly greater biomasses than Riverside and Bird Area (Figure 4).

Energy Demand of Fishes versus Energy Availability across Trophic Levels

In contrast with our predictions, the consumption of primary production by primary consumer fishes never approached values of gross primary productivity, with nearly two orders of magnitude separating primary production and fish consumption of primary production across sites, thus suggesting no energy limitation (Figure 7). Native fishes were responsible for >99%

of total fish consumption of primary production across sites. In agreement with our predictions, fish consumption of primary consumers never approached values of production, suggesting no energy limitation (Figure 7). Production was 6-10 times greater than consumption at the three most upstream sites, and was 38-105 times greater at the three downstream sites. Similar to consumption of primary production, native fishes were responsible for the largest percentage of total fish consumption of primary consumer production, accounting for 86-99% across sites. Overlap of 95%CIs of secondary consumer production and consumption by fish was in contrast with our predictions at all sites except Gila Farm, where tertiary consumers fishes might be energy-limited (Figure 7). Differences between consumption and production were small (2-39% of total production consumed by fishes) at other sites, even if there was no overlap. Nonnative consumption comprised the majority of total fish consumption of secondary production, ranging from 62-99% of secondary production consumed across four of our study sites. At Middle Fork nonnative consumption only accounted for 33% of total consumption, due to the native headwater chub (*Gila nigra)*, while at Bird Area nonnatives only accounted for 23%. Total consumption was extremely low (near 0) at Bird Area when compared with other sites however.

Primary Production and Food Chain Length

In contrast with our predictions, no significant relationship between gross primary production and proportional consumption of secondary consumers (fish + predaceous invertebrates) by fish was found across the upper Gila Basin (R^2=0.42, d.f.=5, p=0.16) (Figure 8). Proportional consumption of secondary consumers by fish was greatest at Gila Farm at 22% of total fish diet, but was less than 10% at all other sites.

Productivity and Native Dominance

The ratio of native fish production to production of nonnative predatory species ranged from 0.78 at Gila Farm to 21.7 at Grapevine, with all other values <10. No significant relationship was found between this ratio and gross primary production (R^2=0.0006. d.f.=5, p=0.96), violating our prediction of decreasing dominance with increased productivity and suggesting that native fish dominance is dictated by some environmental factor other than production of basal trophic resources (Figure 9). The prediction of decreased native fish dominance with increased GPP relied on an increase in abundance of nonnative predators with increases in productivity, but what was observed was a marginally significant negative relationship between nonnative predator production and GPP (R^2=0.53, d.f.=5, p=0.10) (Figure 10). Indeed, no relationship between native fish production and nonnative fish production was found either (R^2=0.0007, d.f.=5, p=0.96), suggesting neutral interactions or the interactions between native and nonnative species being overridden by other environmental factors (Figure 11).

DISCUSSION

Spatial Variation of Production

A large amount of spatial variability was found in values of production across all trophic levels in the upper Gila, with amount of variation among sites decreasing with an increase in trophic level. However, these values fall within the range of values reported in other studies, especially in similar ecosystems. Gross primary production calculated for Sycamore Creek, AZ (11,008 kcal m^{-2} yr^{-1}) (Busch and Fisher 1981) was within the range of GPP calculated in the present study (range= 1,526-16,272; mean= 6,075 kcal m^{-2} yr^{-1}) but values calculated in the heavily-forested Walker Branch, TN, were generally much less than these (1,732-1,842 kcal m^{-2} yr^{-1}) (Roberts et al. 2007). Community macroinvertebrate production across the upper Gila

(range= 258-892 kcal m^{-2} yr^{-1}; mean= 557 kcal m^{-2} yr^{-1}) also was much greater than values reported for most locations in the literature (<100 kcal m^{-2} yr^{-1}) (Stagliano and Whiles 2002 and references therein), but were similar to values reported for Sycamore Creek, AZ (600-675 kcal m^{-2} yr^{-1}) (Fisher and Gray 1983; Jackson and Fisher 1986). The short turnover times, small length at maturity, abundant food resources, and warm temperatures that contributed to the high community production values of Sycamore Creek are also found in the upper Gila Basin, which coupled with similar taxonomic composition, likely contributed to these similarities. Also, high turnover rates were probably responsible for the lack of concordance between production and biomass of primary consumer taxa across some sites (Riverside and Bird Area), exemplified in such taxa as the Chironomidae. Rapid turnover rates lead to high production, even while biomass remains low. Community fish production across the upper Gila (range= 5.27-27.7 kcal m^{-2} yr^{-1}; mean= 16.1 kcal m^{-2} yr^{-1}) was well within the range of values reported in a review of production values for rivers (2.6-280 kcal m^{-2} yr^{-1}), but were generally ≤ the mean reported value in the review (27.3 kcal m^{-2} yr^{-1}) (Randall et al. 1995). Across the upper Gila, primary producer and macroinvertebrate production are among the highest production values reported thus far, yet fish production is average. To our knowledge, our fish production estimates represent the first from a southwestern desert stream, making this study the first to identify the pattern of much above average primary and macroinvertebrate productivity occurring at locations with below average fish production. This pattern would suggest that something other than energy availability is limiting fish production in this system, and investigation into the mechanisms limiting fish production would provide insight into our observed patterns.

Generally, predicted responses of biomass and production of trophic levels to variation in gross primary production failed to demonstrate patterns predicted by food web theory. Those

trophic levels that did illustrate the predicted pattern (no response) likely did so not as a result of the proposed mechanisms, but probably through response to some environmental factors not measured in the current study. For example, secondary consumers were predicted to demonstrate no response to increased energy availability, and indeed that response was observed. However, the lack of response was predicted to result from top-down control, yet this was not apparent owing to the negative relationship between energy availability and tertiary consumer biomass. This negative response of the top trophic level to increases in primary production, which was in opposition to the predicted response, was also probably a result of unmeasured environmental factors. Violations of assumptions from food web theory do not appear likely as responsible for these deviations, because violation of assumptions generally result in increased abundance of all trophic levels with increased primary productivity (Abrams 1993). Further exploration into the biotic and abiotic factors responsible for the observed patterns might identify main drivers of consumer production across trophic levels.

Lack of response by trophic levels to variation in energy availability could also be a function of the metric of energy availability we chose, which was GPP. This metric assumes that energy availability in our system originates from autochthonous sources, but it is well known that allochtonously-derived carbon can be an important and sometimes dominant source of energy in stream ecosystems (Dodds and Cole 2007). However, it does not appear that inclusion of allochtonous energy availability in our energy budget through addition of heterotrophic respiration, a proxy of allochtonous energy availability, would change our overall conclusions or patterns observed. The significant relationship between GPP and community respiration would indicate that autochthonous and allochtonous energy availabilities vary along a similar gradient across the upper Gila River basin (Figure 2), thus leaving the observed response by other trophic

levels unchanged. We also note that some circularity may exist between our response and predictor variables in these relationships (i.e. GPP vs. chl *a*), but use of other metrics of energy availability (nutrient concentration, temperature, light) would still not change the patterns observed or our overall conclusions. Many of these proxies for autochthonous energy availability vary in a similar downstream manner as GPP (Table 1), such as the relationship between nitrate concentration and GPP (R^2=0.64, d.f.=5, p=0.05). Because of these reasons we believe our choice of metric for energy availability is justified.

Most studies of benthic macroinvertebrate production encompass a small spatial extent, with the vast majority of studies conducted at one site. This study highlights the degree of variability inherent in production values across a system, thus identifying the complexity of generalizing system production from a single site. However, with an increase in spatial extent (more than one site) comes a decrease in temporal resolution of sampling, unless major resources in the form of time and money are available. Most studies rely on monthly to twice-monthly sampling for macroinvertebrate production estimates at one site, whereas our study had five samples throughout the year at six sites. The tradeoff between decreased temporal resolution of sampling with an increase in spatial extent creates either high temporal variability among samples with low temporal resolution of sampling, or high spatial variability among samples with low spatial resolution of sampling. However, the continuous reproduction, high turnover rates, and asynchronous life cycles of dominant macroinvertebrate taxa (mayflies and midges) (Gray 1981) likely make increased temporal resolution of sampling less necessary in this system for accurate secondary production estimates when compared with other systems that have slower growing taxa and only 1-2 generations per year. Temporal resolution of sampling influences the estimate for the average cohort of a population, which is the crucial step in the size-frequency

method. Less temporal resolution is needed when all size classes are continuously present in the system throughout the year due to the aforementioned life history characteristics for construction of the average cohort when compared with systems where there is only one cohort per year and size classes are present for only days to weeks. An understanding of the life history attributes of taxa is thus necessary when planning the sampling regime of a production study.

Non-fish Nonnatives

Both the northern crayfish (*Orconectes virilis*) and the American bullfrog tadpole (*Rana catesbeiana*) reached extremely high productivities at some sites in this study; the production of the northern crayfish (6.35 kcal m^{-2} yr^{-1}) was more than any fish species at Bird Area, the production of the American bullfrog tadpole (3.74 kcal m^{-2} yr^{-1}) was third in productivity of aquatic vertebrates to Sonora sucker and desert sucker at Middle Fork (Appendix B). These high productivities create the potential for strong effects on community structure and ecosystem function by these nonnatives. Northern crayfish have been shown to compete with and cause decreased growth in native fishes of the Colorado River Basin (Carpenter 2005), whereas bullfrog tadpoles have been demonstrated to compete with native tadpoles (Kupferberg 1997) and feed on larval stages of native fish (Mueller et al. 2006) in the Colorado Basin. Predatory fish do not readily feed on American bullfrog tadpoles, owing to a predation deterrent produced by the tadpole (Kruse and Francis 1977). Released from predation, these tadpoles could sequester primary production in their tissues, and thus shorten food chain length from four to two trophic levels across where they are present across the upper Gila, harming both native and nonnative fishes. Furthermore, northern crayfish could also potentially shorten food chain length from four to three trophic levels in the Gila through consumption of algae, detritus, and invertebrates and then being consumed by nonnative predators, and via negative effects on native

fishes created via apparent competition (Tablado et al. 2010). Characterizing the effects of crayfish and bullfrogs on community structure, function, and food chain length is necessary to elucidate their role in the Gila River food webs.

Energy Limitation and Consumption

Across sites there was little evidence of energy limitation to fishes of any trophic level, with the exception of secondary consumer production and fish consumption at Gila Farm. Multiple caveats need to be mentioned in this interpretation however. In terms of herbivorous fish consumption, herbivorous fishes made up a very small proportion of total primary consumer production, with macroinvertebrates accounting for the vast majority. Assuming a rough gross production efficiency (production/ingestion) of 0.15 (Benke and Huryn 2006) for these herbivorous macroinvertebrates, invertebrate consumption approaches or exceeds GPP at West Fork and Gila Farm, thus creating potential energy limitation for primary consumers and supporting our predictions (Figure 12). This pattern is similar to what was found in Sycamore Creek, AZ by Fisher and Gray (1983), where grazing macroinvertebrate consumption exceeded production of primary producers, thus highlighting the importance of invertebrate feces and detritus in supplementing invertebrate diets. Indeed, inclusion of detrital energy sources through addition of a proxy for detrital energy availability, heterotrophic respiration, to GPP provides a balanced energy budget and large surpluses of energy for primary consumer macroinvertebrates and fishes, thus alleviating this observed energy limitation and providing stability to these food webs (Figure 13).

Energy in the form of primary consumers was always sufficient to meet the demands of secondary consumer fishes. Even with the addition of predaceous macroinvertebrates as

secondary consumers through division of predaceous macroinvertebrate production by a gross production efficiency of 0.35, primary consumer production is still sufficient to meet to secondary consumer demands across sites (Figure 12). This finding would be in accord with our predictions if secondary consumer populations had been regulated by predation, but we do not have evidence this was the case.

With the exception of Gila Farm, secondary consumer production was always sufficient to meet the consumptive demands of predatory fishes. Actual amount of fish production available for consumption is probably less that the values reported, since production of large-bodied individuals (Sonora sucker, desert sucker) are not available for consumption due to gape limitation of predators. The contribution of large-bodied fish to total fish production is probably small however, owing to the low densities and low P/B ratios of large individuals. Measured fish production estimates are thus likely to close to estimates of total fish production available for consumption.

Considering the aforementioned caveats, energy limitation is not apparent across the upper Gila. This finding is in contrast to findings in trout streams, where energy limitation to fishes is the rule rather than the exception (Waters 1988; Huryn 1996). The Allen Paradox, wherein all available food resources are required to sustain fish production, is a common property of trout streams (Huryn 1996). In the Gila River and other desert streams, where high primary and macroinvertebrate production are the norm, factors besides energy limitation appear to be shaping consumer productivity and biomass. Longer development times required for fish could prevent them from becoming abundant in this system, due to the frequent disturbances created by floods. The rapid life cycles of primary producers and macroinvertebrates allow for rapid recolonization after disturbance (Fisher et al. 1982), and thus accounts for their high

biomass and productivity across the upper Gila. The coupling between primary production and macroinvertebrate consumer production has been observed across many locations, yet this production of basal resources is rarely related to the production of higher trophic levels. This pattern is consistent with the findings of McQueen et al. (1986), who found an attenuation of bottom-up effects (energy availability) in pelagic ecosystems. Also found by McQueen et al. (1986) was that top-down effects of predators were more prevalent in low-energy systems. This may explain why Propst et al. (2008) observed extirpation of natives by nonnatives at low-productivity headwater but not high-productivity downstream sites in the upper Gila.

Food Chain Length

In the present study, little evidence was found supporting energy availability as the primary determinant of food chain length, thus failing to explain the abundance of nonnative predatory fishes and variation in food chain length. Indeed Post (2002) concluded that energy availability is predicted to be a primary determinant of food chain length in only the most unproductive of ecosystems (i.e. 10-100 kcal m^{-2} yr^{-1}). These conditions are far exceeded across all locations of the upper Gila, indicating that some factor or combination of factors besides energy availability is/are responsible for food chain length. Prior to anthropogenic introductions of nonnative predatory fishes, a likely determinant of food chain length in the upper Gila and throughout the Colorado Basin was the history of community organization (Kitching 2001; Post 2002). In isolated systems where colonization is limited food chain length will be dictated by the species of the highest trophic position which can either colonize the system or evolve (Post 2002). With the Rocky Mountain chain impeding colonization of predator fauna from the Rio Grande drainage and the evolution of only one (and maybe two) partially-piscivorous cyprinid predators in situ, history of community organization in the upper Gila probably had a strong

influence of food chain length before nonnative introductions. Introductions of Siluriform and Perciform predatory fishes, which were completely absent from the Colorado River Basin, has bypassed this historical limitation to food chain length, thus suggesting other responsible mechanisms for the variation in food chain length which we observed. Continuing along the hierarchy of Post (2002) and bypassing energy limitation, the next potential mechanism dictating food chain length is predator-prey interactions. If predator and prey are of a similar size, the evolutionarily-stable food chain length is three trophic levels (Hastings and Conrad 1979), since energetically it does not make evolutionary sense to feed on a secondary consumer when a primary consumer of the same size is available. This mechanism seems implausible in the upper Gila, because predatory nonnatives are typically much larger than their native prey. This takes us to the final step of the hierarchy, where disturbance is predicted to be the primary constraint on food chain length (Pimm and Kitching 1987; Post 2002). In systems which are not frequently disturbed, food chain length is predicted to be influenced by ecosystem size, with larger ecosystems having longer food chain length. Disturbances in the form of high and low discharge events and ash flows following forest fires are a common occurrence in the upper Gila, and suggest that food chain length will be dictated not by ecosystem size but by some aspect of stability and colonization following disturbance with an increasing amount of disturbance resulting in either shorter (Pimm and Lawton 1977) or longer (Sterner 1997; Marks et al. 2000) food chains. Post (2002) predicts that streams subject to frequent and strong disturbance events should have shorter food chain lengths when compared with more stable streams. Anecdotally increased downstream disturbance frequency and intensity was seen during the present study, which is in the same direction as our pattern of decreasing food chain length (Figure 8). Thus, do nonnative predators do better in upstream regions of the Gila because they are adapted to

different flow conditions, or are they adapted to different flow conditions because they are predators (i.e. variable flows and disturbance do not favor predators since it discourages longer food chains)? Similarly, was the diversification of predatory fauna limited by evolutionary time, or simply because evolution did not favor species occupying higher trophic positions due to disturbance frequency? Longitudinal variation in disturbance and its relationship with food chain length and thus nonnative predator success deserves further investigation.

Native Dominance and Energy Availability

We found no support for energy availability as an important component of the environmental context under which native dominance over nonnative predators or extirpation of natives by nonnatives occurs. However, the conclusions of this study are limited by their temporal extent with one year being barely adequate to determine these complex interrelationships. Interestingly, our observation of a downstream increase in primary producer and consumer production over one year was in the same direction that Propst et al. (2008) witnessed increased persistence of native fishes over 19 years. To the extent of inter-annual stability of our observed pattern, longitudinal increases in basal energy availability could be an important component of native persistence over longer time scales. In the environmental context of flow, January 2008-June 2009 represented a best case scenario for native fishes, in that flows were much above average during this period (USGS Gauge 09430500). The importance of basal productivity to native dominance could be superseded by discharge. However, during low flow years, basal energy availability may increase in importance with its effect on native/nonnative interactions, potentially driving persistence of natives. Further investigation into the environmental context under which native and nonnative species coexist should be conducted not only in the upper Gila, but in other systems as well.

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TABLES AND FIGURES

Table 1 Physical and chemical characteristics of six sampling sites located on the Upper Gila River Basin, NM. Excluding elevation, all values represent means of data collected between June 2008 and June 2009. Values in parentheses correspond to the ranges for all variables except depth, which equals maximum depth. No temperature data is available for Bird Area.

Site	Elevation (m)	water temperature (°C)	baseflow discharge (m^3/s)	depth (m)	[NO_3^-] (µg/L)
West Fork	1735	11.9 (0.19-25.6)	0.29 (0.2-0.4)	0.17 (0.58)	54 (2-107)
Middle Fork	1725	14.6 (1.3-29.1)	0.41 (0.3-0.6)	0.16 (0.61)	53 (5-101)
Grapevine	1695	10.8 (0.73-27.9)	1.51 (0.9-1.9)	0.31 (0.77)	68 (10-127)
Gila Farm	1410	15.0 (3.3-28.3)	2.04 (1.1-2.7)	0.40 (0.70)	56 (7-105)
Riverside	1360	15.7 (3.7-28.3)	2.23 (1.2-3.9)	0.20 (0.55)	182 (28-335)
Bird Area	1327		2.66 (1.5-3.5)	0.28 (0.76)	243 (198-288)

Table 2 Production method, 365/cohort production interval (CPI), mean P/B ratio, and trophic level assignment for macroinvertebrate taxa in the Upper Gila River Basin, NM. Size-frequency production was used to calculate production for abundant taxa, whereas the P/B method was used for rare taxa. If a taxon was rare at some sites and abundant at others, both methods were used for that taxon. CPI's were determined from either length-frequency histograms or from Gray (1981). Mean P/B ratio represents the mean across macrohabitats and sites for a taxon. Trophic levels were determined from Thorp and Covich (2001), Merritt et al. (2008), and Pilger et al. (2010).

Taxon	Production Method	(365/CPI)	Mean P/B Ratio	Trophic Level
Acari	P/B Ratio	N/A	100	Primary consumer
Baetidae	Size-Frequency	35	158	Primary consumer
Ceratopogonidae	Both	41	111	Secondary consumer
Chironomidae	Size-Frequency	38	249	Primary consumer
Corixidae	Both	17	59	Primary consumer
Corydalidae	P/B Ratio	N/A	5	Secondary consumer
Crambidae	P/B Ratio	N/A	5	Primary consumer
Dryopidae	P/B Ratio	N/A	5	Primary consumer
Elmidae	Size-Frequency	2	8	Primary consumer
Empididae	P/B Ratio	N/A	3	Secondary consumer
Ephemerellidae	Size-Frequency	2	7	Primary consumer
Gastropoda	P/B Ratio	N/A	5	Primary consumer
Glossosomatidae	P/B Ratio	N/A	17	Primary consumer
Gomphidae	P/B Ratio	N/A	5	Secondary consumer
Helicopsychidae	Both	11	32	Primary consumer
Heptageniidae	Both	35	122	Primary consumer
Hydropsychidae	Size-Frequency	7	3	Primary consumer
Hydroptilidae	P/B Ratio	N/A	17	Primary consumer
Isonychiidae	P/B Ratio	N/A	5	Primary consumer
Leptoceridae	P/B Ratio	N/A	17	Primary consumer
Leptohyphidae	Size-Frequency	35	177	Primary consumer
Leptophlebiidae	Both	2	8	Primary consumer
Libellulidae	P/B Ratio	N/A	5	Secondary consumer
Naucoridae	P/B Ratio	N/A	5	Secondary consumer
Nemouridae	P/B Ratio	N/A	5	Secondary consumer
Oligochaeta	P/B Ratio	N/A	10	Primary consumer
Orconectes virilis	Both	1	2	Primary consumer
Perlodidae	P/B Ratio	N/A	5	Secondary consumer
Polycentropodidae	P/B Ratio	N/A	85	Primary consumer
Psephenidae	Both	2	7	Primary consumer
Simuliidae	Both	35	75	Primary consumer
Tabanidae	Both	2	3	Secondary consumer
Tanyderidae	P/B Ratio	N/A	250	Primary consumer
Tipulidae	P/B Ratio	N/A	85	Primary consumer

Table 3 Production method, cohort production interval (CPI), mean P/B ratio, and introduction status for fish species collected in the Upper Gila River Basin, NM. The size-frequency method was used for abundant taxa, the P/B method for rare taxa, and a combination of both for taxa that were abundant at some sites and rare at others. CPI's were estimated using the life history of species, with larger-bodied species receiving a value of 3 and smaller-bodied species a value of 2. The only non-fish taxon in the table, *Rana catesbeiana*, received a value of 1. Mean P/B ratio was an average across sites. Native/nonnative status is from Sublette et al. (1990).

Taxon	Production Method	CPI	Mean P/B Ratio	Native/Nonnative
Agosia chrysogaster	Both	2	1.5	Native
Ameiurus natalis	Both	3	1.2	Nonnative
Catostomus clarki	Size-frequency	3	2.5	Native
Catostomus insignis	Size-frequency	3	2	Native
Cyprinella lutrensis	Both	2	1	Nonnative
Gambusia affinis	P/B Ratio	N/A	1	Nonnative
Gila nigra	Size-frequency	3	2.2	Native
Ictalurus punctatus	Both	3	0.7	Nonnative
Lepomis cyanellus	Both	2	0.7	Nonnative
Meda fulgida	Both	2	1.5	Native
Micropterus dolomieu	Both	3	0.6	Nonnative
Oncorhynchus gilae	P/B Ratio	N/A	0.5	Native
Oncorhynchus mykiss	Both	3	0.7	Nonnative
Pimephales promelas	Both	2	1.6	Nonnative
Pylodictis olivaris	Both	3	0.4	Nonnative
Rana catesbeiana	Both	1	1	Nonnative
Rhinichthys osculus	Size-frequency	2	1.6	Native
Salmo trutta	Both	3	0.7	Nonnative
Tiaroga cobitis	Both	2	1.1	Native

Table 4 Percent gut contents of five diet items found in fish of the Upper Gila River Basin, NM. Percentages represent an average of individuals collected between 2007 and 2009 across six locations. Trophic level assignments were based on this data in addition to the isotopic data of Pilger et al. (2010), with the largest percent diet item value and ^{15}N signature dictating trophic level. No diet data is available for *Oncorhynchus gilae*.

Species	% Algae	% Detritus	% Fish	% Herb. Invert.	% Pred. Invert.	Trophic Level
Agosia chrysogaster	22	32	0	46	0	Secondary Consumer
Ameiurus natalis	0	28	18	46	8	Tertiary Consumer
Catostomus clarki	60	7	0	34	0	Primary Consumer
Catostomus insignis	22	23	0	53	1	Secondary Consumer
Cyprinella lutrensis	1	94	0	5	0	Primary Consumer
Gambusia affinis	0	27	0	73	0	Secondary Consumer
Gila nigra	48	9	25	17	2	Tertiary Consumer
Ictalurus punctatus	0	0	6	94	0	Tertiary Consumer
Lepomis cyanellus	0	4	36	60	0	Tertiary Consumer
Meda fulgida	0	15	0	85	0	Secondary Consumer
Micropterus dolomieu	0	8	29	39	24	Tertiary Consumer
Oncorhynchus mykiss	2	10	21	57	11	Tertiary Consumer
Pimephales promelas	92	8	0	0	0	Primary Consumer
Pylodictis olivaris	0	0	84	16	0	Tertiary Consumer
Rhinichthys osculus	1	22	0	74	2	Secondary Consumer
Salmo trutta	0	5	23	53	19	Tertiary Consumer
Tiaroga cobitis	0	4	0	96	0	Secondary Consumer

Table 5 Percent composition of production by macroinvertebrates and vertebrates across three trophic levels in the Upper Gila Basin, NM.

	Primary Consumer		Secondary Consumer		Tertiary Consumer	
Site	%Invert	%Vert	%Invert	%Vert	%Invert	%Vert
West Fork	99	1	26	70	0	100
Middle Fork	96	4	25	74	0	100
Grapevine	99	1	27	73	0	100
Gila Farm	99	1	58	41	0	100
Riverside	99	1	50	50	0	100
Bird Area	99	1	37	63	0	100

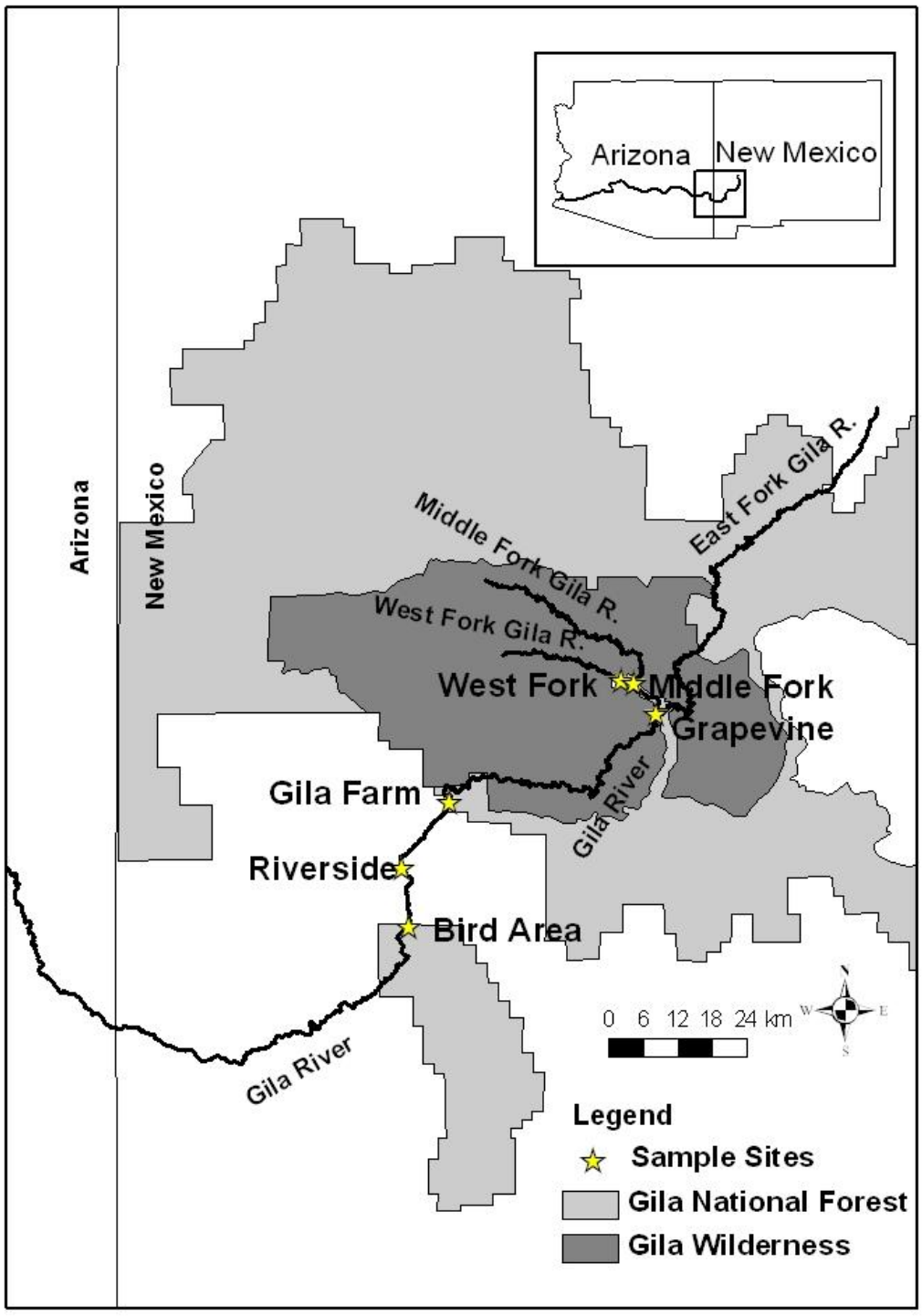

Figure 1 . Map of study sites in the upper Gila River Basin, NM, USA.

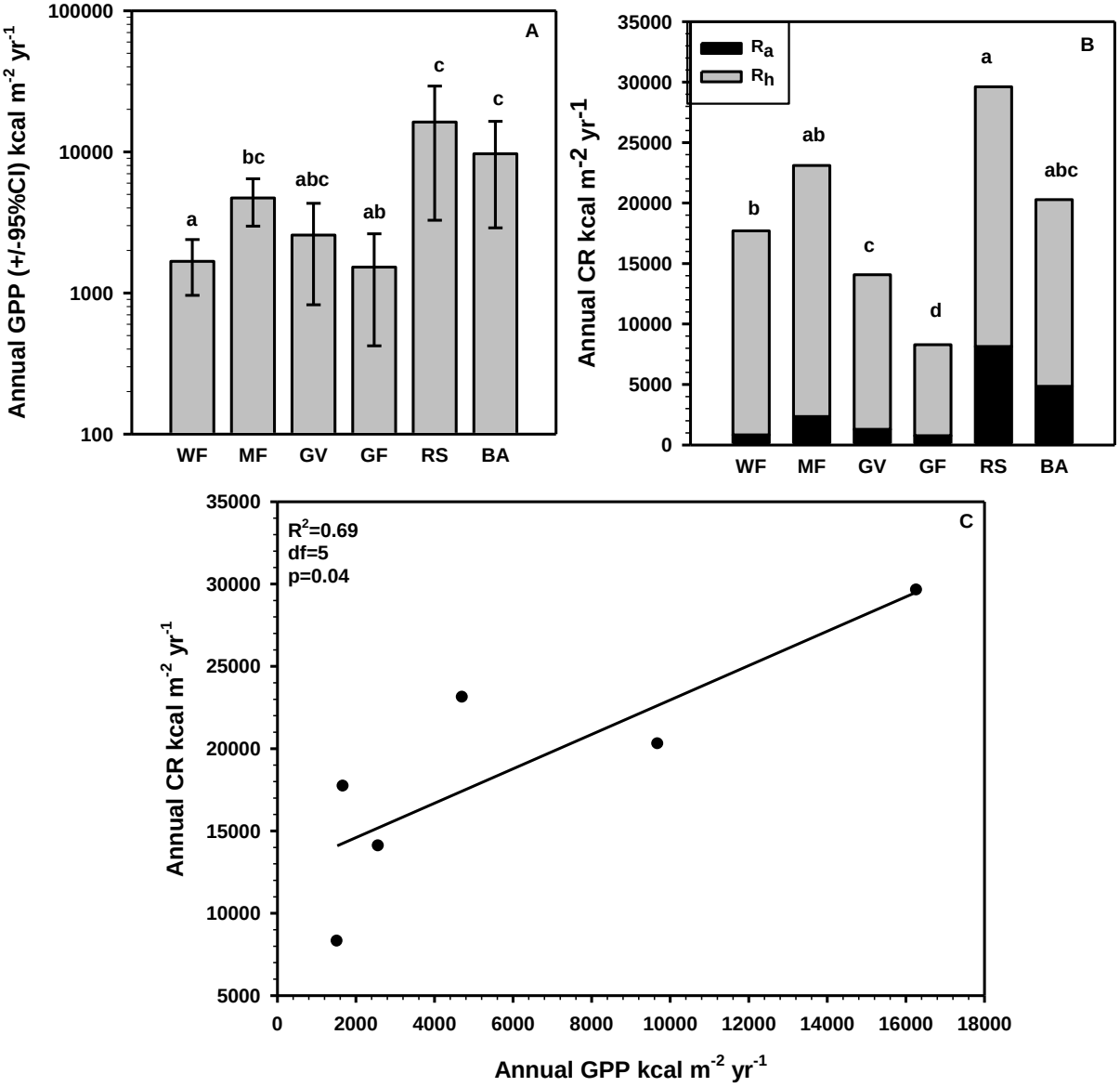

Figure 2 Graphs depicting (A) annual gross primary production (GPP), (B) annual community respiration, and (C) the relationship between annual GPP and CR. All units are in kcal m^{-2} yr^{-1}. Significant differences in GPP and CR are denoted by letter codes and were determined through overlap of 95%CIs. Annual CR is divided into autotrophic (black) and heterotrophic (grey) respiration, assuming that 50% of GPP is used in autotrophic respiration (Dodds and Cole 2007). The relationship between GPP and CR was statistically significant (R^2=0.69, d.f.=5, p=0.04).

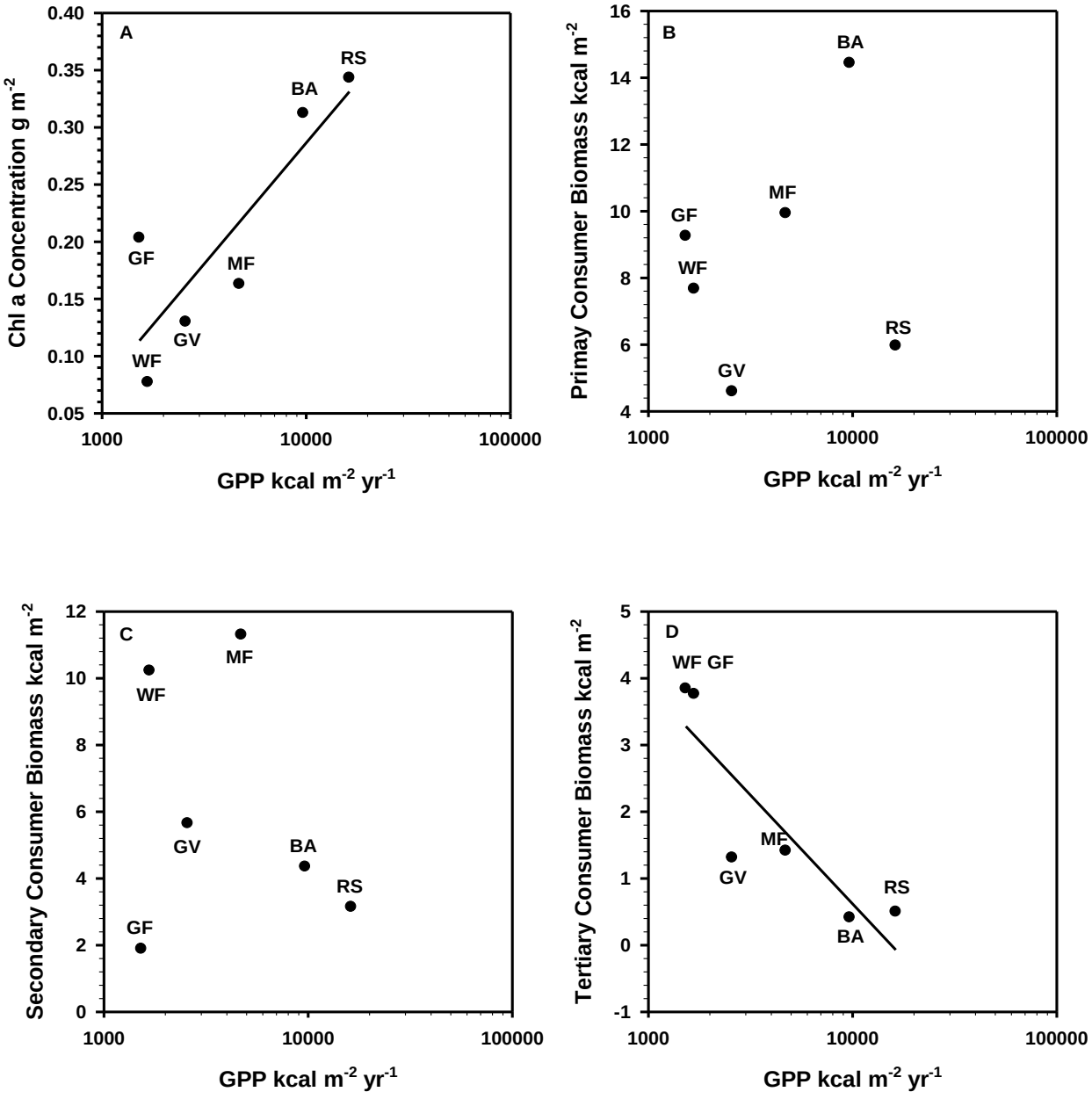

Figure 3 Regressions between GPP and (A) primary producer biomass, (B) primary consumer biomass, (C) secondary consumer biomass, and (D) tertiary consumer biomass. Solid lines represent significant relationships. Predicted relationships were as follows: A=none, B=positive, C=none, D=positive. GPP was $\log_{10}$ transformed prior to analysis due to unequal variances. Regression results are as follows: GPP vs. primary producer biomass R^2=0.72, df=5, p=0.03; GPP vs. primary consumer biomass R^2=0.05, df=5, p=0.68; GPP vs. secondary consumer biomass R^2=0.05, df=5, p=0.67, GPP vs. tertiary consumer biomass R^2=0.78, df=5, p=0.02.

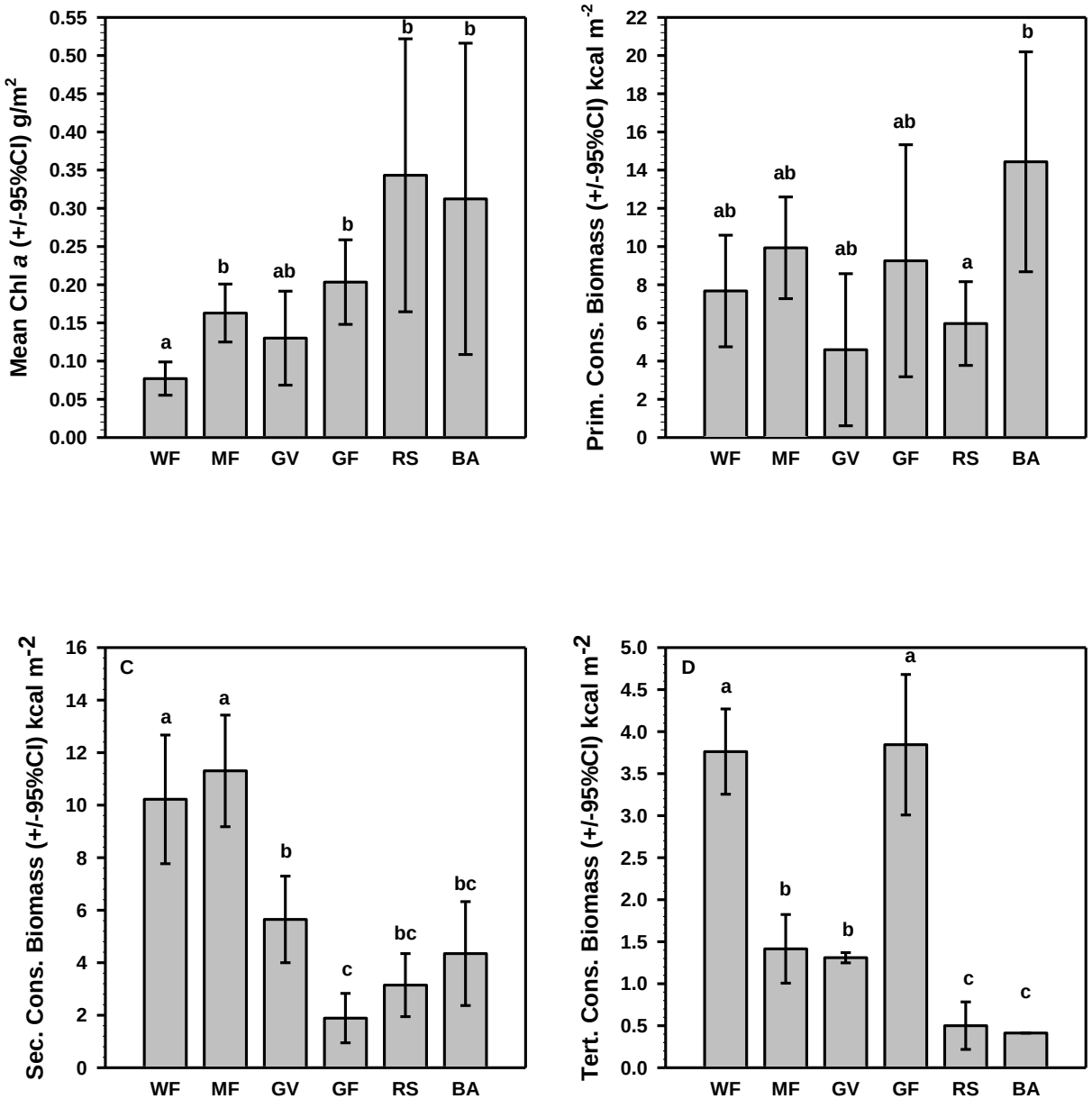

Figure 4 Biomass values of primary producers (A), as well as energy density of primary (B), secondary(C), and tertiary consumers (D) in the upper Gila River Basin of New Mexico. Error bars indicate 95% confidence intervals. Significant differences among sites were determined by overlap of 95%CI's. Units of primary producers are in g chl *a* m^{-2}, while all other units are in kcal m^{-2}. Note that the scale of consumer values decreases with an increase in trophic level.

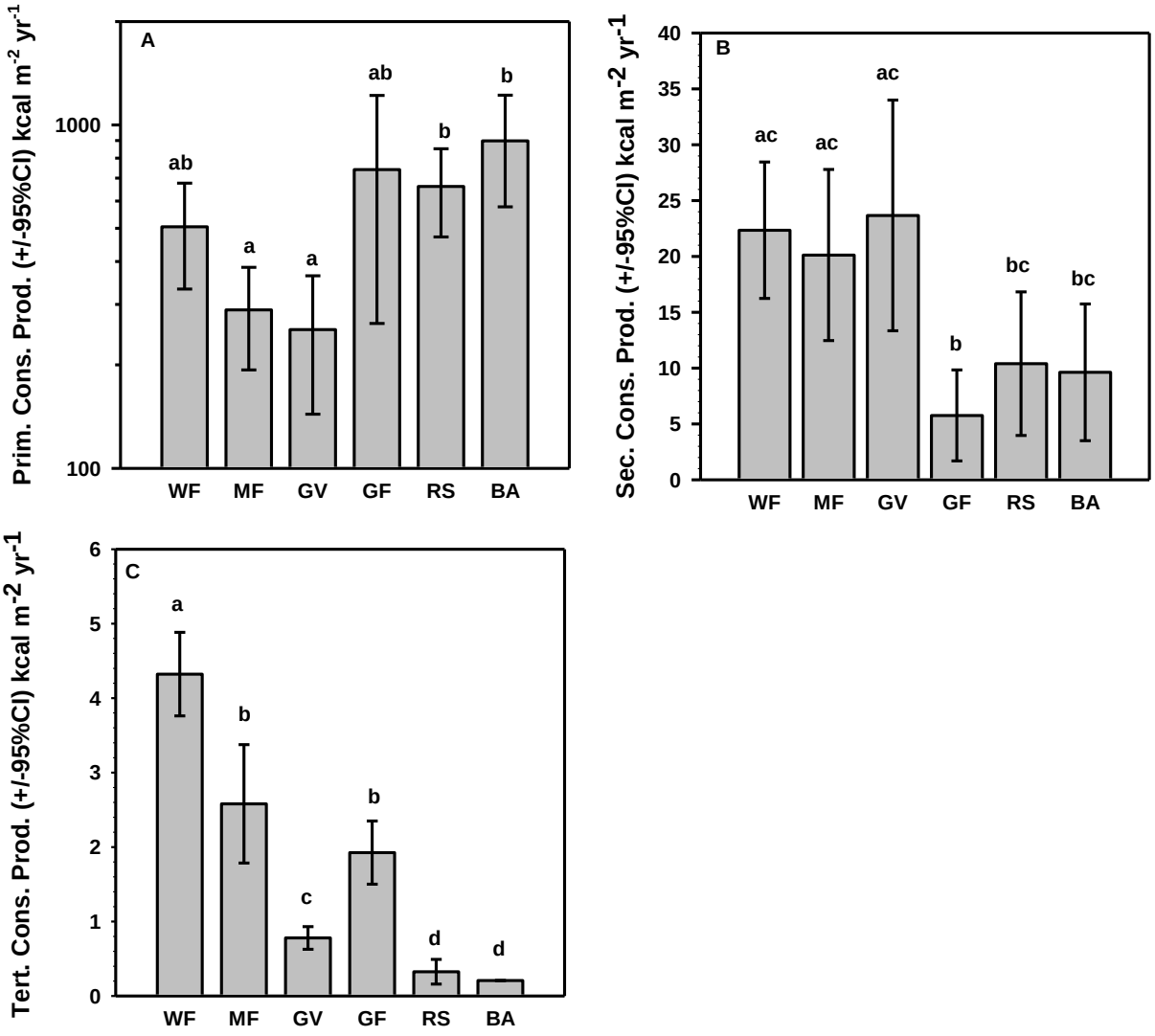

Figure 5 Production values of (A) primary, (B) secondary, and (C) tertiary consumers in the upper Gila River Basin of New Mexico. Note that y-axis of (A) is $\log_{10}$ transformed due to unequal variances. Error bars indicate 95% confidence intervals. Significant differences among sites were determined by overlap of 95%CI's. All units are in kcal m^{-2} yr^{-1}, but note that the scale of the y-axis decreases with an increase in trophic level. Sites along the x-axis are arranged from upstream to downstream. Site codes are as follows: WF=West Fork, MF=Middle Fork, GV=Grapevine, GF=Gila Farm, RS=Riverside, BA=Bird Area.

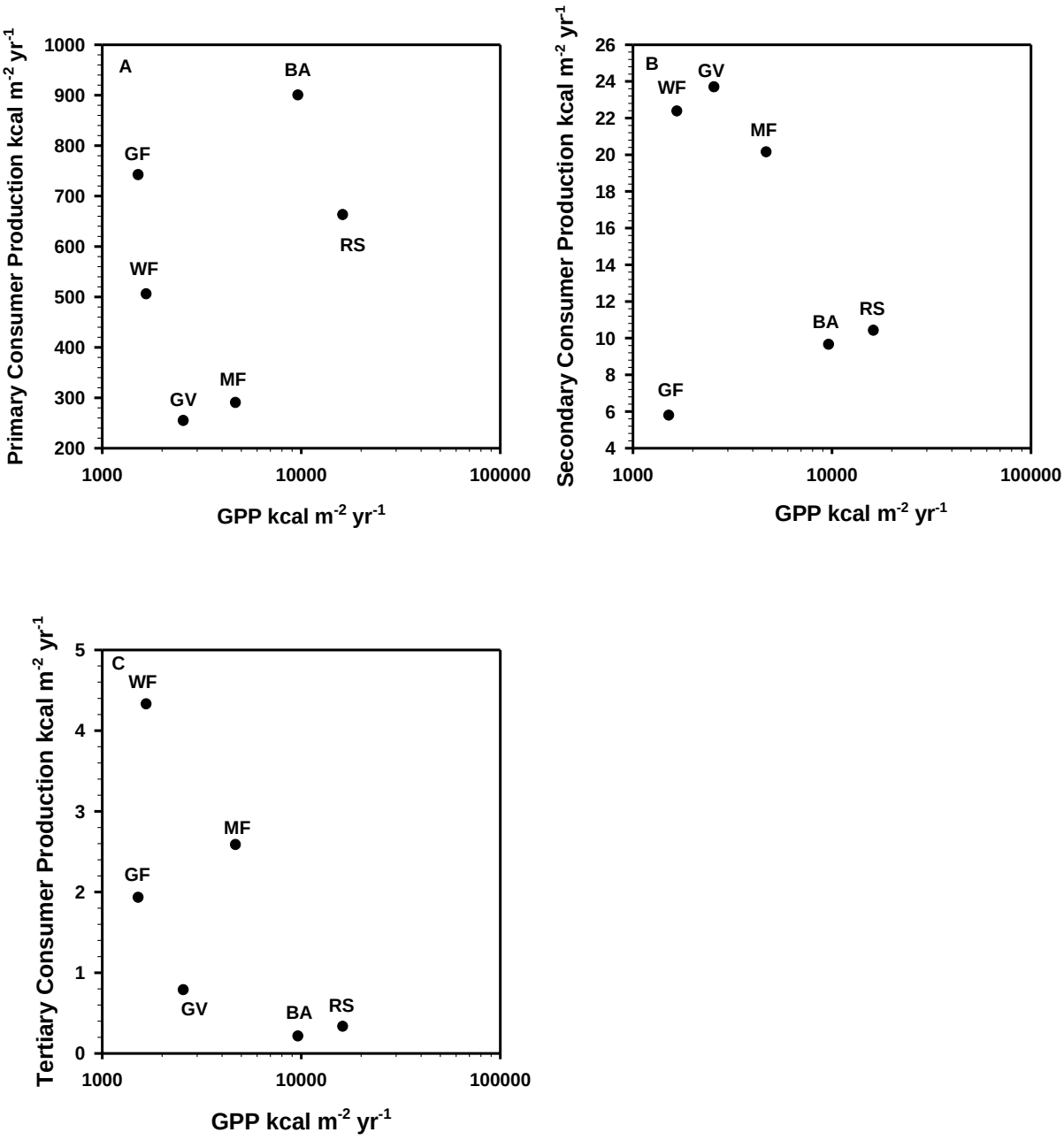

Figure 6 Regression between gross primary production (GPP) and (A) primary consumer production, (B) secondary consumer production, and (C) tertiary consumer production. Predicted relationships were as follows: A=positive, B=none, C=positive. GPP was $\log_{10}$ transformed prior to analysis due to unequal variances. Regression results are as follows: GPP vs. Primary Consumer Production (A) R^2=0.11, df=5, p=0.52; GPP vs. Secondary Consumer Production (B) R^2=0.11, df=5, p=0.54; GPP vs. Tertiary Consumer Production (C) R^2=0.46, df=5, p=0.14. Site codes are as follows: WF= West Fork, MF= Middle Fork, GV= Grapevine, GF= Gila Farm, RS= Riverside, BA= Bird Area.

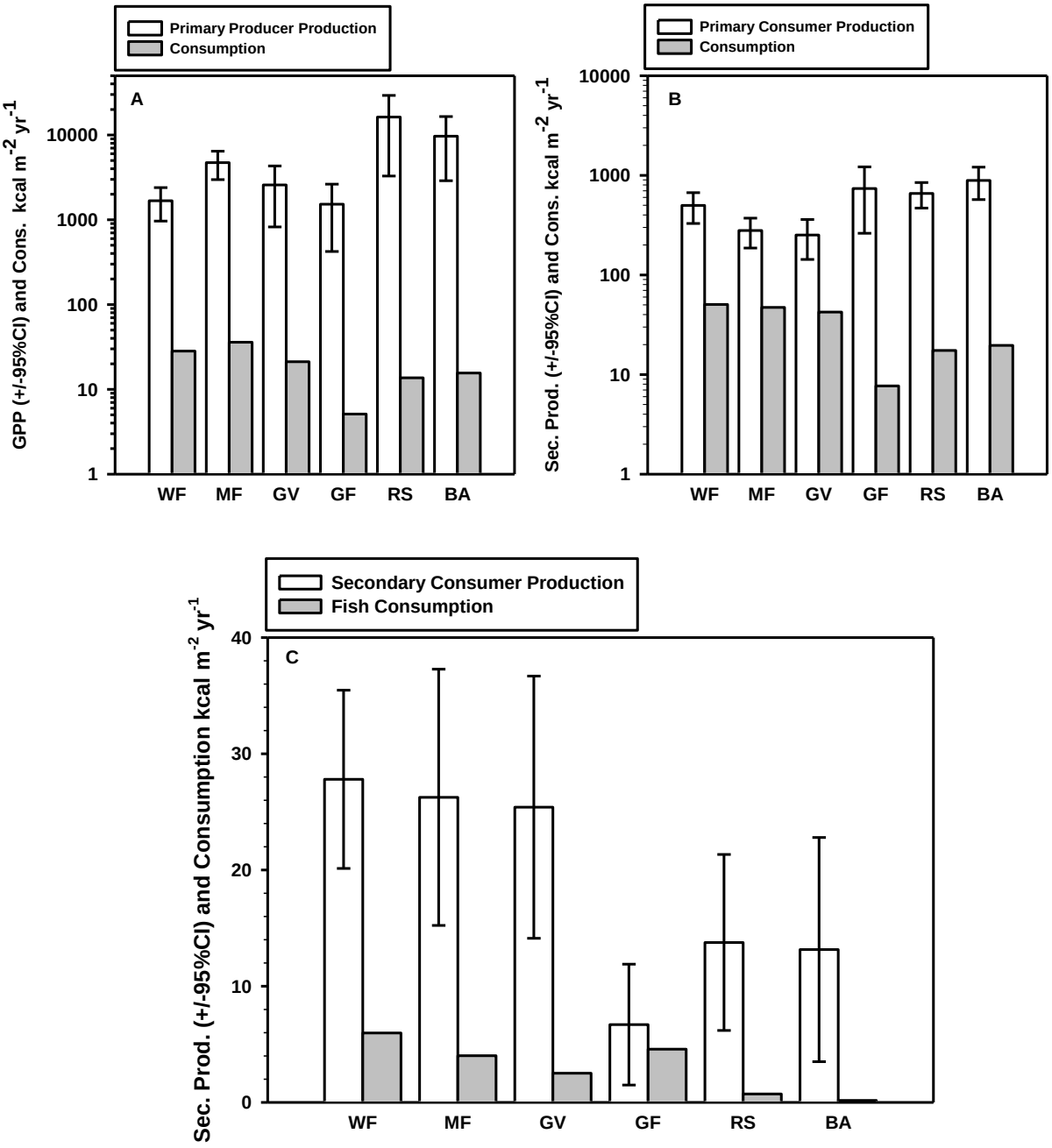

Figure 7 Production of primary producers (A), primary consumers (B), and secondary consumers (C) coupled with consumption of that production by fish. Production and consumption values are in units of kcal m^{-2} yr^{-1}, with error bars on production indicating 95% confidence intervals. Production of primary consumers does not include fish primary consumers, since the only herbivorous fishes are large-bodied adults not available for consumption. Secondary consumer production includes both predaceous invertebrates and fish. Asterisks denote sites where fish consumption of a trophic level approaches production of that level. Not the $\log_{10}$ scale of the y-axis on the top two graphs.

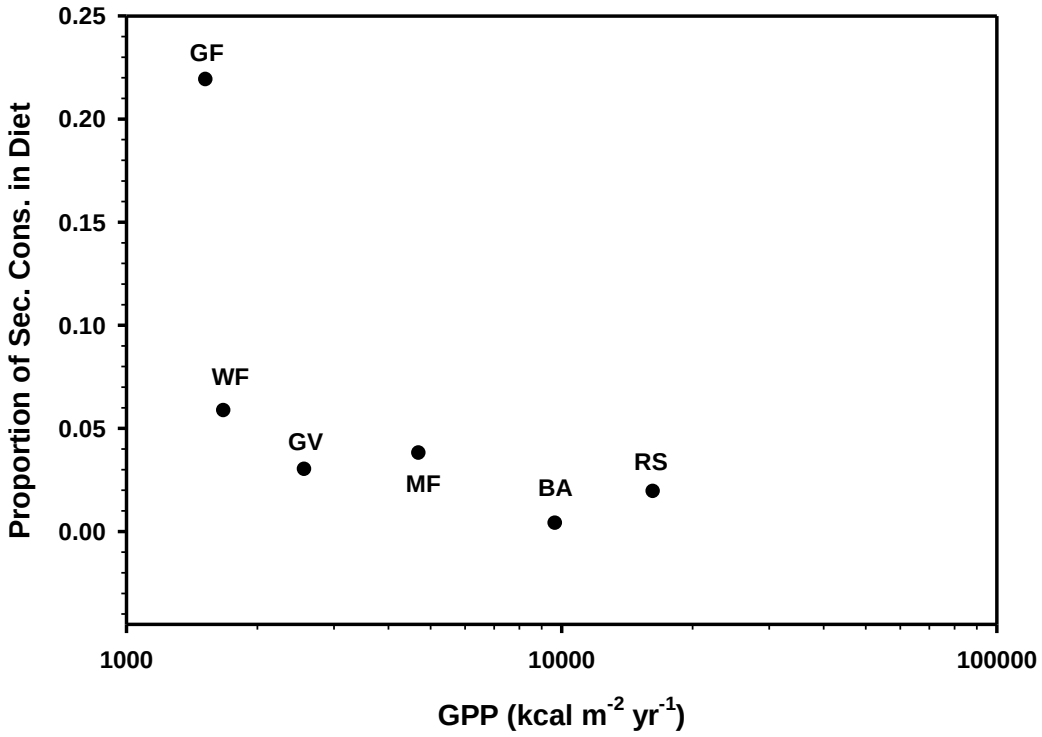

Figure 8 Regression between gross primary production and proportion of secondary consumers in diet of predatory fishes, which represents a metric of food chain length (R^2=0.42, d.f.=5, p=0.16). The predicted relationship was positive. All tertiary consumers were nonnative except the headwater chub (*Gila nigra)*. Units of GPP are in kcal m^{-2} yr^{-1} werelog_{10} transformed prior to analysis.

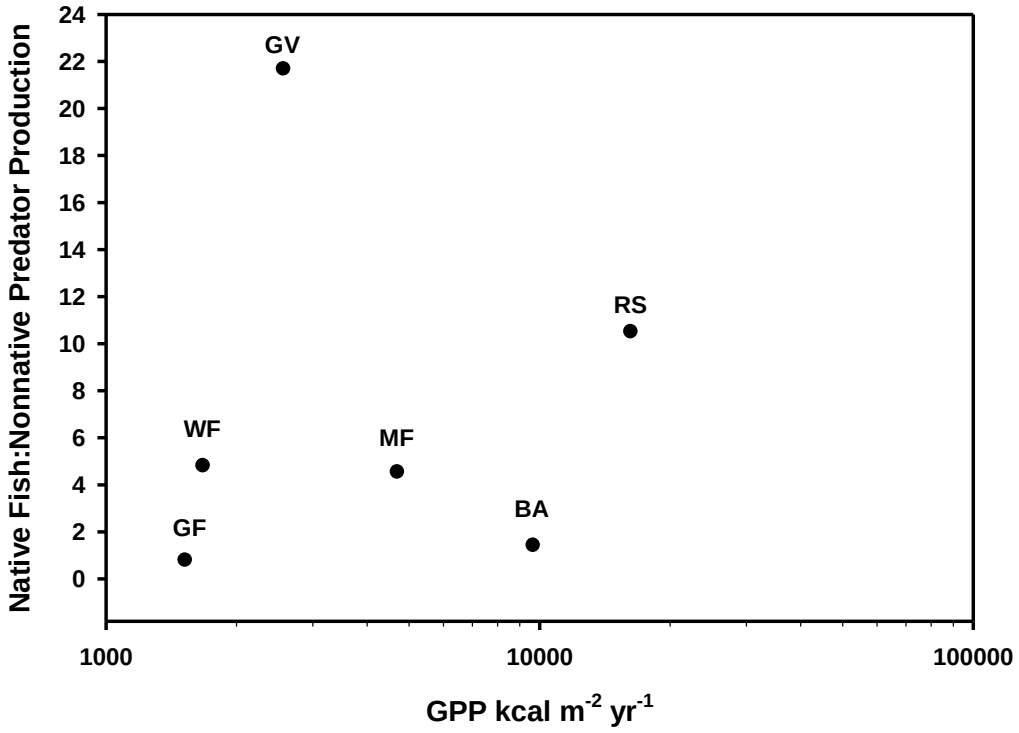

Figure 9 Regression between gross primary production and the ratio of native fish production to nonnative predator production (native dominance) (R^2=0.0006, d.f.=5, p=0.96). The predicted relationship was negative. Note that GPP was $\log_{10}$ transformed due to unequal variances.

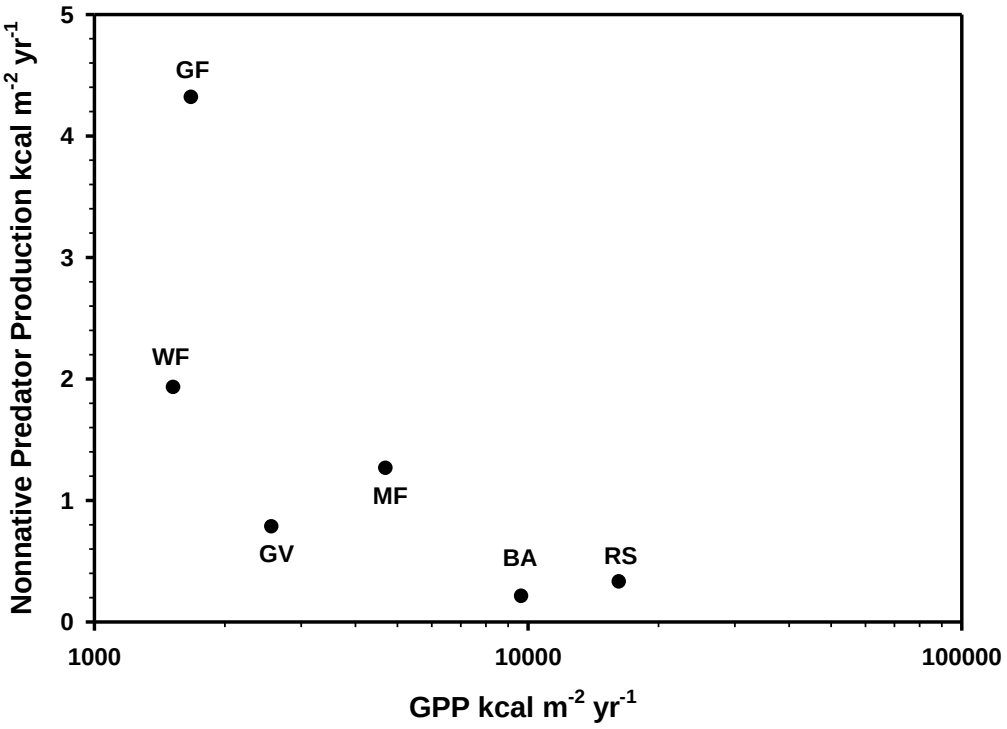

Figure 10 Regression between gross primary production and nonnative predator production. GPP was log10 transformed prior to analysis due to unequal variances. The predicted relationship was positive. Results of the regression are R^2=0.53, d.f.=5, p=0.10.

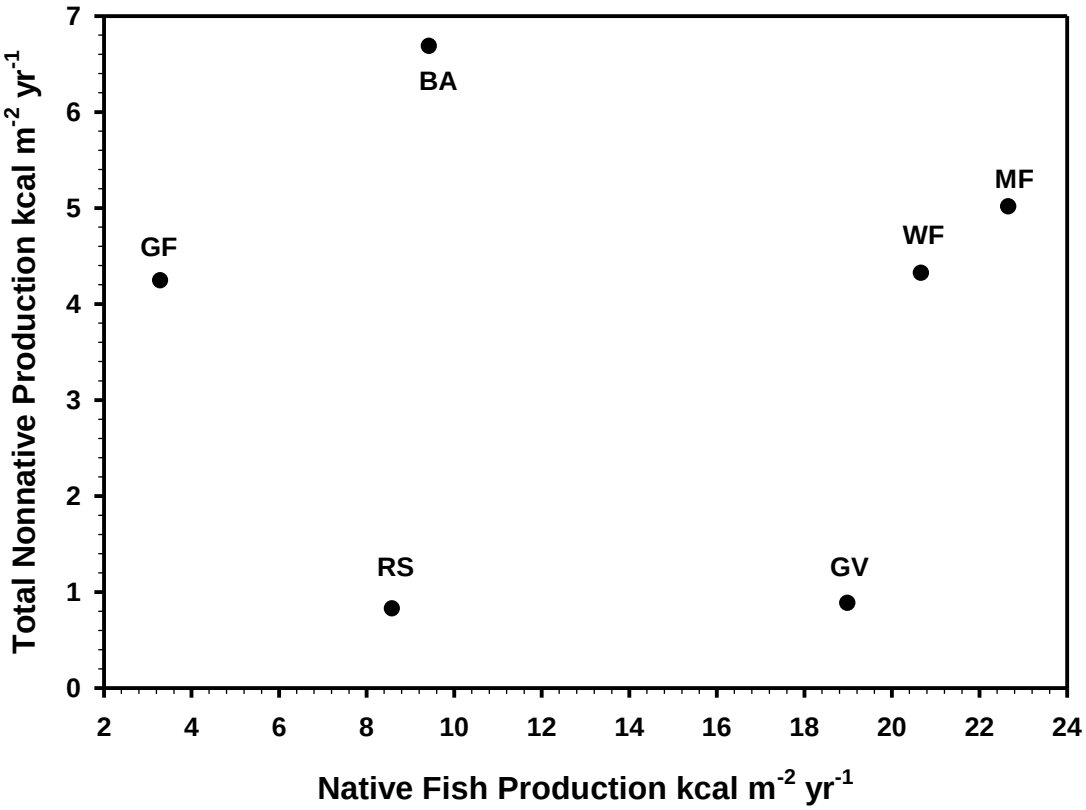

Figure 11 Regression between native fish production and total nonnative production (R^2=0.0007, d.f.=5, p=0.96). Native fish production was the summed productivity of all native fishes, whereas total nonnative production was the sum of production for nonnative crayfish, tadpoles, and fish.

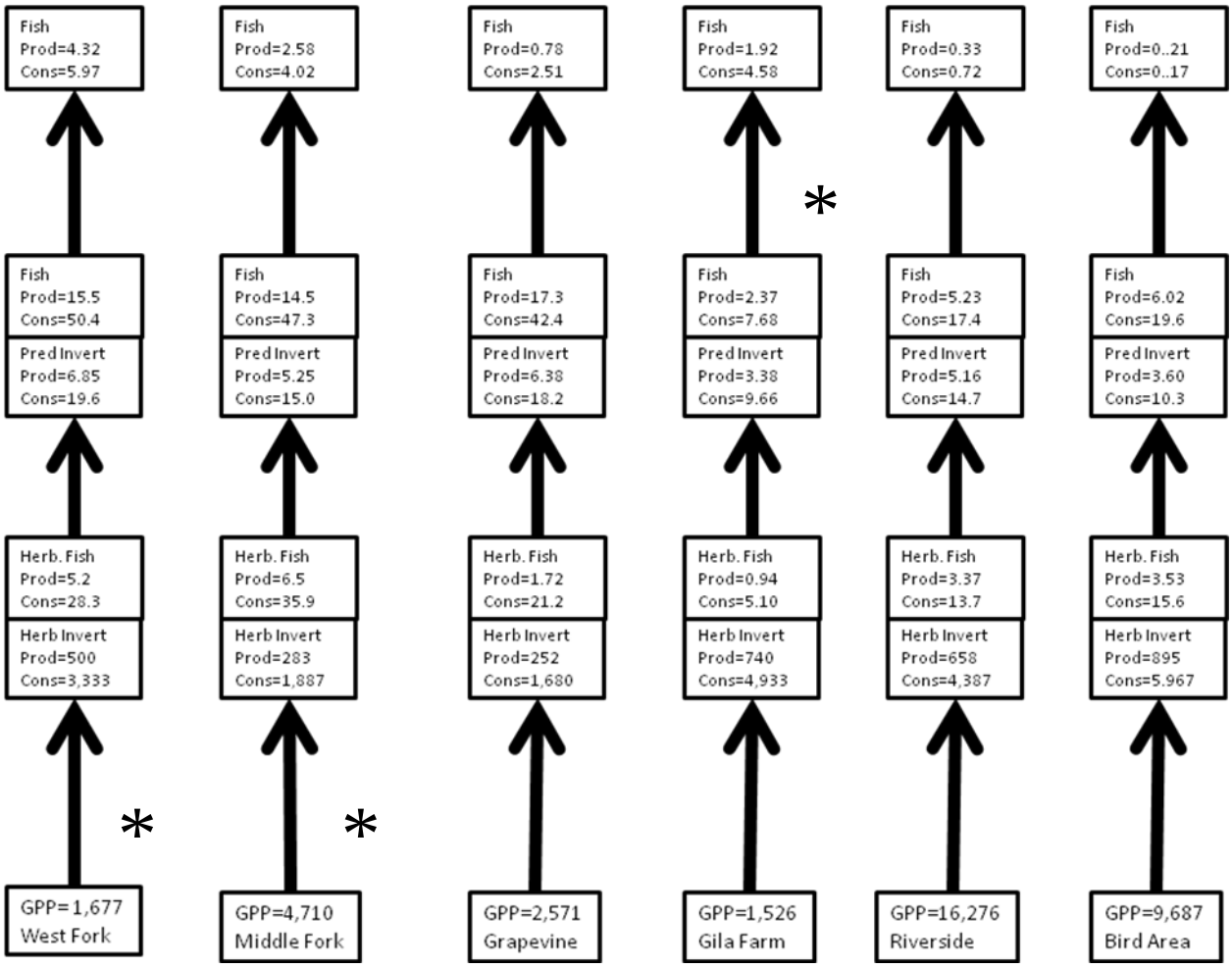

Figure 12 Energy flow across six sites of the upper Gila River. All units are in values of kcal m^{-2} yr^{-1}. Prod stands for production, whereas Cons stands for consumption. Herb. Stands for herbivorous and Pred stands for predaceous. Herbivorous macroinvertebrate consumption was calculated by dividing production by a gross production efficiency of 0.15. Predaceous macroinvertebrate consumption was calculated by dividing production by a gross production efficiency of 0.35. Fish consumption values were calculated based on % gut contents, production, and varying gross production efficiencies based on food type. (GPP gross production efficiency= 0.15, invertebrate and fish gross production efficiency =0.35). Asterisks denote those sites and trophic levels where production of the supporting trophic level is not sufficient to meet the demands of the consumer trophic level.

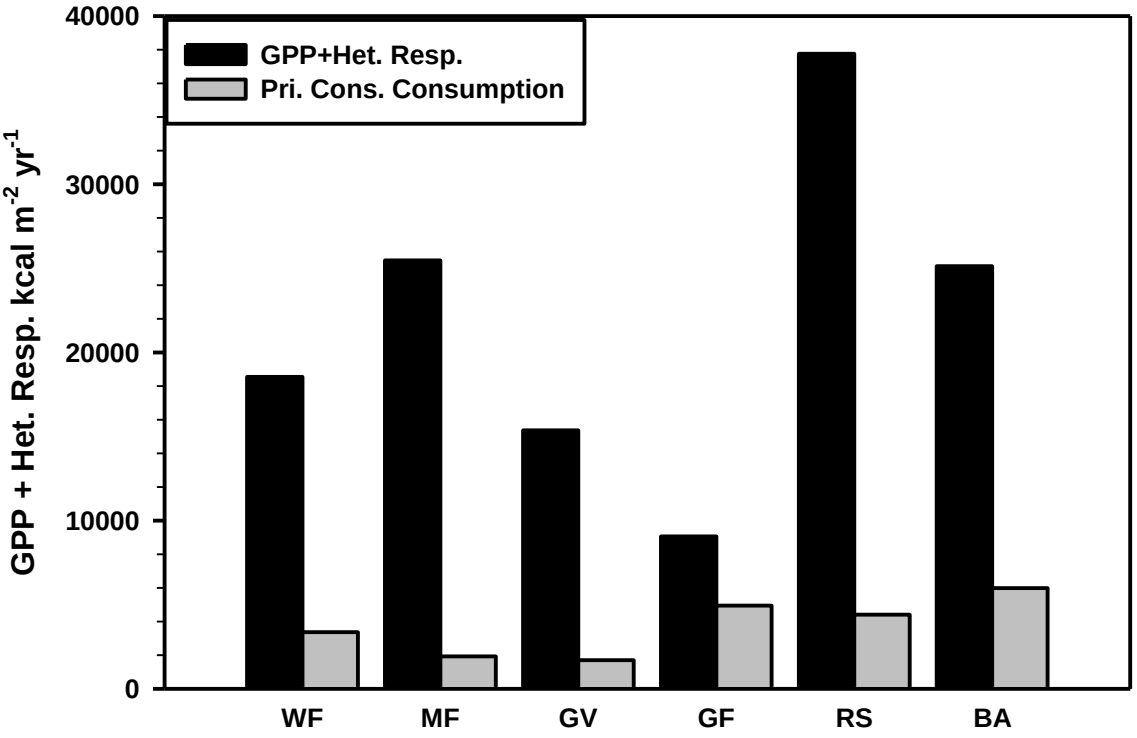

Figure 13 Inclusion of detrital energy availability via addition of heterotrophic respiration to gross primary production. All units are in kcal m^{-2} yr^{-1}. Black bars represent energy availability whereas grey bars represent primary consumer consumption. Autotrophic respiration was calculated by multiplying GPP by 0.5 (because half of GPP goes towards autotrophic respiration (Dodds and Cole 2007)) and this value was then subtracted from total respiration to calculate heterotrophic respiration.

Appendix A - Detailed Sampling Methods

Chlorophyll *a* Extraction Methods

After collection of six composite samples across each site, samples were frozen and kept in the dark until pigment extraction, which generally occurred within 1-2 weeks. Pigment extraction was accomplished using 90% ethanol, which was poured into an autoclave bag holding the three rock composite sample, heated at 78°C for 5 minutes, and then kept in the dark at 4°C overnight. Determination of chlorophyll *a* concentration was done using spectrophotometry at 664nm with a Hitachi U-2900 UV/VIS Spectrophotometer and corrected for chlorophyll *a* degradation products (pheophytin) through acidification with 0.1 N HCl at 665 nm. Turbidity in samples was controlled for through spectrophotometric analysis at 750nm before and after acidification. The surface area of sampled rocks was measured by tracing outlines of the three rocks of each sample on a piece of white paper and comparing the total area of those rocks with a known area ($4cm^2$) using the program SigmaScan Pro Version 5. A mean chlorophyll *a* concentration of the six samples for each site during each sample period was calculated and represented a site-level estimation of standing stock algal biomass in the units of g chl a/m^2. Sampled period means were averaged across the year to obtain an annual mean estimate with associated standard error. The standard error multiplied by 1.96 was used to approximate a 95% confidence interval for each site.

Macroinvertebrate Secondary Production Methods

The size-frequency method (Hynes 1961; Hynes and Coleman 1968; Hamilton 1969) was used to estimate secondary production of abundant macroinvertebrate taxa which had an adequate mass-survivorship curve (i.e., detectable densities in each size group present) (Table 2). Secondary production was estimated separately for each macrohabitat type (pool, riffle, LWD). The size-frequency method multiplies the change in density between successive size groups by the geometric mean of individual masses between size groups, sums those tissue losses across all size groups, and is then multiplied by the number of size groups, since it is assumed that there are as many cohorts per year as there are size groups (Krueger and Martin 1980; Benke 1993; Benke and Huryn 2006). The conceptual basis of this method is that all the tissue produced by a population is eventually removed through mortality, so estimating mortality (tissue losses)

between size groups should approximated production (Boysen-Jensen 1919; Waters 1977). This concept was originally devised for use in the removal-summation method of secondary production, but differs in its summation of tissue losses between size groups (non-cohort technique) instead of between sample periods (cohort technique) (Boysen-Jensen 1919; Waters 1977). In the first step of this method, the mean density and associated variance was calculated for each length group of each macroinvertebrate taxa during each sampling period following the equations of Krueger and Martin (1980). Annual mean density and variance for each 1mm length group was then calculated and weighted by the number of days between sampling periods (Krueger and Martin 1980). Using the annual mean density and associated variance for each 1mm length group combined with the individual mass for each size group, production and approximate 95% confidence intervals were calculated, with calculation of 95% CI equal to 2 multiplied by the standard error of production (Krueger and Martin 1980). Individual mass by length group for each taxon was determined using the power equations of Burgherr and Meyer (1997), Benke et al. (1999), and Sabo et al. (2002) which relate total body length to dry mass (DM). To obtain an estimate of total site production for each taxon, macrohabitat production values were multiplied by their proportional areas in the reach and then summed (Smock et al. 1985). Mean annual biomass of taxa were calculated by multiplying mean annual density of each size group by the length-specific mass of the size group and summing across size groups for each macrohabitat. Variance of mean annual biomass was calculated from the equation of Hayes et al. (2007), assuming that the variance of mean individual weight within a size class was equal to zero. Site levels biomass estimates were calculated in the same manner as site-level production through weighted proportions.

To obtain an accurate estimate of annual secondary productivity, the production value obtained by the size-frequency method must be multiplied by the cohort production interval (CPI), which is equal to 365 divided by larval development time (time from hatching to reaching pupal or adult stages) (Benke 1979). The CPI has a strong impact on estimates of secondary production and requires detailed life-history studies for correct estimation (Benke and Huryn 2006). We reasoned that the collection of this detailed life-history data was beyond the scope of our current study, so we utilized CPIs derived by Gray (1981) for taxa of Sycamore Creek, AZ, a tributary of the Gila River in Arizona. The taxa of Sycamore Creek were found to have some of the most rapid larval development times ever reported, thus creating very large CPIs. It was

reasoned by Gray (1981) that these large CPIs were an evolutionary response to the disturbance regime of Sycamore Creek. When compared with the Upper Gila, Sycamore Creek has a very similar temperature and flood regime, although its drying regime appears to be more frequent. As a result of the geographic proximity of Sycamore Creek with the Gila River creating a high probability of taxonomic overlap coupled with the similar physical conditions, we believe we are justified is the use of CPIs derived for Sycamore Creek taxa. For the calculation of production of abundant taxa which Gray (1981) did not provide larval development times, we estimated CPIs from length-frequency histograms.

The size-frequency method requires that taxa included in each production calculation be from the same trophic group, have the same voltinism, reach the same maximum size, and have linear growth rates (i.e. no change in growth rate with increases in size) (Waters 1977). We likely violated some or all of these assumptions by only having our taxonomic resolution at the family or higher scale. However, the size-frequency method is robust to violations of some of these assumptions (linear growth rates), so our estimates should not be too biased by our taxonomic resolution (Hamilton 1969).

For those rare taxa which lacked an adequate mass-survivorship curve, secondary production was estimated using the P/B ratio for each macrohabitat by multiplying mean annual biomass by the P/B ratio (Benke and Huryn 2006) (Table 2). P/B ratios were assumed to be the theoretical value of 5 for univoltine taxa, 10 for bivoltine taxa, or 2 for hemivoltine taxa (Waters 1977; Benke and Huryn 2006). Mean annual biomass (B) for each taxon was estimated by multiplying mean annual densities for each size group of each taxon by the length group specific mass, and then summing across size groups. Variance of P/B production calculated was calculated by multiplying the variance of biomass by the P/B ratio. The square-root of this variance multiplied by 1.96 approximated the 95% confidence interval for production estimates. Total production estimates of the P/B ratio for each habitat were weighted by multiplication with proportional macrohabitat area, similar to total production of the size-frequency method. Summations of size-frequency production and 95%CI estimates of abundant taxa with estimates from the P/B ratio of rare taxa allowed us to calculate community level macroinvertebrate secondary production and associated 95%CI's. Production values were in units of g DM m^{-2} yr^{-1} and were converted to kcal m^{-2} yr^{-1} (1g DM = 5kcal) (Waters 1977).

Fish, Crayfish, and Tadpole Production Methods

Annual secondary production and mean annual biomass was estimated for each species encountered across sites using a combination of the size-frequency method corrected for the cohort production interval (CPI) for abundant taxa and the P/B ratio for rare taxa in a similar manner as macroinvertebrate methods (Table 3). The equations of Garman and Waters (1983) were used to estimate the weighted annual mean and variance of density and individual weight, as well as size-frequency production with associated 95%CI's. Small-bodied fish species (maximum length <100mm) were broken into 10-cm length groups, whereas larger bodied species (maximum length >200mm) were categorized into 50-cm length groups. Tadpoles and crayfish were broken into 20cm length groups (maximum length ≈ 130mm). P/B ratios were assumed to be 1.0 for smaller-bodied species, 0.5 for larger species, and 2.0 for crayfish and tadpoles. Production and biomass estimates were not weighted by proportional habitat area as was done with macroinvertebrate production, since population and production estimates were conducted at the reach scale. The cohort production interval for these larger, slower-growing taxa with long-lived adult life stages is approximated by the average maximum age in years of individuals within the population (Garman and Waters 1983; Hayes et al. 2007). Estimation of these CPI's thus requires knowledge of age structure, which currently is not available for the Gila community. As a result of this, we estimated CPI's based on the life history of species, with smaller bodied fish species receiving a value of 2, larger bodied species a value of 3, and crayfish and tadpoles a value of 1. Production estimates from the size-frequency method were multiplied by 1 over the CPI to obtain accurate production estimates in units of g WM m^{-2} yr^{-1} (Garman and Waters 1983). All production values were converted to units of kcal m^{-2} yr^{-1} (1g WM = 1 kcal) (Waters 1977).

Appendix B - Density, Biomass, and Production of Macroinvertebrate and Fish Taxa

Table B.1 Density (# of individuals m^{-2}), biomass (kcal m^{-2}), and production (kcal m^{-2} yr^{-1}) of collected macroinvertebrates from the Upper Gila River Basin, NM. Values equal the sum of weighted values from large woody debris, riffle, and pool habitats except for *Orconectes virilis*, which was estimated at the site scale.

Taxon		West Fork	Middle Fork	Grapevine	Gila Farm	Riverside	Bird Area
Acari	Density	384.4	293.4	188.3	147.1	258.6	88.3
	Biomass	0.098	0.074	0.050	0.039	0.065	0.022
	Production	9.821	7.409	5.046	3.932	6.464	2.217
Baetidae	Density	581.1	258.4	184.1	194.2	184.9	215.8
	Biomass	0.8	0.4	0.3	0.3	0.2	0.2
	Production	140.8	82.9	47.6	44.3	36.0	26.2
Ceratopogonidae	Density	62.2	46.3	21.4	6.9	6.4	4.4
	Biomass	0.0	0.0	0.0	0.0	0.0	0.0
	Production	5.7	3.6	2.7	0.8	1.7	1.0
Chironomidae	Density	4701.8	3572.0	2877.8	6402.1	16552	8400.9
	Biomass	0.4	0.3	0.2	1.2	1.6	2.2
	Production	114.1	79.8	75.3	259.5	450.2	449.3
Corixidae	Density	7.3	5.0	42.5	6.9	60.3	52.0
	Biomass	0.0	0.0	0.0	0.0	0.0	0.1
	Production	0.4	0.7	2.1	1.4	3.7	5.4
Corydalidae	Density	3.8	7.1	10.7	36.4	8.1	5.3
	Biomass	0.1	0.0	0.1	0.4	0.1	0.1
	Production	0.3	0.2	0.7	1.9	0.7	0.3
Crambidae	Density	4.1	2.8	4.0	4.0	15.1	55.3
	Biomass	0.0	0.0	0.0	0.0	0.0	0.0
	Production	0.2	0.1	0.1	0.1	0.0	0.1
Dryopidae	Density	0.9	2.7	0.6	0.2	0.0	0.5
	Biomass	0.0	0.0	0.0	0.0	0.0	0.0
	Production	0.0	0.0	0.0	0.0	0.0	0.0
Elmidae	Density	117.2	163.1	51.3	28.2	25.9	38.8
	Biomass	0.1	0.1	0.0	0.0	0.0	0.0
	Production	0.4	0.6	0.2	0.1	0.1	0.1
Empididae	Density	7.3	3.4	7.0	8.1	11.5	7.5
	Biomass	0.0	0.0	0.0	0.0	0.0	0.0
	Production	0.0	0.0	0.0	0.0	0.0	0.0
Ephemerellidae	Density	89.3	122.8	199.8	87.4	4.9	156.0
	Biomass	0.1	0.5	1.6	0.3	0.0	1.2
	Production	1.1	3.9	8.7	1.9	0.1	8.1

Table B.1 Continued

Taxon		West Fork	Middle Fork	Grapevine	Gila Farm	Riverside	Bird Area
Gastropoda	Density	0.9	3.4	17.3	8.2	1.4	18.1
	Biomass	0.0	0.0	0.1	0.0	0.0	0.2
	Production	0.0	0.1	0.7	0.0	0.0	0.9
Gastropoda	Density	50.9	35.9	36.1	8.2	39.5	53.9
	Biomass	0.1	0.0	0.0	0.0	0.0	0.0
	Production	1.0	0.6	0.3	0.1	0.1	0.3
Gomphidae	Density	2.8	2.7	10.8	7.8	16.8	11.1
	Biomass	0.0	0.0	0.2	0.0	0.3	0.1
	Production	0.2	0.0	0.8	0.2	1.6	0.6
Helicopsychidae	Density	5.2	22.7	4.1	11.2	13.9	57.7
	Biomass	0.0	0.1	0.0	0.0	0.0	0.1
	Production	0.1	2.1	0.3	1.0	0.9	3.7
Heptageniidae	Density	14.8	5.4	22.9	5.3	0.8	3.3
	Biomass	0.1	0.0	0.1	0.0	0.0	0.0
	Production	15.3	4.2	21.0	6.3	0.9	2.5
Hydropsychidae	Density	182.3	137.5	67.6	132.1	163.5	601.0
	Biomass	1.2	1.0	0.4	0.6	1.1	3.1
	Production	25.7	25.2	10.4	18.2	25.6	77.3
Hydroptilidae	Density	6.8	3.2	3.7	11.3	26.3	10.9
	Biomass	0.0	0.0	0.0	0.0	0.0	0.0
	Production	0.0	0.1	0.0	0.0	0.2	0.1
Isonychiidae	Density	0.0	6.3	3.3	1.2	3.7	0.7
	Biomass	0.0	0.0	0.0	0.0	0.0	0.0
	Production	0.0	0.2	0.1	0.1	0.2	0.1
Leptoceridae	Density	9.9	12.1	12.4	0.8	1.5	14.7
	Biomass	0.0	0.0	0.1	0.0	0.0	0.2
	Production	0.1	0.5	1.5	0.0	0.0	3.8
Leptohyphidae	Density	162.2	225.9	180.4	86.0	435.2	795.1
	Biomass	0.2	0.2	0.3	0.0	0.8	1.6
	Production	33.4	44.3	47.6	7.7	127.5	295.8
Leptophlebiidae	Density	6.0	23.6	14.1	1.3	10.8	17.7
	Biomass	0.0	0.1	0.0	0.0	0.0	0.0
	Production	0.0	0.4	0.3	0.1	0.1	0.3
Libellulidae	Density	1.7	4.5	2.5	2.1	0.0	3.5
	Biomass	0.0	0.1	0.0	0.0	0.0	0.1
	Production	0.1	0.6	0.0	0.2	0.0	0.4
Naucoridae	Density	3.7	1.0	0.1	0.1	1.3	0.1
	Biomass	0.0	0.0	0.0	0.0	0.0	0.0
	Production	0.1	0.1	0.0	0.0	0.1	0.0
Nemouridae	Density	19.8	20.7	82.8	5.1	0.0	2.0
	Biomass	0.0	0.0	0.0	0.0	0.0	0.0
	Production	0.1	0.0	0.0	0.0	0.0	0.0

Table B.1 Continued

Taxon		West Fork	Middle Fork	Grapevine	Gila Farm	Riverside	Bird Area
Oligochaeta	Density	1905.9	1419.9	1101.8	1589.9	9507.0	13020.8
	Biomass	0.1	0.1	0.1	0.3	0.2	0.5
	Production	1.0	0.8	1.1	2.6	1.8	5.0
Orconectes virilis	Density	0.0	0.0	0.0	0.1	0.0	0.2
	Biomass	0.0	0.0	0.01	0.79	0.18	3.34
	Production	0.0	0.0	0.02	2.27	0.48	6.35
Perlodidae	Density	15.2	10.7	12.8	6.0	4.7	4.2
	Biomass	0.1	0.1	0.4	0.0	0.0	0.0
	Production	0.3	0.5	2.0	0.2	0.1	0.1
Polycentropodidae	Density	1.5	0.1	0.2	0.0	0.0	0.9
	Biomass	0.0	0.0	0.0	0.0	0.0	0.0
	Production	0.2	0.0	0.0	0.0	0.0	0.5
Psephenidae	Density	0.8	8.2	2.9	15.4	8.1	10.6
	Biomass	0.0	0.0	0.0	0.2	0.1	0.2
	Production	0.0	0.4	0.2	1.2	0.8	1.2
Simuliidae	Density	443.5	191.2	227.0	2871.2	178.2	89.5
	Biomass	0.8	0.1	0.4	4.5	0.0	0.0
	Production	56.2	4.8	21.0	387.6	1.5	2.5
Tabanidae	Density	3.2	9.1	9.0	0.2	28.6	34.4
	Biomass	0.0	0.1	0.1	0.0	0.3	0.3
	Production	0.1	0.3	0.3	0.0	0.9	1.1
Tanyderidae	Density	117.2	163.1	51.3	28.2	25.9	38.8
	Biomass	0.0	0.0	0.0	0.0	0.0	0.0
	Production	2.3	2.8	1.3	0.7	0.5	1.1
Tipulidae	Density	1085.9	190.1	83.6	23.6	21.5	15.3
	Biomass	1.1	0.2	0.1	0.0	0.0	0.0
	Production	97.2	17.0	6.8	0.8	1.2	2.3
Total	Density	9999	6974	5534	11737	27616	23829
	Biomass	5.45	3.69	4.87	8.18	5.12	10.38
	Production	506	284	258	741	663	892

Table B.2 Density (# of individuals m^{-2}), biomass (kcal m^{-2}), and production (kcal m^{-2} yr^{-1}) values of collected fish and American bullfrog tadpoles (*Rana catesbeiana*) from the Upper Gila River Basin, NM.

Taxon		West Fork	Middle Fork	Grapevine	Gila Farm	Riverside	Bird Area
Agosia chrysogaster	Density	0.0013	0.1378	0.0198	0.3272	0.0951	0.6382
	Biomass	0.0011	0.3957	0.0599	0.8528	0.2417	1.6183
	Production	0.0011	0.3569	0.0481	1.6227	0.4569	3.0891
Ameiurus natalis	Density	0.0000	0.0457	0.0035	0.0000	0.0000	0.0001
	Biomass	0.0000	0.5652	0.0657	0.0000	0.0021	0.0024
	Production	0.0000	1.0668	0.1183	0.0000	0.0011	0.0012
Catostomus clarki	Density	0.1251	0.3066	0.0539	0.0506	0.2127	0.1260
	Biomass	2.4995	2.4230	0.4227	0.7698	1.4823	1.3485
	Production	5.1806	6.4909	1.7164	0.9364	3.3684	3.5044
Catostomus insignis	Density	0.1644	0.3328	0.3284	0.0272	0.0860	0.1365
	Biomass	9.1704	10.446	4.7741	0.5038	1.6200	1.6400
	Production	14.246	14.444	17.216	0.7416	3.8778	2.3312
Cyprinus carpio	Density	0.0000	0.0000	0.0000	0.0000	0.0000	0.0001
	Biomass	0.0000	0.0000	0.0000	0.0000	0.0000	0.1397
	Production	0.0000	0.0000	0.0000	0.0000	0.0000	0.0698
Cyprinella lutrensis	Density	0.0000	0.0013	0.0000	0.0004	0.0000	0.0052
	Biomass	0.0000	0.0032	0.0001	0.0018	0.0000	0.0152
	Production	0.0000	0.0032	0.0001	0.0018	0.0000	0.0080
Gambusia affinis	Density	0.0000	0.0000	0.0000	0.0002	0.0001	0.0006
	Biomass	0.0000	0.0000	0.0000	0.0003	0.0001	0.0008
	Production	0.0000	0.0000	0.0000	0.0003	0.0001	0.0008
Gila nigra	Density	0.0008	0.0905	0.0002	0.0000	0.0000	0.0000
	Biomass	0.0182	0.3279	0.0005	0.0000	0.0000	0.0000
	Production	0.0079	1.3210	0.0005	0.0000	0.0000	0.0000
Ictalurus punctatus	Density	0.0000	0.0000	0.0000	0.0037	0.0018	0.0004
	Biomass	0.0000	0.0000	0.0000	0.0170	0.0222	0.4079
	Production	0.0000	0.0000	0.0000	0.0085	0.0249	0.2040
Lepomis cyanellus	Density	0.0000	0.0001	0.0030	0.0054	0.0020	0.0002
	Biomass	0.0000	0.0028	0.0017	0.0559	0.0227	0.0025
	Production	0.0000	0.0028	0.0017	0.0311	0.0098	0.0013
Meda fulgida	Density	0.0120	0.0068	0.0000	0.0008	0.1618	0.1376
	Biomass	0.0216	0.0110	0.0000	0.0019	0.3104	0.2201
	Production	0.0231	0.0110	0.0000	0.0019	0.6750	0.4598
Micropterus dolomieu	Density	0.0000	0.0057	0.0037	0.0002	0.0088	0.0000
	Biomass	0.0000	0.3445	0.2108	0.0018	0.3086	0.0000
	Production	0.0000	0.1024	0.1430	0.0009	0.2481	0.0000
Oncorhynchus gilae	Density	0.0005	0.0000	0.0000	0.0000	0.0000	0.0000
	Biomass	0.2520	0.0000	0.0000	0.0000	0.0000	0.0000
	Production	0.1260	0.0000	0.0000	0.0000	0.0000	0.0000

Table B.2 Continued

Taxon		West Fork	Middle Fork	Grapevine	Gila Farm	Riverside	Bird Area
Oncorhynchus mykiss	Density	0.0149	0.0025	0.0001	0.0000	0.0000	0.0000
	Biomass	0.9367	0.0902	0.0108	0.0000	0.0000	0.0000
	Production	1.1937	0.0451	0.0054	0.0000	0.0000	0.0000
Pimephales promelas	Density	0.0000	0.0000	0.0000	0.0018	0.0000	0.0051
	Biomass	0.0000	0.0000	0.0000	0.0039	0.0000	0.0125
	Production	0.0000	0.0000	0.0000	0.0039	0.0000	0.0280
Pylodictis olivaris	Density	0.0000	0.0000	0.0004	0.0019	0.0014	0.0000
	Biomass	0.0000	0.0000	1.0085	3.7687	0.1442	0.0000
	Production	0.0000	0.0000	0.5043	1.8844	0.0416	0.0000
Rana catesbeiana	Density	0.0000	0.1891	0.0037	0.0014	0.0008	0.0004
	Biomass	0.0000	4.2234	0.0810	0.0333	0.0022	0.0118
	Production	0.0000	3.7450	0.0810	0.0333	0.0148	0.0118
Rhinichthys osculus	Density	0.2249	0.0213	0.0027	0.0000	0.0000	0.0000
	Biomass	0.4968	0.0471	0.0053	0.0000	0.0000	0.0000
	Production	1.0952	0.0494	0.0080	0.0000	0.0000	0.0000
Salmo trutta	Density	0.0745	0.0012	0.0008	0.0000	0.0000	0.0000
	Biomass	2.8066	0.0833	0.0104	0.0000	0.0000	0.0000
	Production	3.1203	0.0417	0.0052	0.0000	0.0000	0.0000
Tiaroga cobitis	Density	0.0000	0.0000	0.0069	0.0004	0.0795	0.0293
	Biomass	0.0000	0.0000	0.0158	0.0012	0.1490	0.0620
	Production	0.0000	0.0000	0.0126	0.0012	0.2177	0.0576
Total	Density	0.6184	1.1415	0.4271	0.4212	0.6500	1.0798
	Biomass	16.2029	18.9635	6.6674	6.0123	4.3056	5.4817
	Production	24.9935	27.6800	19.8603	5.2680	8.9362	9.7669