Longer food chains and crowded niche space: effects of multiple invaders on desert stream food web structure

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Abstract – Tributaries of the Colorado River Basin, historically home to a complex of endemic omnivores collectively referred to as the ‘three species’; flannelmouth sucker (Catostomus latipinnis), bluehead sucker (C. discobolus) and roundtail chub (Gila robusta), have experienced the establishment of numerous non-native fish species. In this study, we examine the impacts of the trophic ecology of non-native fishes on the ‘three species’ in the San Rafael River, Utah, USA. We employ a suite of abundance comparisons, stable isotope techniques and size-at-age back-calculation analyses to compare food web structure and growth rates of the ‘three species’ in study areas with and without established populations of non-native species. We found that the ‘three species’ are more abundant in areas with few non-native fishes present, regardless of habitat complexity. Stable isotope analyses indicate non-native fishes lengthen the food chain by 0.5 trophic positions. Further, the trophic niche spaces of the native fishes shift and are narrower in the presence of non-native fishes, as several non-native species’ trophic niche spaces overlap almost entirely with each of the ‘three species’ (bluehead sucker and flannelmouth sucker 100%, roundtail chub 98.5%) indicating strong potential for competition. However, the ‘three species’ demonstrated no evidence of reduced growth in the presence of these non-native fishes. Collectively, these results suggest that while non-native fishes alter the food web structure presenting novel sources of predation and competition, mechanisms other than competition are controlling the size-structure of ‘three species’ populations in the San Rafael River.

Key words: non-native species; competition; novel predators; growth; stable isotope analysis

Introduction

The impact of human development increasingly threatens the native biodiversity of freshwater ecosystems (Ricciardi & Rasmussen 1999; Dudgeon et al. 2006). Anthropogenic alterations to rivers result in physical (e.g., flow alteration, sedimentation, channelisation), chemical (e.g., pollution, nutrient loading) and biological (e.g., invasive species, disease) degradation of natural habitats. These alterations can favour novel life-history strategies (Olden et al. 2006), decrease resource availability (Tyus & Karp 1990; Brouder 2001), alter the flow of energy through ecosystems (Sousa et al. 2008) and increase predation and competition pressure on native species (Tyus & Saunders 2000). As such, anthropogenic alterations can result in new evolutionary and contemporary pressures on native biota that evolved under a specific suite of environmental conditions, often dramatically restructuring communities.

Biotic communities are structured not only by the environmental tolerances of the species present, but also by interactions among the species of the community. Interspecific competition for resources can limit growth and survival of inferior competitors (e.g., Schoener 1983) and thus limit the distribution and abundance of species. However, negative population-level effects resulting from competition have proven...
difficult to detect in many, though not all, studies (reviewed in Connell 1983). In addition, predator species can have a particularly strong role in shaping community structure through both direct (e.g., Kitchell et al. 1997) and indirect pathways (e.g., Werner et al. 1983; Romare & Hansson 2003). Alterations to trophic structure, such as the establishment of non-native species, can have significant impacts on community structure (e.g., Reissig et al. 2006). However, the impact of invasive predators and competitors is not consistent for all recipient systems and is influenced by ecosystem complexity (Case 1990; Carey & Wahl 2010, 2011) and evolutionary history (Kitchell et al. 1997; Shea & Chesson 2002).

Rivers and streams of the Colorado River Basin, home to a historically depauperate and highly endemic fish fauna, have been particularly affected by anthropogenic disturbances (Minckley & Deacon 1968), due in part to the region’s arid climate and rapidly expanding human population. While degradation of the physical environment is often argued to be the primary cause of population and range reductions of native fishes (Ross 1986), interactions with non-native fishes may be equally or even more influential than habitat loss in the extinction of species (Tyus & Saunders 2000; Woodford 2009a). Invasion by non-native fishes has the potential to alter the energetic pathways of the historic food web, resulting in significant and negative ecosystem impacts, such as modified habitat coupling, nutrient cycling rates and ecosystem resilience (Eby et al. 2006; Britton et al. 2010; Pilger et al. 2010). Non-native species often maintain a competitive advantage over native fishes (Shea & Chesson 2002; Cox & Lima 2006) and can have particularly strong impacts on simple food webs (Carey & Wahl 2010), such as those of the historical Colorado River Basin (Tyus & Nikirk 1990; Tyus & Saunders 2000; Unmack & Fagan 2004).

In addition, the interaction between a degraded physical habitat and non-native species presence can result in complex synergistic effects on native species and their habitat (Brook et al. 2008). Physical habitat degradation, for example, can aid in the establishment and dispersal of invasive species (Marvier et al. 2004). While change in flow regimes may decouple the life histories of native fishes from their current environmental template, many invasive fishes are pre-adapted to the new conditions (Olden et al. 2006; Johnson et al. 2008). In addition, the impact of non-native fishes has been suggested to be strongest at times of low flow (Pilger et al. 2010), a nearly perpetual state in degraded desert rivers. This combination of physical degradation and biotic invasions in the Colorado River Basin has contributed to the extirpation and the federal listing of many endemic fishes under the Endangered Species Act (Minckley & Deacon 1968; USDI, Fish & Wildlife Service 1994) and the protection of many others under conservation agreements between states of the Colorado River Basin (UDWR, Utah Division of Wildlife Resources 2006).

The bluehead sucker (*Catostomus discobolus*), flannelmouth sucker (*C. latipinnis*) and roundtail chub (*Gila robusta*) represent a highly imperilled ecological complex of fishes, hereafter, collectively the ‘three species’, native to the upper Colorado River Basin, U.S.A. These endemic fishes are listed as state species of concern and subject to a range-wide conservation agreement aimed at ensuring their persistence throughout their range (UDWR 2006). Many of the non-native fishes present in the basin have the potential to negatively impact populations of these native fishes through competition or predation (e.g., Bestgen & Propst 1989; Tyus & Saunders 2000; Johnson et al. 2008). In fact, predation on early life stages of native fish by non-native fish has been implicated in total recruitment failure for native fishes in the Colorado River Basin and other systems (Meffe 1985; Woodford 2009b).

Populations of imperilled species may be able to persist in an area if recruitment cannot balance with mortality, provided there is a source habitat capable of supplying colonisers to the sink habitat (Pulliam 1988). Previous study has suggested that populations of the ‘three species’ in the downstream, degraded portions of the San Rafael River, a tributary of the Green River, occupy a sink habitat, and are maintained through colonisation from sources in both the upper portions of the San Rafael River and the main-stem Green River (e.g., Bottcher 2009). Identification of the mechanisms (i.e., competition and/or predation) by which non-native fishes interact with the ‘three species’ may illuminate the causes of source-sink structure. In this article, we address the following questions: (i) do non-native fishes occupy piscivorous trophic positions and/or change the trophic position occupied by native fishes and (ii) does the presence of non-native fishes alter the growth of native fishes? In addressing these questions, we explore a combination of food web and growth analyses among patches of a river with alternate invasion histories to advance our understanding of how trophic interactions impact community composition and population structure.

**Study area**

The San Rafael River (hereafter ‘SRR’), Utah, U.S.A., is an ideal study stream as it has experienced degradation representative of many tributaries of the Colorado River Basin (i.e., altered hydrograph, water...
loss, channelisation, homogenisation of habitat, invasive species establishment; Walker & Hudson 2004; Bottcher 2009). The SRR drains 4500 km² of southeastern Utah and is formed by the confluence of Ferron, Cottonwood, and Huntington creeks (Fig. 1). The SRR is a spring snowmelt and autumn monsoon driven system, and flows approximately 175 km from its headwaters in the Manti–La Sal National Forest to its confluence with the Green River near the town of Green River, Utah. The SRR is one of the most over-allocated rivers in Utah (Walker & Hudson 2004) and the lower 64 km are frequently dewatered during the summer irrigation season (Bottcher 2009).

Native fish species currently occupying the SRR for at least a portion of their life history include the flannelmouth sucker, bluehead sucker, roundtail chub, speckled dace (*Rhinichthys osculus*), as well as occasional, transient bonytail (*Gila elegans*), razorback sucker (*Xyrauchen texanus*) and Colorado pikeminnow (*Ptychocheilus lucius*). Non-native species present include red shiner (*Cyprinella lutrensis*), sand shiner (*Notropis stramineus*), fathead minnow (*Pimephales promelas*), channel catfish (*Ictalurus punctatus*), black bullhead (*Ameiurus melas*), common carp (*Cyprinus carpio*), white sucker (*Catostomus commersoni*), green sunfish (*Lepomis cyanellus*) and virile crayfish (*Orconectes virilis*).

In this study, we delineate the upper and lower SRR by the San Rafael Reef, dividing the river into the section flowing through the San Rafael Swell, characterised by deep canyons (upper SRR), and the section flowing through the San Rafael Desert, characterised by primarily open desert terrain (lower SRR). Natural and anthropogenic barriers in the San Rafael Reef and at the Hatt Ranch diversion dam limit upstream movement of fishes. Twelve 300 m long sampling sites were established in total (Fig. 1). The sites in the upper SRR (*N* = 4) were chosen opportunistically due to extremely rugged terrain, while sites in the lower SRR (*N* = 8) were chosen by a systematic sample design with random seed start (Bottcher 2009).

### Methods

#### Collection of biotic community data

Sampling events occurred during the spring (i.e., prior to spring snowmelt run-off; April and May), summer (i.e., immediately after recession of spring runoff; June and July) and autumn (i.e., October) of 2010. Fish from all habitat types were sampled via canoe electrofishing, and all native and non-native fishes were identified to species, anesthetised with tricaine methanosulphate (MS-222), weighed, measured for total length and clipped (lower caudal fin) for stable isotope analysis. Tissue samples were preserved and stored in 95% ethanol until processing later in the lab, and native fishes were fin-clipped for age determination (see below). Storing tissue samples in ethanol has been shown to enrich δ¹³C signatures in some studies (Kaehler & Pakhomov 2001; Kelly et al. 2006), to have no significant effect in other studies (Sarakinos et al. 2002; Serrano et al. 2008) and to cause small shifts relative to ecological variation (Kelly et al. 2006). We were confident using these tissues given that all indices were relative and as long as carbon signatures were interpreted with caution.

Following sample collection, native fishes were held in a recovery tank until they showed no effects of the anaesthetic before being returned to the river.

Benthic invertebrates were sampled at each food web site with a Surber sampler. For each sampling event, eight 0.09 m² samples were taken from riffles in each site. Samples within a site and date were combined in 95% ethanol, returned to the lab where they were sorted, identified to family (or lower) and functional feeding group, and counted.

Relative abundance of native fishes in presence of non-native species

The sampling sites were placed into three categories of degradation (Fig. 1). The high quality category

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*Fig. 1.* Map of the San Rafael River watershed. Inset shows location of watershed (cross-hatched) in Utah, USA.
(all located in the upper SRR) had widely available complex habitat (i.e., riffles, pools and backwaters) and very low to zero densities of non-native fishes present. The medium quality category (all located in the lower SRR, with one site upstream of the Hatt Ranch diversion dam, yet downstream of the San Rafael Reef) had widely available complex habitat, but high densities of non-native fishes present. The poor quality category (all in the lower SRR) all had very limited complex habitat available and high densities of non-native fishes. Habitat complexity was calculated as the per cent of the reach consisting of riffle, pool or backwater habitat as determined by in-stream habitat surveys (Walsworth 2011). While the surrounding terrain is somewhat different between the upper and lower SRR (Fortney et al. 2011), the in-stream habitat in high and medium quality reaches was similar. A repeated measures analysis of variance, repeated on sampling site, was run to compare the catch-per-unit-effort (CPUE) of native fishes and of non-native fishes between sites in the different quality categories.

Stable isotope analysis of food web structure

Once returned to the lab, caudal fin clips and benthic invertebrates of the collector-filterer functional feeding groups (most abundant) were prepared for stable isotope analysis. Tissue samples were dried for 48 h at 70 °C, crushed into a homogeneous powder with mortar and pestle and placed in tin capsules for shipment. To examine the effect of non-native species on the trophic structure of the SRR, samples from the upper SRR (high quality sites) and from the lower SRR (medium and poor quality sites) were analysed for stable isotope signatures separately. We chose SRR (medium and poor quality sites) were analysed for stable isotope signatures to characterise the food web structure throughout the upper and lower SRR.

Due to limited sample sizes for the ‘three species’, especially in the lower SRR, stable isotope data were pooled across seasons (spring, summer, and autumn). Species’ trophic niche space was analysed using methods presented in Layman et al. (2007). For each species, the following measures were calculated: trophic position (TP), nitrogen range (NR), carbon range...
(CR), trophic niche width, trophic niche overlap and food chain length. Trophic position was calculated using the following equation:

\[ \text{TP}_i = \frac{\delta^{15}\text{N}_{\text{cor}} - \delta^{15}\text{N}_{\text{cor},i}}{3.4} + 2, \]

where TP\(_i\) is the trophic position of species \( i \), \( \text{N}_{\text{cor}} \) is the corrected nitrogen signature of species \( i \), and \( \text{N}_{\text{cor},i} \) is the corrected nitrogen signature of collector filterer invertebrates (Vander Zanden & Rasmussen 1999). Collector-filterer invertebrates were assumed to have a trophic position of 2 and we assumed trophic fractionation of \( \delta^{15}\text{N} \) to be 3.4\% as trophic level increases (Minagawa & Wada 1984). Trophic position and \( \delta^{13}\text{C}_{\text{cor}} \) signatures for each of the ‘three species’ were compared between the upper and lower SRR with Student’s \( t \)-tests. Nitrogen range and carbon range were calculated from the following equations:

\[ \text{NR} = \delta^{15}\text{N}_{\text{cor,max}} - \delta^{15}\text{N}_{\text{cor,min}}, \]

\[ \text{CR} = \delta^{13}\text{C}_{\text{cor,max}} - \delta^{13}\text{C}_{\text{cor,min}}, \]

for each species (Layman et al. 2007). Niche width was calculated as the convex hull area of isotopic signatures of each species plotted in C-N bivariate space (Layman et al. 2007). Niche overlap was calculated as the per cent of a species’ niche width area that is overlapped by the niche width area of another species in the food web. Food chain length was calculated as the highest TP detected in the upper or lower SRR.

Calculation of native fish growth rates

The basal portion of the second dorsal fin ray was collected from each individual of the ‘three species’ captured during sampling, and stored in vials until returned to the lab. The fin rays were placed in molds and heated at 70 °C for 12 h to allow the mold to harden. The molds were then mounted on metal chucks and cut using a Buehler Isomet low-speed saw (Buehler Ltd., Lake Bluff, IL, USA). The fresh edge was sanded, polished and a second cut was made to produce a thin (~1.5 mm) section. The section was placed on a microscope slide and polished if necessary. Fin ray sections were placed under a camera-mounted microscope and back-lit to reveal annuli. Digital images of each section were captured and analysed for length-at-age using the Frasier-Lee back-calculation:

\[ L_t = c + (L_T - c) \left( \frac{S_i}{S_T} \right) \]

where \( L_t \) is the length of the fish at time \( t \), \( L_T \) is the total length of the fish, \( c \) is the length of the fish at age 1, \( S_i \) is the length of the fin ray at time \( t \) and \( S_T \) is the total length of the fin ray (Francis 1990). The length of each species at age 1 \( (c) \) was estimated from length-frequency plots. Length-at-age data for each species were then fit to a repeated measures non-linear Von Bertalanffy growth curve (VBGC; Jones 2000):

\[ L_t = L_\infty \left( 1 - e^{-k(t - t_0)} \right) \]

where \( L_\infty \) represents the maximum possible length achieved by the fish, \( L_t \) is the fish’s length at time \( t \), \( t_0 \) is the theoretical age of the fish when its length equals zero and \( k \) is the Brody growth rate coefficient (Ricker 1975), a measure of the rate of approach to \( L_\infty \). Growth rates of fish in the upper and lower SRR were examined by comparing the standardised residuals from the VBGC of individual fish captured in each section. A Student’s \( t \)-test was used to compare the residuals between groups. All statistical analyses were run in the R Statistical Environment (R Development Core Team 2011) with an \textit{a priori} \( \alpha \) of 0.05.

Effects of multiple invaders on imperiled desert fishes

Relative abundance

The lower SRR fish community species composition was dominated by non-native fishes, while the fish collections in the upper SRR were almost entirely composed of native fishes (Table 1). In addition, juvenile individuals of the ‘three species’ were uncommon in the electrofishing samples (Table 1). The ‘three species’ were captured in significantly greater numbers in the high-quality sites (CPUE = 26.22 ± 3.69 fish per hour [mean ± 1.96 SE]) than in either the medium (CPUE = 3.93 ± 1.14 fish per hour) or low-quality sites (CPUE = 4.30 ± 1.04 fish per hour; repeated measures \textit{ANOVA}, \( P = 0.001; \) Fig. 2a), while non-native fishes were captured in significantly greater numbers in both the medium (CPUE = 61.01 ± 11.60 fish per hour) and low-(CPUE = 53.09 ± 6.13 fish per hour) quality sites than in the high-quality sites (CPUE = 0.79 ± 0.46 fish per hour; repeated measures \textit{ANOVA} \( P < 0.001; \) Fig. 2b). No significant seasonal or interaction effects were detected for CPUE of either native or non-native fishes (all repeated measures \textit{ANOVA} \( P > 0.05 \). The only non-native fishes captured upstream of the San Rafael Reef were 2 green sunfish and 1 Utah chub (\textit{Gila atraria}). Non-native white sucker were captured in the lower SRR for the first time in 2010.

The relative abundances of benthic invertebrates were not significantly different between the upper and lower SRR (\textit{ANOVA}, \( P = 0.432 \). When compar-
ing only densities of collector filterer insects only, there was still no significant difference between the upper and lower SRR (ANOVA, \( P = 0.319 \)).

### Stable isotope analysis

The upper SRR can be broadly characterised by a short food chain (food chain length = 3.51; Table 2, Fig. 3a) and food web populated by few species. The bluehead sucker (‘BHS’, TP = 2.75 ± 0.18 [mean ± 1.96-SE]), flannelmouth sucker (‘FMS’, TP = 2.95 ± 0.22) and roundtail chub (‘RTC’, TP = 2.80 ± 0.24) occupied similar trophic positions (ANOVA \( P = 0.38 \)) that signify the assimilation of benthic invertebrates. The ‘three species’ displayed significantly different \( \delta^{13}C_{\text{cor}} \) signatures (BHS \( \delta^{13}C_{\text{cor}} = -0.65 ± 0.18 \); FMS \( \delta^{13}C_{\text{cor}} = 0.77 ± 0.24 \); RTC \( \delta^{13}C_{\text{cor}} = 1.91 ± 0.40 \); ANOVA \( P < 0.001 \)). The bluehead sucker was more depleted in carbon than either the flannelmouth sucker (t-test \( P < 0.001 \)) or the roundtail chub (t-test \( P < 0.001 \)), and the flannelmouth sucker was more depleted in carbon signature than the roundtail chub (t-test \( P < 0.001 \)). Speckled dace occupied the highest mean trophic position in the upper SRR (TP = 3.18 ± 0.08) and demonstrated an intermediate \( \delta^{13}C \) signature among the upper SRR fish community (\( \delta^{13}C_{\text{cor}} = 0.64 ± 0.59 \)).

While the food web of the upper SRR was structurally simple, the food web of the lower SRR was populated by more species distributed across a broader range of trophic positions (food chain length = 4.01; Table 2, Fig. 3b). As in the upper SRR, the bluehead sucker (TP = 2.82 ± 0.06) and flannelmouth sucker (TP = 2.84 ± 0.06) occupied

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### Table 1. Number and mean, minimum (‘Min’) and maximum (‘Max’) total lengths of individuals sampled in the San Rafael River by species and location. Cells with no data available marked with ‘-’.

<table>
<thead>
<tr>
<th>Species</th>
<th>Upper San Rafael River</th>
<th>Lower San Rafael River</th>
</tr>
</thead>
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<tr>
<td></td>
<td>( N )</td>
<td>Mean Length</td>
</tr>
<tr>
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<td></td>
<td></td>
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<tr>
<td>Age-0 sucker</td>
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<td>26.7</td>
</tr>
<tr>
<td>Bluehead sucker (BHS)</td>
<td>155</td>
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<tr>
<td>Flannelmouth sucker (FMS)</td>
<td>110</td>
<td>284.7</td>
</tr>
<tr>
<td>Roundtail chub (RTC)</td>
<td>40</td>
<td>145.2</td>
</tr>
<tr>
<td>Speckled dace (SDD)</td>
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<td>63.9</td>
</tr>
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<td><strong>Non-native Species</strong></td>
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<tr>
<td>Black bullhead (BBH)</td>
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<td>–</td>
</tr>
<tr>
<td>Channel catfish (CLC)</td>
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<td>–</td>
</tr>
<tr>
<td>Common carp (CNC)</td>
<td>0</td>
<td>–</td>
</tr>
<tr>
<td>Fathead minnow (FHM)</td>
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<td>Green sunfish (GNS)</td>
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<td>Red shiner (RDS)</td>
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<td>White sucker (WES)</td>
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</tbody>
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**Fig. 2.** Catch-per-unit-effort (fish/hr) of native (a) and non-native (b) fish in the San Rafael River by site quality. The high-quality sites have significantly greater CPUE of native fishes (ANOVA \( P = 0.001 \)) and significantly lower CPUE of non-native fishes (ANOVA \( P < 0.001 \)) than either the medium or poor quality sites.
Effects of multiple invaders on imperiled desert fishes

Table 2. Stable isotope signatures by species and location in the San Rafael River. Sample size (N), mean corrected stable isotope signature values and standard errors are reported. Cells with no data available marked with ‘—’.

<table>
<thead>
<tr>
<th>Species</th>
<th>Upper San Rafael River</th>
<th>Lower San Rafael River</th>
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<tr>
<td></td>
<td>N</td>
<td>$\delta^{13}C_{cor}$ (SE)</td>
</tr>
<tr>
<td><strong>Native Species</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Collector-Filterer Insects (ColFil)</td>
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<td>0.09 (0.09)</td>
</tr>
<tr>
<td>Bluehead sucker (BHS)</td>
<td>10</td>
<td>-0.53 (0.06)</td>
</tr>
<tr>
<td>Flannelmouth sucker (FMS)</td>
<td>10</td>
<td>0.77 (0.12)</td>
</tr>
<tr>
<td>Roundtail chub (RTC)</td>
<td>9</td>
<td>1.91 (0.20)</td>
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<tr>
<td>Speckled dace (SDD)</td>
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<td>0.64 (0.30)</td>
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<td><strong>Non-native Species</strong></td>
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<td></td>
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<tr>
<td>Black bullhead (BBH)</td>
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<td>—</td>
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<td>Channel catfish (CLC)</td>
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<td>Green sunfish (GNS)</td>
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<td>Sand shiner (SDS)</td>
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<tr>
<td>White sucker (WES)</td>
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</table>

Fig. 3. Stable isotope signatures (mean values ± 1.96 SE) and food web structure of the upper (a) and lower (b) San Rafael River. The ‘three species’ icons are enlarged. Mean values ± 1.96 SE shown. See Table 2 for abbreviations.

similar trophic positions (t-test P = 0.70), and the two species demonstrated significantly different carbon signatures (BHS $\delta^{13}C_{cor} = 1.26 ± 0.18$; FMS $\delta^{13}C_{cor} = 2.02 ± 0.37$; t-test P = 0.002). The roundtail chub had a significantly elevated trophic position (TP = 3.34 ± 0.27) in the lower SRR compared to the two native suckers (ANOVA P < 0.001), and was significantly elevated from its trophic position in the upper SRR (t-test P = 0.009). The bluehead sucker and flannelmouth sucker carbon signatures were significantly enriched in the lower SRR compared to the upper SRR (both t-tests P < 0.001). All remaining stable isotope measures for the ‘three species’ were similar between the upper and lower SRR (t-tests, all P > 0.05). Green sunfish held the highest trophic position in the lower SRR (TP = 3.54 ± 0.24), and five other non-native species occupied higher trophic positions than at least two of the ‘three species’.

The stable isotope signatures of fishes in the upper SRR spanned a broad array of carbon sources and trophic positions (CR = 3.71, NR = 4.08, niche width = 12.79). Bluehead sucker occupied a narrow trophic niche (CR = 0.53, NR = 3.37, niche width = 6.96; Fig. 4a), aligning closely with collector-filterer insects with respect to carbon signature. The bluehead sucker niche space did not overlap with other native species trophic niches. Flannelmouth sucker had a slightly wider, less distinct, trophic niche space than the bluehead sucker (FMS CR = 1.27, NR = 3.24, niche width = 7.14, overlap = 22.4%). The roundtail chub occupied the widest trophic niche space out of the ‘three species’ in the upper SRR, and had less niche overlap than the flannelmouth sucker (CR = 1.89, NR = 3.32, niche width = 8.41, overlap = 6.9%).

The stable isotope signatures of fishes in the lower SRR was similar to that used in the upper SRR, although a slightly wider range of trophic positions were inhabited and there was greater variation in resource use at all given trophic positions (CR = 5.15, NR = 4.96, niche width = 18.12; Fig. 4b).
lower SRR was much narrower and less distinct than in the upper SRR (CR = 0.77, NR = 1.21, niche width = 3.25, overlap = 100%). Flannelmouth sucker trophic niche space was also considerably more narrow and less distinct than in the upper SRR (CR = 1.89, NR = 1.22, niche width = 5.03, overlap = 100%). Roundtail chub trophic niche space was slightly wider in the lower SRR (CR = 2.95, NR = 3.69, niche width = 9.89), but was overlapped with other species’ trophic niche spaces to a much greater degree (overlap = 98.5%) than in the upper SRR. Red shiners, sand shiners, channel catfish, common carp and white suckers each occupied a trophic niche that overlapped substantially with those of the ‘three species’.

Growth

The oldest bluehead suckers (age = 6 year) were captured in the upper SRR, while those captured in the lower SRR had a greater mean age than those captured in the upper SRR (lower SRR mean age = 4.27 year, upper SRR mean age = 4.00 year). Flannelmouth sucker and roundtail chub attained the same maximum age measured in the SRR (maximum age = 8 year). Flannelmouth sucker in the upper SRR exhibited an older maximum age (8 year) measured, as well as an older mean age (5.07 year) than those aged in the lower SRR (maximum = 7 year; mean = 4.39 year). The lower SRR exhibited both the oldest individual (8 + year) and a greater mean roundtail chub age (4.59 year) than the upper SRR (4.20 year). More individuals were analysed for age and growth than were analysed for stable isotope signature (Upper SRR BHS N = 43, FMS N = 31, RTC N = 10; Lower SRR: BHS N = 15, FMS N = 23, RTC N = 17).

Flannelmouth sucker demonstrated the greatest model-estimated maximum length (L∞ = 481.46 mm; Fig. 5) and roundtail chub the smallest model-estimated maximum length (L∞ = 267.00 mm) of the ‘three species’. Bluehead sucker exhibited the greatest Brody growth rate coefficient (k = 0.21) and flannelmouth sucker the lowest predicted Brody growth rate coefficient (k = 0.19). No differences in length-at-age were detected between fish captured in the upper and lower SRR for either flannelmouth sucker (t-test P = 0.72) or roundtail chub (t-test P = 0.48). However, bluehead sucker captured in the lower SRR were significantly larger at age than those captured in the upper SRR (t-test P = 0.012).

**Fig. 4.** Trophic niche spaces occupied by fish species in the upper (a) and lower (b) San Rafael River. The ‘three species’ are shown with solid lines. Solid lines: blue = bluehead sucker, green = flannelmouth sucker and yellow = roundtail chub; Dashed lines: blue = sand shiner, red = red shiner, grey = channel catfish, yellow = green sunfish, light blue = fathead minnow, black = collector filterer insects; Dotted lines: yellow = common carp, red = white sucker, black = black bullhead; Dash-dotted lines; red = speckled dace.

**Fig. 5.** Size-at-age with Von Bertalanffy growth function for flannelmouth sucker (a), bluehead sucker (b), and roundtail chub (c) in the San Rafael River. Black triangles represent fish captured in the lower San Rafael River; grey circles represent fishes captured in the upper San Rafael River. Note different y-axes.
Discussion

In this study, we analysed stable isotope signatures and growth (a fitness-related measure) to examine the effect of non-native species on trophic status and growth of populations of imperilled desert fishes. Our analysis of catch rates between areas with and without complex habitat and non-native fishes revealed that areas of the San Rafael River without non-native fishes held significantly greater abundances of the ‘three species’ than those areas with non-native species present, regardless of habitat quality. Results of the stable isotope analysis revealed that non-native fish species have significantly altered food web structure in the San Rafael River. After detecting these changes to the trophic structure of the river, we examined the relative growth and condition of the ‘three species’ to determine whether the establishment of the non-native fish populations has had an effect on the relative fitness of these imperilled native fishes. Greater understanding of these issues is critical to the effective conservation and management of these endemic species, and has implications for the conservation of species threatened by habitat loss and non-native species introductions worldwide.

Non-native species can alter the flow of nutrients and energy through an ecosystem through alteration of the number and strength of trophic linkages in a food web (Eby et al. 2006; Sousa et al. 2008; Britton et al. 2010). In the process, they may also facilitate the establishment of other non-native species (Simberloff & Von Holle 1999). The stable isotope signatures of the ‘three species’ detected in this study indicate trophic levels consistent with the diets observed in previous studies (Childs et al. 1998; Bezzrides & Bestgen 2002; Quist et al. 2006). The establishment of non-native fishes has increased the number of resident fish species in the food web from four in the upper San Rafael River (and assumed pre-invasion lower San Rafael River) to eleven (including seven non-native) species in the lower San Rafael River. Although the food web of the upper San Rafael River consists primarily of a few native, secondary consumers (the ‘three species’ and speckled dace), the food web of the lower San Rafael River consists of a crowded level of secondary consumers, as well as a diverse level of tertiary consumers. Acknowledging that the potential ecological impact of an invading species is context dependent (i.e., on the abiotic conditions and biotic community of the invaded ecosystem; Ruesink 2003), the high diversity of invading species in the San Rafael River increases the likelihood that at least one of the established non-native species will be a high-impact invader (Ricciardi & Kipp 2008).

Due to the inherent isolation and insularity of rivers and lakes, freshwater ecosystems often display high rates of endemism (Dudgeon et al. 2006). Ecosystems comprised of highly endemic faunas, such as streams in the Colorado River Basin, are more likely to be negatively impacted by invading species, as the invader often represents a novel predator or competitor archetype (Ruesink 2003; Cox & Lima 2006). In isolation, prey species may not evolve defences (e.g., behavioural or morphological) against predators not native to their range (Ruesink 2003), and often experience strong negative effects of introduced non-native predators (Kitchell et al. 1997). Three non-native fishes in the lower San Rafael River (i.e., channel catfish, black bullhead and green sunfish) have trophic positions indicative of at least partial piscivory. While previous studies suggest the large-bodied piscivore trophic niche was occupied seasonally by endangered Colorado pikeminnow in Colorado River tributaries (Tyus & Saunders 2000; Bottcher et al. in press), the established populations of channel catfish, black bullhead and green sunfish present a novel, year-round source of predation pressure for juveniles of the ‘three species’. Our limited catches of juveniles in the river suggest that they occur at low abundances, are highly patchy in distribution, or are less susceptible to our sampling methods. Additional samples with a stick seine in backwater and slow, marginal habitats also had very limited catches of juveniles, suggesting that gear bias was not the cause of the limited catch numbers. Red shiners have been shown to be significant predators on larval and juvenile stages of Colorado River fishes (Tyus & Nikirk 1990; Tyus & Saunders 2000). While we argue that novel predators likely have substantial negative effects on juveniles of the ‘three species’, our data show that more juveniles of the ‘three species’ were captured in the lower San Rafael River than were captured in the upper San Rafael River. This occurrence is likely due to the habitat characteristics of the sampling sites in the upper San Rafael, which, while having extensive complex habitat, did not have backwater habitats, the preferred habitats of juvenile native fishes, available. The contemporary suite of novel predator archetypes in the river presents the potential for substantial impacts on recruitment success and viability of the ‘three species’ (Meffe 1985).

In addition to the negative effects of predation from invasive species, these invaders may also compete with native species for resources. Competition for resources can be demonstrated by a numerical response (Pell & Tidemann 1997), a shift in resource usage (Werner & Hall 1979; Davey et al. 2006), change in morphology (Crowder 1984), and/or a change in vital rates in the presence of potential com-
petitors (Davey et al. 2006). Competition cannot be inferred from stable isotope signatures alone (Newsome et al. 2007), as multiple combinations of basal resources and prey items can result in similar isotopic signatures. Nonetheless, our trophic niche space analysis suggests that the presence of numerous non-native species in the lower San Rafael River has the potential to increase competition for food resources for the ‘three species’ (DeNiro & Epstein 1978; Zambrano et al. 2010). The vast majority of the trophic niche space of each of the ‘three species’ is overlapped by multiple non-native fishes. Furthermore, the trophic niches of the bluehead sucker and flannelmouth sucker are altered in the presence of non-native fishes. In the lower San Rafael River, both species demonstrated a more enriched δ13C signature than in the upper San Rafael River, potentially indicative of a shift from riffle to more pool-derived resources (Finlay et al. 2002). It is important to note, however, that this shift in carbon signature could result from competitive exclusion by the non-native fishes, the scarcity of riffle habitats in the degraded lower San Rafael River, or some combination of both. The reduction in the range of nitrogen signatures demonstrated by both bluehead sucker and flannelmouth sucker may be indicative of niche displacement whereby non-native species are limiting the native fishes’ food resource use to lower trophic level items, potentially through exploitative competition over the resource or interference competition relegating the native species to less preferred habitats (Douglas et al. 1994).

As resources become concentrated into smaller areas, competition can intensify over an increasingly limited resource pool (Mills et al. 2004), reducing the energy available to native species. Competition-based changes to a fish’s energy intake (i.e., quantity or quality) can result in less favourable growth patterns, as the fish may not be able to obtain necessary resources, or may have to increase energy expenditure to feed (Mills et al. 2004; Davey et al. 2006). Decreased growth rates can negatively affect fish populations, as fecundity (Bagenal 1978), age-at-maturity (Alm 1959), and, often, survival (Quinn & Peterson 1996) are strongly correlated with body size. For example, faster growth rates can enable fish to escape gape-limited predators and avoid starvation during extreme environmental conditions (Post & Evans 1989; Quinn & Peterson 1996). However, the ‘three species’ do not demonstrate lower growth rates in the lower San Rafael River relative to the upper San Rafael River, even in the face of lesser resource abundance (Walsworth 2011) and greater potential for competition. Previous studies have suggested that source-sink dynamics control the populations of the ‘three species’ in the San Rafael River (Bottcher 2009), with the upper San Rafael River and the main-stem Green River providing colonists to the lower San Rafael sink habitat. The ‘three species’ are each highly mobile species that make long distance movements in both downstream and upstream directions, either through larval drift or directed adult migration (e.g., Chart & Bergersen 1992; Robinson et al. 1998; Compton et al. 2008). Movement of individuals from the Green River into the San Rafael River could mask any differences in growth resulting from competition. Flannelmouth sucker and bluehead sucker have been shown to grow faster and to larger sizes in larger rivers (Sweet et al. 2009). In addition, unidirectional movement downstream over the Hatt Ranch diversion dam, a barrier to upstream movement, could mask any fitness-related effects of competition with non-native species in the lower river.

In addition to disrupting connectivity, dams and diversions often result in more stable flow regimes. In a static environment, Menge & Sutherland (1987) predicted that the effect of predation outweighs the effects of competition or physical factors on intermediate level consumers, such as the ‘three species’, especially in systems with high levels of omnivory. The highly altered contemporary flow regime of the San Rafael River has led not only to habitat homogenisation, but also to frequent low flow and dewatering events (Bottcher 2009). Predation should have a stronger impact on populations in homogeneous habitat (Caroffino et al. 2010) and at times of low flow (Pilger et al. 2010), as the fish are concentrated into smaller habitat areas with less refuge. The lack of significant growth differences in the San Rafael River, coupled with the greater abundances of the ‘three species’ in the upper San Rafael River, regardless of habitat quality, suggest that predation by the non-native fishes in the lower river has a stronger impact on the ‘three species’ than does greater competition for resources, similar to the findings of others (Pilger et al. 2010).

Many of the fish species in our stable isotope analysis demonstrated elevated carbon signatures relative to the collector-filterer invertebrates used as a baseline, suggesting the contribution of an alternative carbon source to the food web. As consumer carbon stable isotope signatures are elevated relative to the collector-filterers, it is likely that the additional resources contributing to the food web are detritus and invertebrates from slow-water habitats (Finlay et al. 2002). An alternative basal resource could have implications for our interpretation of trophic position if the nitrogen signature of the primary consumers demonstrating elevated δ13C is different than the signature demonstrated by the collector-filterers used in our analysis. However, the results of a previous desert stream study (Gido et al. 2006) suggest that...
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algae and detritus have similar δ15N signatures. Previous studies have demonstrated that each of the ‘three species’ is omnivorous, consuming benthic invertebrates, algae, detritus and in the case of roundtail chub, fish and terrestrial invertebrates (Childs et al. 1998; Bezzerides & Bestgen 2002; Quist et al. 2006). Thus as collector-filterer insects dominated our benthic invertebrate samples, we believe that the use of collector-filterer insects as a baseline is sound.

We recognise there are potential limitations to our inference of both the trophic structure and relative growth rates between the upper and lower San Rafael River. Previous research suggests using caution when estimating annual growth from more than the single most recent annuli, as this method inherits uncertainties due to size-selective mortality (i.e., Lee’s phenomenon; Gutreuter 1987). However, by including all annuli in the analysis, we were able to estimate growth in years when the populations were not sampled, or when fin ray sections were not collected. In addition, an analysis of body condition revealed similar results to our size-at-age analysis (Walsworth 2011). Isotopic signatures often vary with fish length and growth rate, as well as over time (Harvey et al. 2002; Vinson & Budy 2011), another potential limitation of our data. However, ontogenetic diet shifts, if present, would result in more conservative estimates of non-native piscivore trophic positions, as smaller individuals would not yet be piscivorous. While the data collected for this study cannot explicitly demonstrate predation, greater competition or a change in fitness for the ‘three species’, the weight of evidence from our stable isotope analysis, abundance comparisons (T.E. Walsworth & P. Budy in review) and the results of previous studies throughout the Colorado River Basin suggest that the non-native fishes are having substantial impacts on populations of the ‘three species’. These negative impacts appear to result from the establishment of novel predators and competitors in the ecosystem and extensive restructuring of the aquatic community.

The reduction or loss of native species in an ecosystem can lead to overwhelming ecosystem level effects, including, but not limited to, further species loss or reduced ecosystem resilience (Wootton & Downing 2003; Lockwood et al. 2007). Given the high densities of non-native fishes in the lower river, the lack of significant increase in native fish density in complex habitat in the presence of non-native fishes, and the associated impacts suggested herein, restoration of physical habitat in the lower river may have little effect on ‘three species’ populations in the absence of efforts to minimise the effects of non-native fish species (Walsworth 2011). Improving the physical habitat template could actually enhance non-native performance and abundance (Bond & Lake 2003). As such, the eradication of non-native fishes may be a necessary step to ensure the persistence of the ‘three species’ throughout their native range, although the effectiveness of such a strategy may be most effective in combination with restoration of a more natural flow regime (Gido & Propst 2012). Our results demonstrate that non-native fish species significantly alter the food web structure of the San Rafael River, presenting novel predators and competitors that threaten the persistence of these endemic and imperilled species. Maintaining connectivity with ‘three species’ populations in the upper San Rafael River (while avoiding upstream expansion by non-native species) and the main-stem Green River may be critical to the persistence of the ‘three species’ in the lower river (Pulliam 1988; Bottcher 2009; Walsworth 2011).

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