

Research Article

Invasive crayfish in a high desert river: Implications of concurrent invaders and climate change

Patrick J. Martinez

Colorado Division of Wildlife, 711 Independent Avenue, Grand Junction, Colorado, 81505, USA

Present address: U. S. Fish and Wildlife Service, 764 Horizon Drive, Building B, Grand Junction, Colorado, 81506, USA

E-mail: patrick_martinez@fws.gov

Received: 28 October 2010 / Accepted: 8 August 2011 / Published online: 18 August 2011

Abstract

No crayfish species are native to the Colorado River Basin (CRB), including the portion of the state of Colorado west of the Continental Divide. Virile crayfish [*Orconectes virilis* (Hagen, 1870)], a recent invader in the middle Yampa River in northwestern Colorado, displayed an abrupt increase in abundance in the early 2000s, which coincided with a drought, a severe decline in the abundance of small-bodied and juvenile native fishes, and a dramatic increase in the abundance of nonnative smallmouth bass [*Micropterus dolomieu* (Lacepède, 1802)]. The annual density of virile crayfish was 6.4/m² in 2005 and 9.3/m² in 2006. The annual biomass density of virile crayfish was 9.0g/m² in 2005 and 15.8 g/m² in 2006, representing a riverwide biomass of 122 kg/ha, which equaled that of other macroinvertebrates and fish combined (120.7 kg/ha). Efforts to recover and preserve native fishes in the Upper Colorado River Basin (UCRB), particularly in the Yampa River, have been hampered by nonnative predatory fishes, but the implications of crayfish may have been overlooked and underestimated. Stream conditions during the drought apparently facilitated proliferation by virile crayfish in the middle Yampa River, likely contributing to hyperpredation on native fishes by invasive smallmouth bass. This trophic interaction between virile crayfish and smallmouth bass, in conjunction with regional projections for climate change, will likely make efforts to reduce the abundance and negative ecological impact of smallmouth bass in this ecosystem more difficult and costly. Given the nonnative status of all crayfishes in the CRB, and their invasive capacity and potential to negatively reconfigure native lotic food webs, all states in the UCRB should prohibit the importation, movement, sale, possession and stocking of any live crayfish.

Key words: *Orconectes virilis*, Upper Colorado River Basin, quadrat sampler, *Micropterus dolomieu*, hyperpredation, drought, climate change

Introduction

The Colorado River Basin (CRB) in western North America drains about one-twelfth of the land area of the 48 contiguous United States (Carlson and Muth 1989; Figure 1a). The Upper Colorado River Basin (UCRB) is functionally separated from the lower basin by Glen Canyon Dam in Arizona, which impounds Lake Powell. The UCRB comprises five states (Arizona, Colorado, New Mexico, Utah, and Wyoming) from which water naturally drains into the Colorado River. The native fish fauna of the UCRB is characterized by low species diversity (14) and high endemism (57%), with five species federally listed as endangered (Valdez and Muth 2005).

No crayfish species are native to the CRB (Hobbs 1989; Inman et al. 1998; Carpenter 2005), but one species, the virile crayfish [*Orconectes virilis* (Hagen, 1870)], is widely

established in the UCRB (Johnson 1986, Hubert 1988; Carothers 1994, Blinn and Poff 2005). The virile crayfish has a broad native distribution in North America where it occupies a wide variety of habitats in lotic and lentic systems (Bovbjerg 1970; Tierny and Atema 1988; Hobbs 1989; Richards et al. 1996). It feeds on plants, detritus, and other animals (dead or alive), and displays grazing, scavenging, cannibalistic and predatory behaviors; hence, its trophic status as an opportunistic rather than indiscriminate omnivore (Chambers et al. 1990; Loughman 2010). These flexible habitat requirements and feeding habits categorize the virile crayfish as a generalist rather than specialist species (Charlebois and Lamberti 1996; Mead 2008; Larson and Olden 2010), which contributes to its success as an invasive species (Phillips et al. 2009; Larson and Olden 2011; Gherardi et al. 2011).

Invasive crayfish can have inordinately large effects on native aquatic species due to their complex role in food webs as prey and their polytrophic feeding habits (Kerby et al. 2005; Usio et al. 2006; Ilheu et al. 2007). Because crayfish are generally larger, longer lived, and more mobile than most other invertebrates in a given ecosystem, these crustaceans can greatly affect the systems they inhabit (Lorman and Magnuson 1978; Momot, 1995). For example, crayfish can dominate the biomass of benthic invertebrates (Lorman and Magnuson 1978; Momot 1995) and may be considered “keystone” species, influencing multiple trophic levels by interacting with various life stages of numerous species (Momot 1995; Charlebois and Lamberti 1996; Whitley and Rabeni 1997; Holdich 2002). Adding nonnative crayfish to food webs can have adverse effects on macrophytes (Elser et al. 1994; Nystrom and Strand 1996), invertebrates (Hanson et al. 1990; Crawford et al. 2006; McCarthy et al. 2006), native crayfish species (Lodge et al. 2000a; Taylor et al. 2007; Larson and Olden 2011), amphibians (Kats and Ferrer 2003; Cruz et al. 2006) and native fishes (Guan and Wiles 1997; Carpenter 2005; Light 2005).

Understanding food web impacts and community consequences of crayfish invasions requires an ability to monitor their density and biomass relative to other community components and crayfish densities elsewhere. There is no single standardized protocol for estimating lotic crayfish abundance due to variations in species behavior, habitat features and preferences, and the clustered distribution of crayfish; however, using a variation of a quadrat sampler has emerged as an effective method (Rabeni 1985; DiStefano et al. 2003; Larson et al. 2008). A modified quadrat sampling method was used in this study to collect virile crayfish in the Yampa River in northwestern Colorado to describe their demographics in relation to recent fish community shifts. This information was used to evaluate the ecological and management implications of this invasive crayfish and other invasive aquatic species in the UCRB.

Materials and methods

Study area

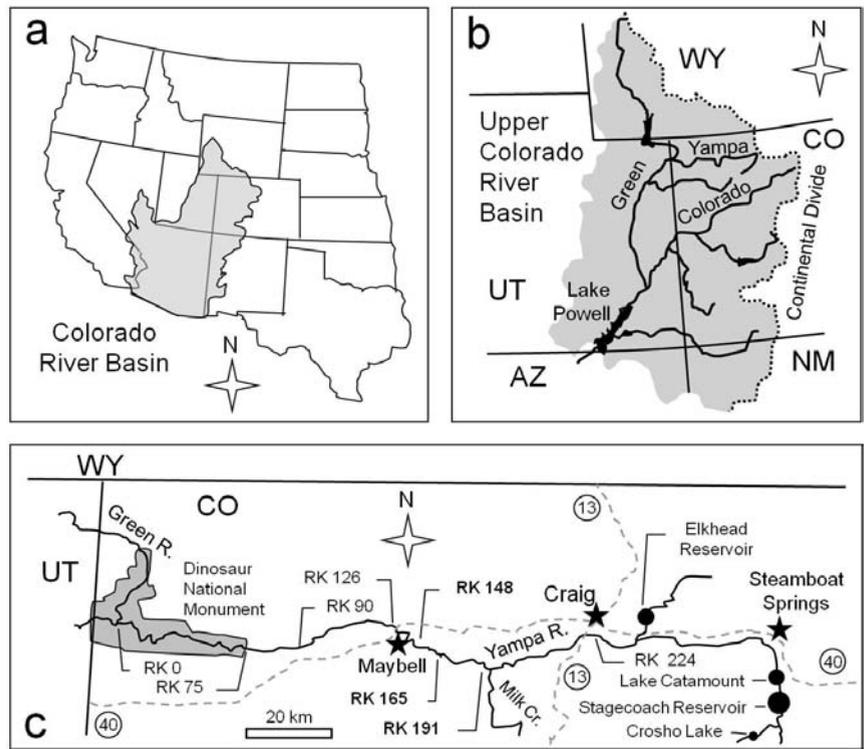
The Yampa River (Figure 1b) has been described as the “crown jewel” among tributaries of the UCRB for its formerly robust native fish

populations (Johnson et al. 2008) and largely unregulated flow (Roehm 2004; Stewart et al. 2005). The river flows westward from the Continental Divide (elevation 3,712 m above sea level [ASL]) until its confluence with the Green River (1,548 m ASL) in Dinosaur National Monument (DNM; U. S. National Park Service; Figure 1c). Draining mountainous and high desert terrain, it is the largest and most important tributary for endangered fish recovery in the Green River sub-basin (Tyus and Saunders 2001). The Yampa River has a snowmelt hydrograph and displays great seasonal flow variability (Van Streeter and Pitlick 1998). While spring discharges remain relatively unaffected, agricultural withdrawals have reduced late summer base flows to about 70% of native conditions (Modde et al. 1999; Stewart et al. 2005). Site locations were designated according to their distance upstream (km) from the Yampa River's confluence with the Green River at river kilometer (RK) 0 (Figure 1c).

Stream flow (U.S. Geological Survey 2009a) and water temperature (U.S. Geological Survey 2009b) data are from the U.S. Geological Survey site (gage 09251000) located at RK 126 (Figure 1c). Mean peak, daily summer (15 June–15 September) and base (August–February) flows from 1979–1999 were about 223, 44, and 10 m³/s, respectively (Bestgen et al. 2007). During the drought of 2000–2006 annual peak flows rivaled the peak flows of 1979–1999 (except in 2002 and 2004 when they were lower), but daily summer flows averaged only about 39% (17 m³/s) of those during the previous period. During the recent period, base flows were much lower and began earlier, reaching seasonal lows in July rather than in August, except in 2005 when the timing and level of base flows were similar to the 1979–1999 average (Bestgen et al. 2007). The effects of the drought were most severe in 2002 when base flows during the summer averaged about 0.3 m³/s (Anderson and Stewart 2007). The Yampa River tends to remain clear, except during spring runoff and after rainstorms (Holden and Stalnaker 1975).

Climatic conditions vary with elevation, but the study area has relatively cool, dry summers (July mean air temperature = 19.5°C at RKM 126 and 224), and cold winters (Johnson et al. 2008). Indices of stream temperature indicated that summertime water temperatures were warmer, and warmed earlier during the drought period from 2000–2006. From 1991–1999 the mean daily summer stream temperature was 19.0°C

Figure 1. Map of (a) the Colorado River Basin in the southwestern USA, (b) the location of the Yampa River in the Upper Colorado River Basin, and (c) the Yampa River in northwestern Colorado showing river kilometer (RK; RK 0 = confluence with the Green river) designations of the three crayfish sampling locations (bold). Other key sites (standard font) mentioned in the text include the upstream boundaries of critical habitat for endangered fishes: RK 75 for bonytail and humpback chub; RK 90 for razorback sucker; and RK 224 for Colorado pikeminnow (Roehm 2004). The middle Yampa River refers to that segment from RK 90 to RK 224.



(Bestgen et al. 2007). Lower flows and likely higher air temperatures during 2000-2006 elevated the mean daily stream temperature to 20.6°C. Average stream temperature was sustained at $\geq 16^{\circ}\text{C}$ from late-May to mid-June from 2000-2006, whereas this same temperature threshold did not occur until late June from 1979-1999 (Bestgen et al. 2007).

The Yampa River contains the 12 fish species native to western Colorado (Holden and Stalnaker 1975; Johnson et al. 2008). The warmer middle (RK 75-224) and lower reaches include critical habitat for four endemic, federally listed endangered fishes, Colorado pikeminnow [*Ptychocheilus lucius* (Girard, 1856)] humpback chub [*Gila cypha* (Miller, 1946)], bonytail [*G. elegans* (Baird and Girard, 1853)] and razorback sucker [*Xyrauchen texanus* (Abbot, 1860)], with Colorado pikeminnow critical habitat extending upstream to RK224 (Figure 1c). This portion of the river also supports three additional native large-bodied fishes, bluehead sucker [*Catostomus discobolus* (Cope, 1871)] and endemic flannelmouth sucker

[*C. luttipinnis* (Baird and Girard, 1853)] and roundtail chub [*G. robusta* (Baird and Girard, 1853)], and two small-bodied native fishes, speckled dace [*Rhinichthys osculus* (Girard, 1856)] and mottled sculpin [*Cottus bairdi* (Girard, 1856)] (Johnson et al. 2008).

Intentional and unintentional stocking and immigration by nonnative fishes has resulted in at least 20 nonnative fish species occupying the Yampa River, including nongame cyprinids and several piscivorous game fish (Bestgen et al. 2007; Johnson et al. 2008). Channel catfish [*Ictalurus punctatus* (Rafinesque, 1818)], introduced in 1944 (Wiltzius 1985), are common in the middle Yampa River, but they are abundant within DNM (Tyus and Nikirk 1988; Fuller 2009). Northern pike [*Esox lucius* (Linnaeus, 1758)] and smallmouth bass [*Micropterus dolomieu* (Lacepède, 1802)] were introduced into the Yampa River basin in the late 1970's by intentional stocking into Elkhead Reservoir (Figure 1c; Tyus and Beard 1990; Johnson et al 2008; Hawkins et al. 2009). These species escaped from the reservoir and northern

pike became abundant in the upper and middle Yampa River below Stagecoach Reservoir since the mid-1980s (Nesler 1995; Hawkins et al. 2005). Smallmouth bass were absent (Baily and Alberti 1952a; Holden and Stalnaker 1975; Carlson et al 1979) or rare (Miller et al. 1982; Wick et al 1985; McAda et al. 1994) in the Yampa River before they were flushed in large numbers from Elkhead Reservoir during its draining in 1992 (Nesler 1995; Martinez 2003). The distribution and abundance of smallmouth bass gradually increased in the middle Yampa River in the mid-1990s (Martinez 2006; Hawkins et al. 2009) and they were first detected in the lower Yampa River within DNM in 2002 (Fuller 2009; Figure 1c). Smallmouth bass abundance increased abruptly in 2001 (Anderson 2002) and increased further in 2005 and 2006 (Hawkins et al. 2009), likely due to benefits accrued as a result of the drought (Anderson and Stewart 2007). Smallmouth bass have become the dominant predator in the middle Yampa River and their increase in abundance coincided with a severe decline in the numbers of native fish (Anderson and Stewart 2007; Bestgen et al. 2007; Hawkins et al. 2009), and an abrupt increase in the abundance of virile crayfish (Anderson and Stewart 2007; Martinez 2006).

Virile crayfish in Crosho Lake near the Yampa River headwaters (Figure 1c) were established prior to or during the early 1950, were abundant by 1954, and may be the oldest known crayfish population in northwestern Colorado (Klein 1955; Carothers 1994). Other lakes in the upper Yampa basin were known to contain established virile crayfish populations or received transplants of virile crayfish by the late 1970s (Carothers 1994). No crayfish were reported in macroinvertebrate surveys ranging from the upper to lower Yampa River in 1951 (Baily and Alberti 1952b) or during the late 1970s (collections made with a D-frame kicknet; Carlson et al. 1979). Johnson (1986) reported that no crayfish were captured in the Yampa River in fish surveys (gill nets and electrofishing) performed from 1978–1984. Crayfish were initially reported in low numbers in the diets of channel catfish and northern pike from the middle and lower Yampa River from 1988–1991 (Nesler 1995). While virile crayfish were collected in the Yampa River during a crayfish survey (traps and lift-nets) conducted in 1991 above Craig (RK 224), no live crayfish were collected at stations located further downstream near the Milk Creek confluence or

near Maybell (Figure 1c; Carothers 1994). Anderson and Stewart (1999) reported low numbers of crayfish in invertebrate samples (Surber sampler) collected within the study area in 1998. Virile crayfish likely appeared in the middle Yampa River by the late 1980s, existing at low densities until the drought beginning in 2000. Fishery workers began to report observations of higher crayfish densities in 2001 (Martinez 2006) with an apparent explosion in their abundance occurring by 2003 (Anderson and Stewart 2007).

Crayfish sampling and measurements

Several factors were considered in selecting the time and locations for the sampling of crayfish in the middle Yampa River. The method of sampling, hand-picking within 1 m² quadrats, relied on good water clarity and the ability for personnel to wade across the width of the river without the need for specialized gear to withstand low water temperatures or high water velocities. These conditions were met as the hydrograph reached base flow by late summer. Low discharge at this time of year can limit access by watercraft, so accessibility from shore was also important in selecting sampling stations. This late season timing ensured that annual reproduction was complete and that young-of-year crayfish would be available for capture. Last, it was desirable that the stations represent as distinctly as possible the river's three major habitats: run, pool, and riffle-rapid (Anderson and Stewart 2007).

Sampling was conducted on 22–24 August 2005 and on 29–30 August 2006. Discharge during these dates, averaged 4.4 m³/s in 2005 and 4.7 m³/s in 2006 (U.S. Geological Survey 2009a). The three stations included the Juniper Springs boat ramp (RK 148; 13T 0248620 UTM 4484633), the Morgan Gulch boat ramp (RK 165; 13T 0256685 UTM 4478085), and the boater's access located downstream of the Milk Creek confluence (RK 191; 13T 0265393 UTM 4475603; Figure 1c). Sampling at these stations was conducted upstream of the boat ramp/access points to avoid to the extent possible human disturbance of the crayfish distribution or density. At each station, six transects spanning the river channel, oriented perpendicular to flow, were spaced 10 m apart. Two of these transects at each station were randomly selected for sampling by placement of 1 m² quadrats spaced 5 m apart. The placement of the first quadrat either

1 m or 5 m from shore was also randomly determined. A laser rangefinder (± 0.5 m) was used to maintain the 5 m spacing between quadrats and to measure stream width at the selected transects.

Quadrats enclosing an area of 1 m² were fabricated from 5 cm inside diameter, schedule 40 PVC pipe, and 90-degree couplers. Prior to final assembly and gluing of the pipe and coupler joints, the pipe was filled with sand to provide sufficient weight to keep the quadrat in place when submerged, while remaining light enough to be easily handled and moved. Transects were approached from downstream and a person onshore used the rangefinder to direct the spacing and placement of the quadrats. As the sampling site was approached and the quadrat was submerged into place on the substrate, the number of crayfish fleeing from within the boundary of the quadrat was counted as "missed". One person held a seine (2 m \times 1 m \times 10 mm aperture) downstream of the quadrat, preventing crayfish escape or drift in that direction, while two others captured and excavated crayfish by hand from inside the quadrat to a maximum substrate depth of about 15 cm (Larson et al. 2008). In water exceeding 60 cm deep, workers used snorkels and masks to facilitate excavation, visual detection and capture of crayfish. Water clarity in both years allowed unfettered visual detection of crayfish fleeing, hiding among the substrate, or burrowed under cobbles or rocks. Fifty eight 1 m² quadrats were sampled for crayfish in each year in 2005 and 2006.

Captured crayfish were counted, recorded, and bagged by quadrat, and placed on ice. Upon completion of sampling, water depth and velocity were measured at the center of each quadrat, and the percentage of major substrate types was visually estimated. Water velocity (m/s) was measured with a Marsh-McBirney flow meter at 60% of total water depth (from the surface). Substrate categories approximated those described by Bain et al. (1985) and included silt, sand, gravel (2–74 mm), cobble (75–250 mm) and rock (>250 mm). Simple linear regression was used to examine the relationship between water depth, water velocity, percent of substrate ≥ 75 mm, and total number of counted crayfish versus the percent of crayfish observed fleeing in each quadrat. The correlation between quadrat densities of crayfish and percentage of smaller substrates (silt, sand and gravel) and percentage of larger substrates (gravel, cobble

and rock) was also examined. Percentages were arcsine transformed prior to computing correlation coefficients. Data transformations and nonparametric tests were conducted with SAS software and all other statistical analyses were performed using Microsoft Excel software.

The method of capture, hand picking, allowed nearly all crayfish to remain intact. Individual crayfish with an undamaged cephalothorax were measured for carapace length (CL; determined as the dorsal distance from the anterior tip of the rostrum protruding between the eyes to the posteriomedian edge of the carapace) to the nearest mm using digital calipers. The CLs of crayfish in 2005 (n=481) and 2006 (n=436) were nonnormal and were compared between years and sexes (Wilcoxon rank-sum test). In 2005, captured crayfish ≥ 20 mm CL that were intact (n=78) were weighed to the nearest 0.5 g. In 2006 captured crayfish that were intact (n=432) were weighed to the nearest 0.1 g. Individual masses of crayfish were used to develop a length-mass relationship. The species identity and sex of all captured crayfish was determined (Hobbs 1989; Pennak 1989), except for 42 crayfish < 15 mm CL in 2005, for which the sex was not identified. Chi-square tests were used to compare sex ratios of crayfish in 2005 and 2006.

Density and biomass estimation

Crayfish density was examined and reported in four ways. First, station-specific mean densities of crayfish (number/m²) in 2005 and 2006 were calculated by dividing the number of crayfish counted (captured and missed) in the two transects at each station by the number of quadrats in both transects. The number of crayfish counted within individual quadrats in both transects was used to calculate the standard error (SE), coefficient of variation (CV), and 95% confidence interval (CI) for the station-specific mean crayfish densities. Crayfish densities were nonnormal (Shapiro-Wilk test) so nonparametric analysis of variance was used to compare station densities in each year. Second, mean counts of crayfish in quadrats in 2005 and 2006 were compared for a significant difference in density between years (Wilcoxon rank-sum test). Third, annual estimates of crayfish density in 2005 and 2006 were made by weighting the station-specific densities by the amount of habitat that each major type represented within the study area. Percentages of major habitat categories reported in Anderson and Stewart

(2007) for the middle Yampa River provided weighting values for three predominant habitat types represented by each station. Run habitat at the Juniper Springs station, was the most prevalent type representing 68% of the study area. Pools dominated the Morgan Gulch station accounting for about 26% of the study area. Riffle-rapids at the Milk Creek station comprised only 6% of the study area. The weighted station densities for each year were summed to provide annual estimates of crayfish density (number/m²). Last, these annual estimates of crayfish density were averaged to provide a riverwide estimate of crayfish density (number/m²) in the middle Yampa River during the mid-2000s. This riverwide estimate derived by weighting provided a better representation of crayfish density for examining potential food web implications in the Yampa River and UCRB in relation to invasive crayfish abundance and impacts reported in the literature. Accordingly, station-specific mean CLs of crayfish were also weighted by the percentage of each major habitat type and summed to provide annual crayfish CLs for 2005 and 2006. Wet masses corresponding to these weighted CLs were determined from the length-mass relationship, and were multiplied by their respective weighted annual crayfish density to provide annual estimates of crayfish biomass density (g/m²). These annual estimates of crayfish biomass density were averaged to estimate the riverwide biomass of crayfish (kg/ha) in the middle Yampa River during the mid-2000s for comparison with the biomass of other macroinvertebrates and fish.

An estimate of non-crayfish macroinvertebrate wet biomass in the middle Yampa River was obtained by converting the ash free dry mass of macroinvertebrates (average=0.48 g/m²) reported for streams and rivers in CRB studies (Haden et al. 1999; Haden et al. 2003; Oberlin et al. 1999) to dry mass using an average of 6.5% ash for major aquatic insect orders (Benke et al. 1999; Benke and Huryn 2007), and then converting dry mass to wet mass by an average factor of 0.18 (Waters 1977; Wetzel and Likens 2000). An average estimate of biomass for fish > 150 mm TL in the middle Yampa River in 2003 and 2004, 53.2 kg/ha, was obtained from Anderson (2005). A similar estimate for fish ≤ 150 mm TL was based on a small-bodied fish density of 30,000/ha and an individual mass of 1.3 g (Johnson et al. 2008).

Results

The width of the Yampa River at each station was similar in 2005 and 2006, ranging from about 40 m at Milk Creek to 67 m at Morgan Gulch (Table 1). Water depth in the quadrats ranged from 14 cm to just over one meter and averaged 42 cm in both years. Measured water velocities in quadrats ranged from zero in the pool habitat at Morgan Gulch to 0.92 m/s in a rapid at the Milk Creek station and averaged about 0.3 m/s in both years (Table 1). In 2005-2006, the dominant (45% cover) substrate inside the quadrats was gravel, followed by cobble and sand (25% each), with silt and rocks being comparatively scarce, (2% each; Table 1).

All crayfish captured (n=923) were identified as virile crayfish; 483 in 2005 and 440 in 2006 (Table 2). Including crayfish that were captured or missed within all 116 quadrats, 631 were counted in 2005 and 566 were counted in 2006 (n=1,197; Table 2). Missed crayfish accounted for 23% (n=148) and 22% (n=126) of the crayfish counted in 2005 and 2006, respectively (Table 2). Mean station-specific densities of virile crayfish ranged from 3.6/m² at Juniper Springs to 22.1/m² at Milk Creek in 2005. Higher variability in the numbers of virile crayfish counted in individual quadrats in 2005 resulted in higher coefficients of variation (CV) for the three stations than in 2006 (Table 2). Station densities were significantly different in 2005 (F=3.57, P=0.035), but not in 2006 (F=2.08, P=0.134). Mean densities of virile crayfish in quadrats in 2005 (10.9/m²) and 2006 (9.6/m²) were not significantly different (Wilcoxon rank-sum test, F=0.142, P>0.5). The quadrat densities of virile crayfish in 2005-2006 had a weak negative relationship with smaller substrates (silt, sand, and gravel; correlation coefficient = -0.13), and a slightly positive relationship with larger substrates (gravel, cobble, rock; correlation coefficient = 0.23).

The number of virile crayfish counted in individual quadrats ranged from zero in 12 quadrats in 2005 and one in 2006 to 108 (92 captured, 16 missed) in a nearshore quadrat at the Morgan Gulch station in 2005. No crayfish were captured in 11% of the quadrats sampled in both years, but single crayfish were missed in two quadrats sampled in 2005, resulting in crayfish being absent from only 9% of all quadrats. There was no apparent pattern in the size of virile crayfish exposed on the substrate

Table 1. Habitat characteristics in 1 m² quadrats sampled for virile crayfish along two randomly selected transects at three sampling stations in the middle Yampa River, Colorado, in 2005 and 2006. Gravel, 2-74 mm; cobble, 75-250 mm; rock > 250 mm.

Station name	Mean stream width (m)	Water depth (cm)		Water velocity (m/s) at 60% below surface		Substrate category (percent)				
		Range	Mean	Range	Mean	Silt	Sand	Gravel	Cobble	Rock
2005										
Juniper Springs	58.5	18.3-42.7	33.2	0.15-0.55	0.38		24	33	43	
Morgan Gulch	67	15.2-88.4	45.3	0.01-0.47	0.19	7	32	43	18	
Milk Creek	39.5	15.2-82.3	44.6	0.03-0.61	0.30	2	11	23	52	12
2006										
Juniper Springs	62	22.9-45.7	33.3	0.21-0.56	0.38	2	38	55	5	
Morgan Gulch	67.5	13.7-103.6	54.6	0-0.41	0.18	4	36	60		
Milk Creek	43	16.8-67.1	40.8	0.12-0.92	0.47		2	49	48	1

Table 2. Numbers of virile crayfish caught and missed at three stations in 1 m² quadrats spaced 5-m apart along two randomly selected transects oriented perpendicular to the current in August 2005 and 2006 in the middle Yampa River, Colorado. The total number of crayfish counted and the percent missed summarize capture success in both transects at each station. Standard error (SE), coefficients of variation (CV), and confidence intervals (CI) describe density estimates derived from the total number of crayfish captured and missed in both transects at each station.

Station name	Stream width (m)	Number of 1 m ² quadrats per transect	Number of crayfish captured/missed (percent)	Total number of crayfish counted (percent missed)	Mean number of crayfish/1 m ² quadrat (SE)	CV	95% CI	
							Lower limit	Upper limit
2005								
Juniper Springs	61	10	25 / 3 (10.7)	72 (9.7)	3.6 (1.3)	36	1.8	7.1
Morgan Gulch	62	11	35 / 28 (44.4)	249 (18.6)	10.4 (4.5)	43	4.6	23.2
Milk Creek	39	7	110 / 37 (25.2)	310 (27.1)	22.1 (7.5)	34	11.6	42.3
2006								
Juniper Springs	67	11	73 / 25 (25.5)	201 (19.9)	9.6 (1.8)	19	6.7	13.7
Morgan Gulch	64	11	66 / 32 (32.6)	164 (25.6)	7.5 (1.7)	23	4.8	11.5
Milk Creek	39	7	70 / 16 (18.6)	201 (21.9)	13.4 (2.7)	20	9.0	19.9

and the sizes of crayfish missed appeared to be in proportion to the size structure of captured virile crayfish. Not all exposed crayfish tried to escape, rather some remained undisturbed, while others attempted to conceal themselves amidst or underneath available cover. Crayfish that swam away did not appear to do so in a particular direction (lateral or upstream), regardless of current velocity. Coefficients of determination for the percent of crayfish missed with water depth, water velocity, percent of substrate \geq 75 mm, and the total number of crayfish counted in each quadrat were < 0.03. This suggested that the propensity for crayfish to flee or escape capture was attributable to random circumstances including the degree of exposure and behavior of

individual crayfish, the disturbance involved in positioning each quadrat, and the occasional mishandling of crayfish.

Mean CLs of virile crayfish in 2005 (16.1 mm, SE=0.31) and 2006 (19.2 mm, SE=0.29) were significantly different (Wilcoxon rank-sum test, approximate Z=9.89, P<0.001) due to the greater proportion of crayfish measuring 15 mm CL or less in 2005 (Figure 2). Length frequencies of virile crayfish sexes (Figure 3) had significantly different mean CLs (Wilcoxon rank-sum test) in 2005 (male = 16.7 mm CL, SE = 0.50; female = 15.5 mm CL, SE = 0.43; approximate Z=2.58, P=0.010), but not in 2006 (male = 19.3 mm CL, SE = 0.38; female = 19.1 mm CL, SE = 0.47; approximate Z=-0.851, P=0.395). Virile crayfish

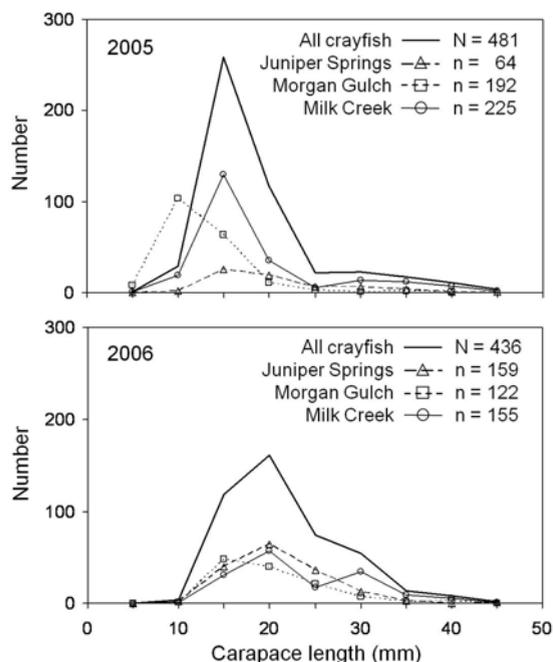


Figure 2. Length frequency of virile crayfish, in 5 mm categories, captured at three sampling stations, Juniper Springs, Morgan Gulch, and Milk Creek, in the middle Yampa River, Colorado in 2005 and 2006.

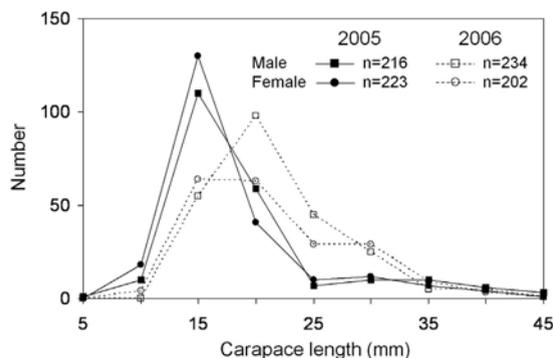


Figure 3. Length frequency of male and female virile crayfish, in 5 mm categories, captured in the middle Yampa River, Colorado in 2005 and 2006.

displayed similar male:female ratios (Figure 3) of 0.97 in 2005 and 1.17 in 2006 (chi-square, $P > 0.5$). The relationship between virile crayfish CL and mass ($n=510$), $M = 0.00014 \text{ CL}^{3.23}$ (where M equals wet mass in g and CL equals carapace length in mm), had a coefficient of determination of 0.99.

Annual estimates of virile crayfish density, made by weighting station-specific densities by

the proportion of available habitat types within the study area, were $6.4/\text{m}^2$ in 2005 and $9.3/\text{m}^2$ in 2006 (Table 3). These annual estimates provided a riverwide density of virile crayfish in the middle Yampa River during the mid-2000s of $7.9/\text{m}^2$. Annual mean CLs of virile crayfish for each station, also weighted by habitat types, and their corresponding masses were 17.3 mm and 1.4 g in 2005, and 18.5 mm and 1.7 g in 2006 (Table 3). These mean annual virile crayfish densities and masses provided biomass densities of $9.0 \text{ g}/\text{m}^2$ and $15.8 \text{ g}/\text{m}^2$ in 2005 and 2006, respectively, and a riverwide biomass for virile crayfish of 122 kg/ha. Non-crayfish macro-invertebrate biomass estimated from literature data for regional streams and rivers and used as a surrogate for the middle Yampa River, was 28.5 kg/ha. A corresponding estimate of fish biomass in the middle Yampa River in the early 2000s was 92.2 kg/ha.

Discussion

Crayfish densities

Station-specific densities of virile crayfish at the three sampling locations of the middle Yampa River ($3.6\text{--}22.1/\text{m}^2$) were similar to those of other single-species crayfish densities in lotic habitats in North America (Momot et al. 1978, $2.0\text{--}33/\text{m}^2$, including common crayfish [*Cambarus bartonii* (Fabricius, 1798)], big water crayfish [*C. robustus* (Girard, 1852)], papershell crayfish [*O. immunis* (Hagen, 1870)], water nymph crayfish [*O. nais* (Faxon, 1885)], northern clearwater crayfish [*O. propinquus* (Girard, 1852)], virile crayfish, rusty crayfish [*O. rusticus* (Girard 1852)], and unidentified species; DiStefano 1993, $0.4\text{--}21.5/\text{m}^2$, including Kentucky crayfish [*O. kentuckiensis* (Rhoades, 1944)], golden crayfish [*O. luteus* (Creaser, 1933)], water nymph crayfish, gap ringed crayfish [*O. neglectus chaenodactylus* (Williams, 1952)], northern clearwater crayfish, spothanded crayfish [*O. punctimanus* (Creaser, 1933)], Sanborn's crayfish [*O. sanborni sanborni* (Faxon, 1884)], and virile crayfish; Nystrom 2002, $0.18\text{--}60/\text{m}^2$, including common crayfish, northern clearwater crayfish, rusty crayfish, Shasta crayfish [*Pacifastacus fortis* (Faxon, 1914)], signal crayfish [*P. leniusculus* (Dana, 1852)], and red swamp crayfish [*Procambarus clarkii* (Girard, 1852)]). Virile crayfish in lotic habitats are most abundant in gravel to cobble-

Table 3 Weighted densities for virile crayfish in the middle Yampa River which were derived by weighting station-specific densities (Table 2) by the proportion of the primary habitat represented at each station (Juniper Springs, run, 68%; Morgan Gulch, pool, 26%; and Milk Creek, riffle-rapid, 6%; Anderson and Stewart 2007) and summed to provide annual estimates of virile crayfish density in 2005 and 2006. Station-specific mean carapace lengths in mm (CL; standard error in parentheses) were similarly weighted and summed to provide weighted mean annual CLs for virile crayfish in 2005 and 2006.

Station	Weighted densities (crayfish/m ²)	Mean CL in
		mm (SE)
	2005	
Juniper Springs	2.4	18.2 (0.90)
Morgan Gulch	2.7	15.1 (0.36)
Milk Creek	1.3	16.5 (0.53)
Weighted mean	6.4	17.3
	2006	
Juniper Springs	6.5	18.6 (0.56)
Morgan Gulch	2.0	17.7 (0.53)
Milk Creek	0.8	21.0 (0.42)
Weighted mean	9.3	18.5

sized substrates (Bovbjerg 1970; Daniels 1980; Mitchell and Smock 1991), which are common in the middle Yampa River, but they are tolerant of fine sediments (50–100% embeddedness; Clark and Lester 2005).

The use of quadrats of varying configurations and various methods to dislodge crayfish is considered to be an effective method for estimating lotic crayfish densities (DiStefano 1993; Roell and Orth 1992; Larson et al. 2008). The method used in this investigation combined quadrats and hand picking, and appeared readily adaptable (due to its portability) to wadeable and even remote reaches of many smaller rivers or streams (< 10 m³/s; ~ 1 m deep) that flow clear during late summer. The similarity in the percentage of counted crayfish that were missed in both years suggests that this quadrat method merits further application and refinement. Flight by some crayfish would be expected when positioning any quadrat sampler on the substrate, regardless of its configuration, but water clarity aids in accounting for this escapement. High variability in crayfish counts among individual quadrats in lotic habitats is common due to clustered distributions, contributing to often high CVs and broad CIs for estimated mean densities (Rabeni et al. 1997; DiStefano et al. 2003; Larson et al. 2008). However, CVs for station density estimates in this study (19–43) were comparable to those reported in similar investigations (DiStefano et al. 2003; Larson et al. 2008).

Potential food web impacts of virile crayfish in the Yampa River

In the middle Yampa River in the mid-2000s, the riverwide density of virile crayfish, 7.9/m², represented a biomass (122 kg/ha) that equaled the combined biomass of other macro-invertebrates and fish (120.7 kg/ha). Relatively low densities of nonnative crayfish (4/m²) can have strong community effects and this impact is intensified at high densities (8/m²; Gherardi and Acquistapace 2007). Thus, the virile crayfish densities observed in the middle Yampa River suggest that potentially severe impacts to the primary and secondary production and unfavorable alterations to the food web for native fishes have occurred within critical habitat for endangered fishes in the Yampa River. These effects would be expected to be detrimental to the native prey resources of the river's endemic apex predator, Colorado pikeminnow. Nonnative crayfish can reconfigure ecosystems they invade in several ways, which may have been overlooked or underestimated by resource managers responsible for the management of the Yampa River and its native and nonnative fishes. As large omnivores, virile crayfish have the capacity to restructure communities due to their simultaneous direct and indirect interactions at multiple trophic levels as primary and secondary consumers, and as predators (Chambers et al. 1990; Hanson et al. 1990; Dorn and Wojdak 2004; Carpenter 2005).

Virile crayfish and native fish in the middle Yampa River also appear to be experiencing apparent competition, a food-web impact that has largely been ignored in invasion biology until recently (Noonburg and Byers 2005). Apparent competition, or hyperpredation, can occur when an introduced prey animal (virile crayfish) that is preyed heavily upon by an introduced predator (smallmouth bass) gains a competitive advantage over native species (small-bodied and juvenile fishes) by increasing and sustaining predator numbers that severely reduce the abundance of the native prey (Vander Zanden et al. 2006). As a result, the introduced prey enjoys a competitive advantage over the native prey and flourishes due to behaviors better adapted to withstand the intense predation. Carter et al. (2010) showed that smallmouth bass selected fish prey over virile crayfish. Apparent competition increases the threat posed by a nonnative competitor where direct competition alone would not exclude the native consumer (Noonburg and Byers 2005; Vander Zanden et al. 2006). Hyperpredation has been described among nonnative mammals and native birds (Courchamp et al. 2000), native frogs and snakes and nonnative trout (Lawler and Pope 2006), and native fishes and nonnative lake trout [*Salvelinus namaycush* (Walbaum, 1792)] and opossum shrimp [*Mysis diluviana* (Audzijonyte and Väinölä, 2005)] (Vander Zanden et al. 2003).

Other data supports hyperpredation as a negative, synergistic outcome of the concurrent invasion by both the virile crayfish and smallmouth bass populations in the middle Yampa River. Managers hoped that smallmouth bass would show a drop in body condition or decline in abundance when the small-bodied fish assemblage, including native speckled dace, mottled sculpin, and young-of-year and juvenile life stages of non-endangered larger-bodied native fishes, declined in the early 2000s (Anderson 2002, 2005; Anderson and Stewart 2007). However, smallmouth bass relative weights remained high in 2003–2004 ($W_r = 102$; Johnson et al. 2008) and in 2007 ($W_r = 104$; John Hawkins, Colorado State University, unpublished data) indicating that body condition had not declined while population estimates of smallmouth bass declined only modestly (20%), despite intensive removal efforts (Hawkins et al. 2009). Virile crayfish dominated the biomass in the diet of smallmouth bass (52–78%) during 2003–2005 when small-bodied fish were scarce in both the river and diet of smallmouth bass

(Martinez 2006; Johnson et al. 2008). Overall, conditions in the middle Yampa River during the drought of the early 2000s proved favorable for virile crayfish with collateral food web benefits for smallmouth bass, including a trophic refuge (Garcia-Berthou 2002) for smallmouth bass as the availability of small-bodied fish declined.

Virile crayfish consumption by other nonnative predators in the middle Yampa River, channel catfish and northern pike, also increased during this period (Martinez 2006; Johnson et al. 2008). Observed levels of crayfish consumption in the 1980s and 1990s by channel catfish (~18%) and northern pike (~5%) increased to 54–82% and 19–25%, respectively, by 2003–2005 (Martinez 2006; Johnson et al. 2008). Elvira et al. (1996) reported nonnative pike thriving on nonnative crayfish after native prey fish had been eliminated. The trophic relationship between virile crayfish and nonnative predatory fishes may further entrench these species, particularly smallmouth bass, in the ecosystem of the middle and lower Yampa River rendering efforts to reduce their abundance more difficult and costly.

Drought and climate change

The three documented community shifts in the middle Yampa River during the 2000s, the increased distribution and abundance of nonnative virile crayfish and smallmouth bass and the decline in the abundance of small-bodied and juvenile native fish, coincided with a drought. Droughts are part of the normal climate pattern in the CRB, but they do not occur in cyclic fashion and they are difficult to forecast (Committee on the Scientific Bases of Colorado River Basin Water Management 2007). However, while the drought of the early 2000s will eventually be followed by wetter conditions, future droughts of varying severity are predicted to recur with increased frequency and duration (Committee on the Scientific Bases of Colorado River Basin Water Management 2007). Resulting reductions in water stores and stream flows due to climate change will likely intensify demand for remaining water supplies and may hasten proposed water development, including in the Yampa River (Northern Colorado Water Conservancy District 2006; Kinsella et al. 2008; Repanshek 2009). Long-term climate and water supply projections suggest that flow scenarios for the Yampa River will functionally mimic drought conditions, including reduced stream

discharge, smaller stream size, and an increase in summertime water temperatures (Roehm 2004; Johnson et al. 2008).

Crayfish populations appear to be highly resistant, if not positively responsive, to drought conditions (Flinders and Magoulick 2003; Light 2003; Adams and Warren 2005). It appears that even severe drought conditions would not eliminate virile crayfish from the Yampa River system; rather it may contribute to a sustained dominance by crayfish. These conditions may predispose the Yampa River to more frequent ecosystem conditions conducive to increased abundance of virile crayfish and smallmouth bass, other invaders, and associated declines in native biota. Further, the ecological effects of crayfish may be stronger in smaller, warmwater stream communities that support higher crayfish production per unit area than larger streams, possibly due to differences in channel structure and habitat availability (Roell and Orth 1992; Helms and Creed 2005). Thus, streams or mid-size rivers in the UCRB with conditions similar to the base flow-depleted middle Yampa River may be susceptible to invasion and dominance by invasive crayfish. In smaller streams, larger crayfish tend to occupy deeper water, presumably as protection against predation by terrestrial predators such as raccoons [*Procyon lotor* (Linnaeus, 1758)] and herons (e.g. [*Ardea herodias* (Linnaeus 1758)]; Butler and Stein 1985; Rabeni 1985; Creed 1994; Englund and Krupa 2000), maintaining adults that sustain reproduction.

Compared to some other crayfishes, virile crayfish experience a significant growth advantage with warming water temperatures, which may facilitate expansion of their range, abundance and ecological impact (Whitledge and Rabeni 2003; Rahel et al. 2008). Similarly, climate change, which reduces streamflow and promotes warmer water temperatures and longer growing seasons, may facilitate survival, growth, and range expansion of smallmouth bass (Shuter et al. 1980; King et al. 1999; Dunlop and Shuter 2006). Both smallmouth bass and virile crayfish were able to exploit the drought conditions in the Yampa River, increasing their abundance in explosive fashion. Maximum daily food consumption rates for both virile crayfish and smallmouth bass have been shown to increase most steeply from 18° C to 22° C (Whitledge et al. 2003; Whitledge and Rabeni 2003). This temperature range encompasses the change in mean summertime water temperature in the

Yampa River before (19.0°C) and during the drought (20.6°C). Virile crayfish become more active above 15° C (Rabeni 1992; Richards et al. 1996) and likely benefitted from the prolonged period of sustained water temperatures $\geq 16^{\circ}\text{C}$ in the middle Yampa River during the early 2000s. In addition to enhancing conditions for growth of virile crayfish and smallmouth bass, higher water temperatures during the drought also likely improved their capacity for reproduction, recruitment, and range expansion (Sharma et al. 2007; Rahel et al. 2008; Rahel and Olden 2008). Climate change could facilitate the colonization of newly or repetitively introduced species into new areas making the restoration and conservation of native aquatic species more difficult (Moyle and Mount 2007; Rahel et al. 2008).

Ongoing introductions and invasion risks

Papershell crayfish, signal crayfish, and unidentified specimens of *Orconectes* were reported in Fish Creek, a tributary in the upper Yampa River drainage, in 1980 and 1981 (Britton 1983). Water nymph crayfish, papershell crayfish, ringed crayfish [*O. neglectus* (Faxon, 1885)] now occur in the upper Yampa River basin (Sovell and Guralnick 2004; Sovell et al. 2005). The rusty crayfish was believed to be established in only one site west of the Continental Divide in Washington (Olden et al. 2009), however, rusty crayfish now occur in the upper Yampa River (Figure 1c) within and below Catamount Reservoir (Brown 2011), and in Stagecoach Reservoir (CDOW 2011). Four of the crayfish species documented in the Yampa River, papershell, ringed, rusty and virile crayfishes are considered to be highly invasive (Larson and Olden 2010, 2011; Gherardi et al. 2011).

Five decades passed following the establishment of virile crayfish in the headwaters of the Yampa River before the species became abundant downstream and it may take more time before other crayfish species reach similar densities. Virile crayfish exploited recent drought conditions in the middle Yampa River and rusty crayfish may respond similarly to climate change (Whitledge and Rabeni 2003), allowing it to become the dominant species. Virile and rusty crayfish have been described as ecological equivalents (Momot et al. 1978), displaying similar adult sizes and diets (Hill et al. 1993), but the rusty crayfish is considered to

be more aggressive and less vulnerable to fish predation (Capelli and Munjal 1982; DiDonato and Lodge 1993; Garvey et al. 1994) Regardless, any invasive crayfish species in the Yampa River would likely continue to be suitable prey for smallmouth bass. The negative synergistic scenario of virile crayfish intensifying the predatory impact of smallmouth bass in the middle Yampa River may be looming across western Colorado. Smallmouth bass and crayfish often produce stable populations that dominate other stream fauna (Probst et al. 1984; Rabeni 1992; Roell and Orth 1992). Historic and ongoing crayfish introductions coupled with smallmouth bass escapement from reservoirs, reproduction and movements in streams and illegal introductions all pose risks for an increase in the sympatry of these invasive species within critical habitat for endangered fishes or in lotic habitats suited for the conservation of non-endangered fishes (Johnson et al. 2009).

Historically, crayfish have been deemed desirable and beneficial components in the food webs of sport fisheries and they have been spread by humans throughout Colorado as prey for fish (Klein 1955; Unger 1978; Carothers 1994). Crayfish regulations among the states in the UCRB range from restrictive (no importation or possession of live crayfish allowed or live crayfish must be immediately returned to the water in which they were collected) to permissive, (importation, possession or movement prohibited only for rusty crayfish). However, definitive identification of crayfish species can be difficult in the field (DiStefano et al. 2009), making the prohibition of individual species ineffective in preventing the spread of nonnative or invasive crayfish species (Peters and Lodge 2009). Management strategies should prevent any transfers of crayfish species outside of their native ranges, including those arising from crayfish culture or used as live bait (Lorman and Magnuson 1978; Lodge et al. 2000a; 2000b; DiStefano et al. 2009), and especially from waters where crayfish invasions have occurred (Peters and Lodge 2009).

Conclusions

The presence of invasive crayfish in UCRB streams and rivers, currently mainly virile crayfish, has direct and indirect negative effects on the local native aquatic ecosystem. Direct effects include dominating the biomass of

consumers, and competition with or predation on native biota. Indirectly, crayfish may help to expand the distribution and abundance of nonnative predatory fishes, particularly invasive smallmouth bass, to the further detriment of native fishes. In the past, low flows during drought periods did not trigger overwhelming shifts in the food web of the Yampa River or other UCRB tributaries toward domination by nonnative species, likely due in large part to the absence or very low abundance of invasive species. Nonnative species whose distribution and abundance are currently constrained by habitat conditions or are believed to present a low risk of invasion or community impact may inflict detrimental effects on native species as a result of climate change (Rahel and Olden 2008).

New and repetitive introductions of nonnative species through escapement from off-stem habitats or via illegal, condoned or permissible movement by humans continues to transform the food web of the Yampa River into one dominated by nonnative species that is less likely to serve as a stronghold for native fishes. Crayfish should not be exempted from concerns about native aquatic species communities or endangered fish recovery, or the ecological and economic consequences posed by the continued introduction and spread of nonnative crayfish (Larson et al. 2010). Given the nonnative status of all crayfishes in the CRB, their invasive capacity and potential to negatively reconfigure native lotic food webs, all states in the UCRB should prohibit the importation, movement, sale, possession and stocking of any live crayfish.

Acknowledgements

This study was funded by the Colorado Division of Wildlife (CDOW) and Great Outdoors Colorado. Maria Ellis, Spring Rivers Ecological Sciences, provided insight into strategies and equipment for sampling crayfish in medium sized streams. Michael Carillo, Kellen Keisling, Ellen Hamann, and Mario Sullivan (CDOW) assisted with fabrication of sampling gear, crayfish collections, or data management. Paul Lukacs (CDOW) and Brett Johnson, Colorado State University, provided statistical assistance. An earlier version of the manuscript benefitted from comments by Anita Martinez (CDOW) and Brett Johnson. Three anonymous reviewers provided critiques and advice that improved the manuscript.

References

- Adams SB, Warren M L (2005) Recolonization by warmwater fishes and crayfishes after severe drought in upper Coastal Plain Hill streams. *Transactions of the American Fisheries Society* 134: 1173–1192, <http://dx.doi.org/10.1577/T04-089.1>
- Anderson R (2002) Riverine fish flow investigations. Colorado Division of Wildlife, Federal Aid in Fish and Wildlife Restoration, Project F–289–R5, Progress Report, 92 pp
- Anderson R (2005) Riverine fish flow investigations. Colorado Division of Wildlife, Federal Aid in Sport Fish Restoration, Project F–288–R8, Progress Report, 105 pp
- Anderson R, Stewart G (1999) Riverine fish flow investigations. Colorado Division of Wildlife, Federal Aid in Fish and Wildlife Restoration, Project F–289, Progress Report, 44 pp
- Anderson RM, Stewart G (2007) Fish-flow investigation: II. Impacts of stream flow alterations on the native fish assemblage and their habitat availability as determined by 2D modeling and the use of fish population data to support instream flow recommendations for the sections of the Yampa, Colorado, Gunnison and Dolores rivers in Colorado. Colorado Division of Wildlife, Special Report Number 80, 66 pp
- Baily C, Alberti R (1952a) Lower Yampa River and tributaries study: fish population inventory. Colorado Division of Wildlife, Federal Aid in Fish and Wildlife Restoration, Project F-3-R-1, Job Completion Report 2, 6 pp
- Baily C, Alberti R (1952b) Lower Yampa River and tributaries study: habitat type studies. Colorado Division of Wildlife, Federal Aid in Fish and Wildlife Restoration, Project F–3–R-1, Job Completion Report 3, 12 pp
- Bain MB, Finn JT, Booke HE (1985) Quantifying stream substrate for habitat analysis studies. *North American Journal of Fisheries Management* 5: 499–506, [http://dx.doi.org/10.1577/1548-8659\(1985\)5<499:QSSFHA>2.0.CO;2](http://dx.doi.org/10.1577/1548-8659(1985)5<499:QSSFHA>2.0.CO;2)
- Benke AC, Huryn AD (2007) Secondary production of macroinvertebrates. In: Hauer FR, Lamberti GA (eds) *Methods in stream ecology*. Academic Press, Burlington, Massachusetts, USA, pp 691–710
- Benke AC, Huryn AD, Smock LA, Bruce JB (1999) Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. *Journal of the North American Benthological Society* 18: 308–343, <http://dx.doi.org/10.2307/1468447>
- Bestgen KR, Walford CD, Hill AA, Hawkins JA (2007) Native fish response to removal of non-native predator fish in the Yampa River, Colorado. Colorado River Recovery Program, Project 140, Final Report. Colorado State University, Larval Fish Laboratory Contribution 150, 40 pp
- Blinn WD, Poff NL (2005) Colorado River basin. In: Benke A, Cushing C (eds) *Rivers of North America*. Elsevier Academic Press, Burlington, Massachusetts, pp 483–526, <http://dx.doi.org/10.1016/B978-012088253-3/50014-6>
- Bovbjerg RV (1970) Ecological isolation and competitive exclusion in two crayfish (*Orconectes virilis* and *Orconectes immunis*). *Ecology* 51: 225–236, <http://dx.doi.org/10.2307/1933658>
- Britton LJ (1983) Data compilation of benthic invertebrates from tributary streams of the Yampa and North Platte River basins, northwestern Colorado. U.S. Department of the Interior, U.S. Geological Survey, Open-file Report 83–140, 99 pp
- Brown E (2011) Combating invasive species: the Colorado Division of Wildlife's state invasive species program. *Colorado Water* 28(3): 13–15
- Butler MJ, Stein RA (1985) An analysis of the mechanisms governing species replacements in crayfish. *Oecologia* 66: 168–177
- Capelli GM, Munjal BJ (1982) Aggressive interactions and resource competition in relation to species displacement among crayfish of the genus *Orconectes*. *Journal of Crustacean Biology* 2: 482–492, <http://dx.doi.org/10.2307/1548090>
- Carlson CA, Muth R (1989) The Colorado River: lifeline of the American Southwest. *Canadian Special Publication of Fisheries and Aquatic Sciences* 106: 220–239
- Carlson CA, Prew itt CG, Snyder DE, Wick EJ, Ames EL, Fronk WD (1979) Fish and macroinvertebrates of the White and Yampa rivers, Colorado. U.S. Bureau of Land Management, Biological Sciences Series 1, 276 pp
- Carothers C (1994) Crayfish distribution in northwest Colorado. Colorado Division of Wildlife, 29 pp
- Carpenter J (2005) Competition for food between an introduced crayfish and two fishes endemic to the Colorado River Basin. *Environmental Biology of Fishes* 72: 335–342, <http://dx.doi.org/10.1007/s10641-004-2588-z>
- Carter MW, Shoup DE, Dettmers JM, Wahl DH (2010) Effects of turbidity and cover on prey selectivity of adult smallmouth bass. *Transactions of the American Fisheries Society* 139: 353–361, <http://dx.doi.org/10.1577/T08-159.1>
- CDOW (2011) Diligence needed to halt invasive species. Colorado Division of Wildlife, Denver, <http://dnr.state.co.us/newsapp/press.asp?PressId=7258> (Accessed August 2011)
- Chambers PA, Hanson JM, Burke JM, Prepas EE (1990) The impact of the crayfish *Orconectes virilis* on aquatic macrophytes. *Freshwater Biology* 24: 81–91, <http://dx.doi.org/10.1111/j.1365-2427.1990.tb00309.x>
- Charlebois PM, Lamberti GA (1996) Invading crayfish in a Michigan stream: direct and indirect effect on periphyton and macroinvertebrates. *Journal of the North American Benthological Society* 15: 551–563, <http://dx.doi.org/10.2307/1467806>
- Clark WH, Lester GT (2005) Range extension and ecological information for *Orconectes virilis* (Hagen 1870) (Decapoda:Cambaridae) in Idaho, USA. *Western North American Naturalist* 65: 164–169
- Courchamp F, Langlais M, Sugihara G (2000) Rabbits killing birds: modeling the hyperpredation process. *Journal of Animal Ecology* 69: 154–164, <http://dx.doi.org/10.1046/j.1365-2656.2000.00383.x>
- Crawford L, Yoemans WE, Adams CE (2006) The impact of the introduced signal crayfish *Pacifastacus leniusculus* on stream invertebrate communities. *Aquatic Conservation: Marine and Freshwater Ecosystems* 16: 611–621, <http://dx.doi.org/10.1002/aqc.761>
- Creed RP (1994) Direct and indirect effects of crayfish grazing in a stream community. *Ecology* 75: 2091–2103, <http://dx.doi.org/10.2307/1941613>
- Committee on the Scientific Bases of Colorado River Basin Water Management (2007) Colorado River Basin water management: evaluating and adjusting to hydroclimatic variability. The National Academies Press, Washington, D. C., 210 pp
- Cruz MJ, Rebelo R, Crespo EG (2006) Effects of an introduced crayfish, *Procambarus clarkii*, on the distribution of southwestern Iberian amphibians in their breeding habitats. *Ecography* 29: 329–338, <http://dx.doi.org/10.1111/j.2006.0906-7590.04333.x>
- Daniels RA (1980) Distribution and status of crayfishes in the Pit River drainage, California. *Crustaceana* 38: 131–138, <http://dx.doi.org/10.1163/156854080X00562>
- DiDonato GT, Lodge DM (1993) Species replacements among *Orconectes* crayfishes in Wisconsin lakes: the role of predation by fish. *Canadian Journal of Fisheries and Aquatic Sciences* 50: 1484–1488, <http://dx.doi.org/10.1139/f93-169>
- DiStefano RJ (1993) Ecology of stream-dwelling crayfish populations: a literature review. Missouri Department of Conservation, Federal Aid in Sport Fish Restoration, Project F–1–R–42, Final Report, 42 pp

- DiStefano RJ, Gale CM, Wagner BA, Zweifel RD (2003) A sampling method to assess lotic crayfish communities. *Journal of Crustacean Biology* 23: 678–690, <http://dx.doi.org/10.1651/C-2364>
- DiStefano RJ, Litvan ME, Horner PT (2009) The bait industry as a potential vector for alien crayfish introductions: problem recognition by fisheries agencies and a Missouri evaluation. *Fisheries* 34(12): 586–597, <http://dx.doi.org/10.1577/1548-8446-34.12.586>
- Dorn NJ, Wojdak JM (2004) The role of omnivorous crayfish in littoral communities. *Oecologia* 140: 150–159, <http://dx.doi.org/10.1007/s00442-004-1548-9>
- Dunlop ES, Shuter BJ (2006) Native and introduced populations of smallmouth bass differ in concordance between climate and somatic growth. *Transactions of the American Fisheries Society* 135: 1175–1190, <http://dx.doi.org/10.1577/T05-218.1>
- Elser JJ, Junge C, Goldman CR (1994) Population structure and ecological effects of the crayfish *Pacifastacus leniusculus* in Castle Lake, California. *Great Basin Naturalist* 54: 162–169
- Elvira B, Nicola GG, Almodovar A (1996) Pike and red swamp crayfish: a new case on predator-prey relationship between aliens in central Spain. *Journal of Fish Biology* 48: 437–446
- Englund G, Krupa JJ (2000) Habitat use by crayfish in stream pools: influence of predators, depth and body size. *Freshwater Biology* 43: 75–83, <http://dx.doi.org/10.1046/j.1365-2427.2000.00524.x>
- Flinders CA, Magoulick DD (2003) Effects of stream permanence on crayfish community structure. *American Midland Naturalist* 149: 134–147, [http://dx.doi.org/10.1674/0003-0031\(2003\)149\[0134:EOSPOC\]2.0.CO;2](http://dx.doi.org/10.1674/0003-0031(2003)149[0134:EOSPOC]2.0.CO;2)
- Fuller M (2009) Lower Yampa River channel catfish and smallmouth bass control program, Colorado, 2001–2006. U. S. Fish and Wildlife Service, Colorado River Recovery Program, Project 110, Synthesis Report, 32 pp
- Garcia-Berthou E (2002) Ontogenetic diet shifts and interrupted piscivory in introduced largemouth bass (*Micropterus salmoides*). *Internationale Revue der Gesamten Hydrobiologie* 87: 353–363
- Garvey JE, Stein RA, Thomas HM (1994) Assessing how fish predation and interspecific prey competition influence a crayfish assemblage. *Ecology* 75: 532–547, <http://dx.doi.org/10.2307/1939556>
- Gherardi F, Acquistapace P (2007) Invasive crayfish in Europe: the impact of *Procambarus clarkii* on the littoral community of a Mediterranean lake. *Freshwater Biology* 52: 1249–1259, <http://dx.doi.org/10.1111/j.1365-2427.2007.01760.x>
- Gherardi F, Aquiloni L, Dieguez-Uribeondo J, Tricarico (2011) Managing invasive crayfish: is there hope? *Aquatic Sciences* 73: 185–200, <http://dx.doi.org/10.1007/s00027-011-0181-z>
- Guan R, Wiles PR (1997) Ecological impact of introduced crayfish on benthic fishes in a British lowland river. *Conservation Biology* 11: 641–647, <http://dx.doi.org/10.1046/j.1523-1739.1997.96073.x>
- Haden GA, Blinn DW, Shannon JP (1999) Driftwood: an alternative habitat for macroinvertebrates in a large southwestern river. *Hydrobiologia* 397: 179–186, <http://dx.doi.org/10.1023/A:1003778222809>
- Haden G A, Shannon JP, Wilson KP, Blinn DW (2003) Benthic community structure of the Green and Colorado rivers through Canyonlands National Park, Utah, USA. *Southwestern Naturalist* 48: 23–35, [http://dx.doi.org/10.1894/0038-4909\(2003\)048<0023:BCSOTG>2.0.CO;2](http://dx.doi.org/10.1894/0038-4909(2003)048<0023:BCSOTG>2.0.CO;2)
- Hanson JM, Chambers PA, Prepas EE (1990) Selective foraging by the crayfish *Orconectes virilis* and its impacts on macroinvertebrates. *Freshwater Biology* 24: 69–80, <http://dx.doi.org/10.1111/j.1365-2427.1990.tb00308.x>
- Hawkins J, Walford C, Hill A (2009) Smallmouth bass control in the middle Yampa River, 2003–2007. Colorado River Recovery Program, Project 125. Colorado State University, Larval Fish Laboratory Contribution 154, Final Report, 53 pp
- Hawkins J, Walford C, Sorensen T (2005) Northern pike management studies in the Yampa River, Colorado, 1999–2002. Colorado River Recovery Program, Project 98a. Colorado State University, Larval Fish Laboratory Contribution 137, 56 pp
- Helms BS, Creed RP (2005) The effects of 2 coexisting crayfish on an Appalachian river community. *Journal of the North American Benthological Society* 24: 113–122, [http://dx.doi.org/10.1899/0887-3593\(2005\)024<0113:TEOCCO>2.0.CO;2](http://dx.doi.org/10.1899/0887-3593(2005)024<0113:TEOCCO>2.0.CO;2)
- Hill AM, Sinars DM, Lodge DM (1993) Invasion of an occupied niche by the crayfish *Orconectes rusticus*: potential importance of growth and mortality. *Oecologia* 94: 303–306, <http://dx.doi.org/10.1007/BF00317102>
- Hobbs HH (1989) An illustrated checklist of the American crayfishes (Decapoda: Astacidae, Cambaridae, and Parastacidae). Smithsonian Contribution to Zoology Number 480, Smithsonian Institution Press, Washington D. C., 236 pp
- Holden PB, Stalnaker CB (1975) Distribution of fishes in the Dolores and Yampa River systems of the upper Colorado River basin. *Copeia* 1970: 403–412
- Holdich DM (2002) Background and functional morphology. In: Holdich DM (ed) Biology of freshwater crayfish, Blackwell Science, Oxford, UK, pp 3–29
- Hubert WA (1988) Survey of Wyoming crayfishes. *Great Basin Naturalist* 48: 370–373
- Ilheu M, Bernardo JM, Fernandes S (2007) Predation of invasive crayfish on aquatic vertebrates: the effect of *Procambarus clarkii* on fish assemblages in Mediterranean temporary streams. In: Gherardi F (ed) Biological invaders in inland waters: profiles, distribution, and threats. Springer, Dordrecht, Netherlands, pp 543–558, http://dx.doi.org/10.1007/978-1-4020-6029-8_29
- Inman TC, Marsh PC, Bagley BE, Pacey CA (1998) Survey of crayfishes of the Gila River basin, Arizona and New Mexico, with notes on occurrences in other Arizona drainages and adjoining states. U. S. Department of the Interior, Bureau of Reclamation, Project 5–FG–32–00470, 22 pp
- Johnson BM, Arlinghaus R, Martinez PJ (2009) Are we doing all we can to stem the tide of illegal fish stocking? *Fisheries* 34(8): 389–394, <http://dx.doi.org/10.1577/1548-8446-34.8.389>
- Johnson BM, Martinez PJ, Hawkins JA, Bestgen KR (2008) Ranking predatory threats by nonnative fishes in the Yampa River, Colorado, via bioenergetics modeling. *North American Journal of Fisheries Management* 28: 1941–1953, <http://dx.doi.org/10.1577/M07-199.1>
- Johnson JE (1986) Inventory of Utah crayfish with notes on current distribution. *Great Basin Naturalist* 46: 625–631
- Kats LB, Ferrer RP (2003) Alien predators and amphibian declines: review of two decades of science and the transition to conservation. *Diversity and Distributions* 9: 99–110, <http://dx.doi.org/10.1046/j.1472-4642.2003.00013.x>
- Kerby JL, Riley SPD, Kats LB, Wilson P (2005) Barriers and flow as limiting factors in the spread of an invasive crayfish (*Procambarus clarkii*) in southern California streams. *Biological Conservation* 126: 402–409, <http://dx.doi.org/10.1016/j.biocon.2005.06.020>
- King JR, Shuter BJ, Zimmerman AP (1999) Empirical links between thermal habitat, fish growth, and climate change. *Transactions of the American Fisheries Society* 128: 656–665, [http://dx.doi.org/10.1577/1548-8659\(1999\)128<0656:ELBTHF>2.0.CO;2](http://dx.doi.org/10.1577/1548-8659(1999)128<0656:ELBTHF>2.0.CO;2)
- Kinsella S, Spencer T, Farling B (2008) Trout in trouble: the impacts of global warming on trout in the interior west. Natural Resources Defense Council, New York, New York, 34 pp
- Klein WD (1955) Crayfish introductions. Colorado Division of Wildlife, Special Purpose Report No. 23, 4 pp

- Larson ER, Busack CA, Anderson JD, Olden JD (2010) Widespread distribution of the non-native crayfish (*Orconectes virilis*) in the Columbia River Basin. *Northwest Science* 84: 108–111, <http://dx.doi.org/10.3955/046.084.0112>
- Larson ER, DiStefano RJ, Magoulick DD, Westhoff JT (2008) Efficiency of a quadrat sampling technique for estimating riffle-dwelling crayfish density. *North American Journal of Fisheries Management* 28: 1036–1043, <http://dx.doi.org/10.1577/M07-029.1>
- Larson ER, Olden JD (2010) Latent extinction risk of crayfishes in the southeastern United States. *Conservation Biology* 24: 1099–1110, <http://dx.doi.org/10.1111/j.1523-1739.2010.01462.x>
- Larson ER, Olden JD (2011) The state of crayfish in the Pacific Northwest. *Fisheries* 36: 60–73, <http://dx.doi.org/10.1577/03632415.2011.10389069>
- Lawler SP, Pope KL (2006) Non-native fish in mountain lakes: effects on a declining amphibian and ecosystem subsidy. University of California Water Resources Center, Technical Completion Report 987, 22 pp
- Light T (2003) Success and failure in a lotic crayfish invasion: the roles of hydrologic variability and habitat alteration. *Freshwater Biology* 48: 1886–1897, <http://dx.doi.org/10.1046/j.1365-2427.2003.01122.x>
- Light T (2005) Behavioral effects of invaders: alien crayfish and native sculpin in a California stream. *Biological Invasions* 7: 353–367, <http://dx.doi.org/10.1007/s10530-004-2510-9>
- Lodge DM, Taylor CA, Holdich DM, Skurdal J (2000a) Nonindigenous crayfishes threaten North American freshwater biodiversity: lessons from Europe. *Fisheries* 25: 7–20, [http://dx.doi.org/10.1577/1548-8446\(2000\)025<0007:NCTNA F>2.0.CO;2](http://dx.doi.org/10.1577/1548-8446(2000)025<0007:NCTNA F>2.0.CO;2)
- Lodge DM, Taylor CA, Holdich DM, Skurdal J (2000b) Reducing impacts of exotic crayfish introductions: new policies needed. *Fisheries* 25:21–23
- Lorman JG, Magnuson JJ (1978) The role of crayfish in aquatic ecosystems. *Fisheries* 3(6):8–19
- Loughman ZJ (2010) Crayfishes of western Maryland: conservation and natural history. *Southeastern Naturalist* 9: 33–62, <http://dx.doi.org/10.1656/058.009.s303>
- Martinez PJ (2003) Westslope warmwater fisheries. Colorado Division of Wildlife, Federal Aid in Sport Fish Restoration, Progress Report, 106 pp
- Martinez PJ (2006) Westslope warmwater fisheries. Colorado Division of Wildlife, Great Outdoors Colorado, Progress Report, 123 pp
- McAda CW, Bates JW, Cranney JS, Chart TE, Elmsblad WR, Nesler TP (1994) Interagency standardized monitoring program: summary of results, 1986–1992. U.S. Fish and Wildlife Service, Colorado River Recovery Program, Final Report, 73 pp
- McCarthy JM, Hein CL, Olden JD, Vander Zanden MJ (2006) Coupling long-term studies with meta-analysis to investigate impacts of non-native crayfish on zoobenthic communities. *Freshwater Biology* 51: 224–235, <http://dx.doi.org/10.1111/j.1365-2427.2005.01485.x>
- Mead KS (2008) Do antennule and aesthetasc structure in the crayfish *Orconectes virilis* correlate with flow habitat? *Integrative and Comparative Biology* 48: 823–833, <http://dx.doi.org/10.1093/icb/01067>
- Miller WH, Archer DA, Tyus HM, McNatt RM (1982) Yampa River fishes study. U.S. Fish and Wildlife Service, Final Report, 78 pp
- Mitchell DJ, Smock LA (1991) Distribution, life history and production of crayfish in the James River, Virginia. *American Midland Naturalist* 126: 353–363, <http://dx.doi.org/10.2307/2426111>
- Modde T, Miller WJ, Anderson R (1999) Determination of habitat availability, habitat use, and flow needs of endangered fishes in the Yampa River between August and October. U.S. Fish and Wildlife Service, Colorado River Recovery Program, Project CAP–9, Final Report, 128 pp
- Momot WT (1995) Redefining the role of crayfish in aquatic ecosystems. *Reviews in Fisheries Science* 3: 33–63, <http://dx.doi.org/10.1080/10641269509388566>
- Momot WT, Gowing H, Jones PD (1978) The dynamics of crayfish and their role in ecosystems. *American Midland Naturalist* 99: 10–35, <http://dx.doi.org/10.2307/2424930>
- Moyle PB, Mount JF (2007) Homogenous rivers, homogenous faunas. *Proceedings of the National Academy of Science USA* 104: 5711–5712, <http://dx.doi.org/10.1073/pnas.0701457104>
- Nesler TP (1995) Interactions between endangered fishes and introduced gamefishes in the Yampa River, Colorado, 1987–1991. Colorado Division of Wildlife, Federal Aid in Sport Fish Restoration, Projects SE-3 and 91–29, Final Report, 184 pp
- Northern Colorado Water Conservancy District (2006) Multi-basin water supply investigation executive summary, 24 pp
- Noonburg EG, Byers JE (2005) More harm than good: when invader vulnerability to predators enhances impact on native species. *Ecology* 86: 2555–2560, <http://dx.doi.org/10.1890/05-0143>
- Nystrom P (2002) Ecology. In: Holdich DM (ed) *Biology of freshwater crayfish*, Blackwell Science, Oxford, UK, pp 192–235
- Nystrom P, Strand JA (1996) Grazing by a native and an exotic crayfish on aquatic macrophytes. *Freshwater Biology* 36: 673–682, <http://dx.doi.org/10.1046/j.1365-2427.1996.d01-508.x>
- Oberlin GE, Shannon JF, Blinn DW (1999) Watershed influence on the macroinvertebrate fauna of ten major tributaries of the Colorado River through Grand Canyon, Arizona. *Southwestern Naturalist* 44: 17–30
- Olden JD, Adams JW, Larson ER (2009) First record of *Orconectes rusticus* (Girard, 1852) (Decapoda, Cambaridae) west of the Great Continental Divide in North America. *Crustaceana* 82: 1347–1351, <http://dx.doi.org/10.1163/156854009X448934>
- Pennak RW (1989) Fresh-water invertebrates of the United States: protozoa to mollusca. John Wiley and Sons, Inc., New York
- Peters JA, Lodge DM (2009) Invasive species policy at the regional level: a multiple weak links problem. *Fisheries* 34(8): 373–381, <http://dx.doi.org/10.1577/1548-8446-34.8.373>
- Phillips ID, Vinebrooke RD, Turner MA (2009) Ecosystem consequences of potential range expansions of *Orconectes virilis* and *Orconectes rusticus* crayfish in Canada - a review. *Environmental Reviews* 17: 235–248, <http://dx.doi.org/10.1139/A09-011>
- Probst WE, Rabeni CF, Covington WG, Marteney RE (1984) Resource use by stream-dwelling rock bass and smallmouth bass. *Transactions of the American Fisheries Society* 113: 283–294, [http://dx.doi.org/10.1577/1548-8659\(1984\)113<283:RUBSR B>2.0.CO;2](http://dx.doi.org/10.1577/1548-8659(1984)113<283:RUBSR B>2.0.CO;2)
- Rabeni CF (1985) Resource partitioning by stream-dwelling crayfish: the influence of body size. *American Midland Naturalist* 113: 20–29, <http://dx.doi.org/10.2307/2425344>
- Rabeni CF (1992) Trophic linkage between stream centrarchids and their crayfish prey. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 1714–1721, <http://dx.doi.org/10.1139/f92-190>
- Rabeni CR, Collier KJ, Parkyn SM, Hicks BJ (1997) Evaluating techniques for sampling stream crayfish (*Parenephrops planifrons*). *New Zealand Journal of Marine and Freshwater Research* 31: 393–700, <http://dx.doi.org/10.1080/00288330.1997.9516799>

- Rahel FJ, Bierwagen B, Taniguchi Y (2008) Managing aquatic species of conservation concern in the face of climate change and invasive species. *Conservation Biology* 22: 551–561, <http://dx.doi.org/10.1111/j.1523-1739.2008.00953.x>
- Rahel FJ, Olden JD (2008) Assessing the effects of climate change on aquatic invasive species. *Conservation Biology* 22: 521–533, <http://dx.doi.org/10.1111/j.1523-1739.2008.00950.x>
- Repanshek K (2009) Yampa River, lifeblood to Dinosaur National Monument, eyed for water diversions. National Park Traveler, <http://www.nationalparkstraveler.com/2009/04/yampa-river-lifeblood-dinosaur-national-monument-eyed-oil-shale-diversions> (Accessed May 2010)
- Richards C, Kutka FJ, McDonald ME, Merrick GW, Devore PW (1996) Life history and temperature effects on catch of northern orconectid crayfish. *Hydrobiologia* 319: 111–118, <http://dx.doi.org/10.1007/BF00016879>
- Roehm GW (2004) Management plan for endangered fishes in the Yampa River Basin and environmental assessment. U.S. Fish and Wildlife Service, Region (6), 194 pp, <http://dx.doi.org/10.1007/BF00006585>
- Roell MJ, Orth DJ (1992) Production of three crayfish populations in the New River of West Virginia, USA. *Hydrobiologia* 228: 185–194, <http://dx.doi.org/10.1007/BF00006585>
- Sharma S, Jackson DA, Minns CK, Shuter BJ (2007) Will northern fish populations be in hot water because of climate change? *Global Change Biology* 13: 2052–2064, <http://dx.doi.org/10.1111/j.1365-2486.2007.01426.x>
- Shuter BJ, MacLean JA, Fry FEJ, Regier HA (1980) Stochastic simulation of temperature effects on first year survival of smallmouth bass. *Transactions of the American Fisheries Society* 109: 1–34, [http://dx.doi.org/10.1577/1548-8659\(1980\)109<1:SSOTEO>2.0.CO;2](http://dx.doi.org/10.1577/1548-8659(1980)109<1:SSOTEO>2.0.CO;2)
- Sovell JR, Guralnick R (2004) Montane mollusk and crustacean survey of western Colorado. Colorado State University, Colorado Natural Heritage Program, Annual Report, 16 pp
- Sovell JR, Guralnick R, Rogers DC (2005) Montane mollusk and crustacean survey of western Colorado. Colorado State University, Colorado Natural Heritage Program, 65 pp
- Stewart G, Anderson R, Wohl E (2005) Two-dimensional modeling of habitat suitability as a function of discharge on two Colorado rivers. *River Research and Applications* 21: 1061–1074, <http://dx.doi.org/10.1002/rra.868>
- Taylor CA, Schuster GA, Cooper JE, DiStefano RJ, Eversole AG, Hamr P, Hobbs HH, Robison HW, Skelton CE, Thoma RF (2007) A reassessment of the conservation status of crayfishes of the United States and Canada after 10+ years of increased awareness. *Fisheries* 32(8): 372–389, [http://dx.doi.org/10.1577/1548-8446\(2007\)32\[372:AROTCS\]2.0.CO;2](http://dx.doi.org/10.1577/1548-8446(2007)32[372:AROTCS]2.0.CO;2)
- Tierny AJ, Atema J (1988) Behavioral responses of crayfish (*Orconectes virilis* and *Orconectes rusticus*) to chemical feeding stimulants. *Journal of Chemical Ecology* 14:123–133, <http://dx.doi.org/10.1007/BF01022536>
- Tyus HM, Beard JM (1990) *Esox lucius* (Esocidae) and *Stizostedion vitreum* (Percidae) in the Green River basin, Colorado and Utah. *Great Basin Naturalist* 50: 33–39
- Tyus HM, Nikirk NJ (1988) Abundance, growth, and diet of channel catfish, *Ictalurus punctatus*, in the Green and Yampa rivers, Colorado and Utah. *Southwestern Naturalist* 35:188–198, <http://dx.doi.org/10.2307/3671541>
- Tyus HM, Saunders JF (2001) An evaluation of the role of tributary streams for the recovery of endangered fishes in the upper Colorado River basin, with recommendations for future recovery actions. University of Colorado Center for Limnology Final report to the Colorado River Recovery Program, 121 pp
- Unger PA (1978) The crayfishes (Crustacea: Cambaridae) of Colorado. Natural History Inventory of Colorado, No. 3. University of Colorado Museum, Boulder, 20 pp
- U.S. Geological Survey (2009a) USGS 09251000 Yampa River near Maybell, Colorado. Calendar year streamflow statistics for the nation. http://nwis.waterdata.usgs.gov/nwis/peak?site_no=09251000&agency_cd=USGS&format=html (Accessed July 2009)
- U.S. Geological Survey (2009b) USGS 09251000 Yampa River near Maybell, Colorado. Surface–water annual statistics for the nation. http://waterdata.usgs.gov/nwis/annual?referred_module=sw&search_site_no=09251000&format=sites_selection_links (Accessed July 2009)
- Usio N, Susuki K, Konishi M, Nakano S (2006) Alien vs. endemic crayfish: roles of species identity in ecosystem functioning. *Archiv fur Hydrobiologie* 166: 1–21, <http://dx.doi.org/10.1127/0003-9136/2006/0166-0001>
- Valdez RA, Muth RT (2005) Ecology and conservation of native fishes in the upper Colorado River Basin. *American Fisheries Society Symposium* 45:157–204
- Vander Zanden, MJ, Chandra S, Allen BC, Reuter JE, Goldman CR (2003) Historical food web structure and restoration of native aquatic communities in the Lake Tahoe (California-Nevada) basin. *Ecosystems* 6: 274–288, <http://dx.doi.org/10.1007/s10021-002-0204-7>
- Vander Zanden MJ, Olden JD, Gratton C (2006) Food-web approaches in restoration ecology. In: Falk DA, Palmer MA, Zedler JB (eds) Foundations of restoration ecology, Island Press, Washington, D. C., pp 165–189
- Van Streeter MM, Pitlick J (1998) Geomorphology and endangered fish habitats of the upper Colorado River: historic changes in streamflow, sediment load and channel morphology. *Water Resources Research* 34: 287–302, <http://dx.doi.org/10.1029/97WR02766>
- Waters TF (1977) Secondary production in inland waters. In: MacFayden (ed) Advances in ecological research, Academic Press, New York, pp 91–151
- Wetzel RG, Likens GE (2000) Limnological analyses. Third edition. Springer Science, New York, 429 pp
- Whitledge GW, Hayward RS, Zweifel RD, Rabeni CF (2003) Development and laboratory evaluation of a bioenergetics model for subadult and adult smallmouth bass. *Transactions of the American Fisheries Society* 132: 316–325, [http://dx.doi.org/10.1577/1548-8659\(2003\)132<0316:DALEOA>2.0.CO;2](http://dx.doi.org/10.1577/1548-8659(2003)132<0316:DALEOA>2.0.CO;2)
- Whitledge GW, Rabeni CF (1997) Energy sources and ecological role of crayfishes in an Ozark stream: insights from stable isotope and gut analyses. *Canadian Journal of Fisheries and Aquatic Sciences* 54: 2555–2563, <http://dx.doi.org/10.1139/cjfas-54-11-2555>
- Whitledge GW, Rabeni CF (2003) Maximum daily consumption and respiration rates at four temperatures for five species of crayfish from Missouri, U.S.A. (Decapoda, *Orconectes* spp.). *Crustaceana* 75: 1119–1132, <http://dx.doi.org/10.1163/156854002763270518>
- Wick EJ, Hawkins JA, Carlson CA (1985) Colorado squawfish and humpback chub population and habitat monitoring: 1981–1982. Colorado Division of Wildlife, Endangered Fish Investigation SE 3–6, Progress Report, 108 pp
- Wiltzius WJ (1985) Fish culture and stocking in Colorado, 1872–1978. Colorado Division of Wildlife, Report No. 12, 102 pp