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REVIEW PAPER

Towards a cohesive strategy for the conservation of the United States' diverse and highly endemic crayfish fauna

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Abstract Freshwater biodiversity of the United States has long been recognized for its high level of species richness. The US crayfish fauna is richer than that found in any other country or continent in the world. Crayfishes are critically important members of freshwater ecosystems and have long been utilized for human consumption. Combined, these factors argue for effective conservation. When compared to other diverse aquatic groups such as fishes or unionid mussels, conservation efforts for US crayfishes are lacking. We review here, knowledge gaps that prevent effective conservation and past and ongoing crayfish conservation and management activities. We conclude by proposing a strategy of actions to improve the conservation standing of this important group of organisms. These action items include improved outreach efforts, funding and research to fill numerous knowledge gaps, and the inclusion of crayfishes in broader scale aquatic conservation activities.

Keywords Aquatic · Review · Knowledge gaps · Management actions · Action items

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Introduction

The United States (US) is home to the richest crayfish fauna in the world with 394 species and subspecies. The number of described species in the US grows annually and currently represents over 65% of the world's crayfish fauna (Crandall & De Grave, 2017). Crayfishes are found natively in most aquatic and semi-aquatic habitat types across the continental US except for the Colorado River drainage of the Pacific Ocean and southern California. A small number of US species are cultured and harvested and form the basis of regionally important commercial markets recently valued at approximately $172 million (https://www.dfw.state.or.us/fish/commercial/landing_stats/2017/index.asp, R. Romaire, Louisiana State University, pers. com.). However, the ecological value of crayfishes to aquatic ecosystems is also noteworthy and often under-appreciated.

Crayfishes are critical components of aquatic ecosystems. Studies suggest that crayfishes can compose dominant amounts of invertebrate biomass in streams (Momot, 1995; Haggerty et al., 2002) and influence multiple aspects of ecosystem structure and function. They increase species richness (Jones et al., 1994, 1997) and influence detrital decomposition rates and nutrient cycling (Huryn & Wallace, 1987; Rabeni et al., 1995; Usio, 2000), the bioturbation of fine organic and inorganic sediments (Statzner et al., 2000; Dorn & Wojdak, 2004), and the modification of interstitial matrices within streambed substrates (Johnson et al., 2010; 2011). Burrowing crayfish species provide habitat (Fig. 1) for many invertebrates (Williams et al., 1974; Glon & Thoma, 2017) and vertebrates (Irwin et al., 1999; Loughman, 2010; Heemeyer et al., 2012), including endangered species (Pintor & Soluk, 2006). Crayfishes also occupy an important intermediate trophic position between other invertebrate consumers and fishes, serving as both consumers and prey items. They are known to consume larval insects (Parkyn et al., 2001), fishes (Rahel & Stein, 1988), and snails (Crowl & Covich, 1990), and often affect primary production by consuming filamentous algae (Creed, 1994) and aquatic macrophytes (Nyström & Strand, 1996). Crayfishes are an important food source for many recreationally and economically important centrarchid fishes (Keast, 1985; Momot et al., 1978; Wheeler & Allen, 2003; Roell & DiStefano, 2010). The importance of crayfish as prey items extends beyond aquatic ecosystems as DiStefano (2005) reported 98 terrestrial vertebrates known to consume crayfishes.

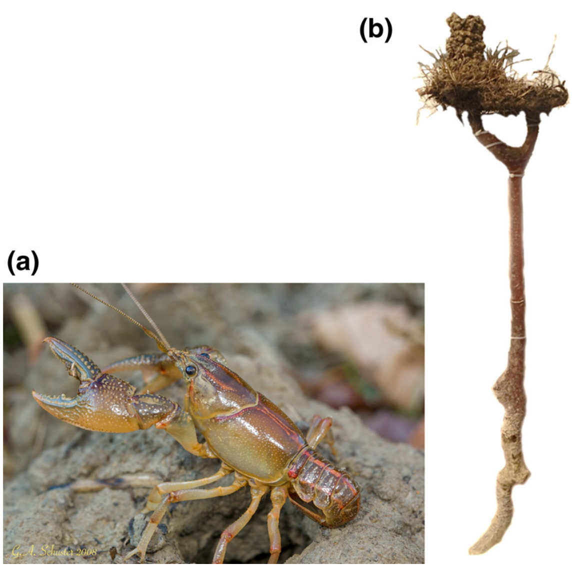

Fig. 1 Burrowing crayfish (**a**) can have highly specialized preferences for soil types and hydroperiods and construct simple to elaborate burrows (**b**) that benefit other taxa including amphibians, reptiles, and invertebrates Image of *Lacunicambarus ludovicianus* courtesy of G. A. Schuster (**a**) and resin cast of crayfish chimney and burrow by J. A. Stoeckel (**b**)

Given its high-species richness, the US crayfish fauna is globally unique. However, it is also recognized for its tenuous conservation position. Master (1990) used data from state natural heritage agencies to first draw attention to US crayfishes. He ranked them second only to unionid mussels in level of imperilment for aquatic taxa in North America. Targeted conservation reviews of US and Canadian crayfishes by Taylor et al. (1996, 2007) found nearly 50% of all US species at some level of conservation concern due to several factors. Richman et al. (2015) more recently reviewed global crayfish extinction risk using International Union for Conservation of Nature (IUCN) criteria. Using the same IUCN criteria, we find that 22.5% of US species meet the definition of Threatened or higher conservation concern categories. Yet, there is a vast disparity in the number of US crayfish species recognized as in need of protection by the federal government and by researchers focusing on crayfish conservation and ecology (Taylor et al., 1996). Until recently, only four species were afforded protection under the Endangered Species Act (ESA). The disparity was negligibly reduced with the 2016 listing of the Big Sandy Crayfish (*Cambarus callainus* Thoma, Loughman, Fetzner 2014) and Guyandotte River Crayfish (*C. veteranus* Faxon 1914) (Fig. 2). While factors such as habitat alteration that are known to impact other aquatic freshwater taxa (Allan & Flecker, 1993; Warren et al., 2000; DeWalt et al., 2005) are concerning, two primary factors identified for many US crayfishes are narrow native ranges and the impact of invasive crayfishes (Lodge et al., 2000; Taylor et al., 2007; Richman et al., 2015).

The conservation of taxa and ecosystems is clearly enhanced when guided by a sound and vetted strategy. Like crayfishes, unionid mussels and freshwater fishes have high levels of species richness and imperilment in the US. Unionid mussels have long experienced dramatic declines from overharvesting, pollution, habitat alteration, and the introduction of invasive species (Williams et al., 1993) and their level of

Fig. 2 Until recently, only four US species received protection under the Endangered Species Act. In 2016 both the Big Sandy Crayfish, *Cambarus callainus* (above), and the Guyandotte Crafish, *C. veteranus*, were listed Image courtesy of G. A. Schuster

imperilment exceeds that of crayfishes (Master, 1990; Haag & Williams, 2014). Recognizing this, mussel workers first proposed a detailed strategy to conserve the US's fauna in 1998 (NNMCC, 1998). That strategy: identified needed research, management, and conservation actions; sought to increase awareness to the plight and value of mussels; and advocated for partnerships among federal, state, tribal, and local governments (NNMCC, 1998). Armed with nearly 14 years of peer-reviewed data (reviewed in Strayer et al., 2004; Haag, 2012) and deeper understanding of threats, the effectiveness of the 1998 strategy was thoroughly assessed by Haag & Williams (2014). Subsequently, a second, revised mussel conservation strategy was published by the Freshwater Mollusk Conservation Society (FMCS, 2016).

Threats to the diverse and ecologically important US crayfish fauna have been identified (Taylor et al., 1996; Lodge et al., 2000; Richman et al., 2015), but a comprehensive strategy to conserve it has not been proposed. We believe that attention to crayfishes is increasing in the US with the two species added to the ESA in 2016, and another 34 to be reviewed under the US Fish and Wildlife Service's (USFWS) seven year National Listing Work Plan (https://www.fws.gov/endangered/esa-library/pdf/Listing%207-Year%20Workplan%20Sept%202016.pdf). When combined with conservation assessments that highlight the precarious position of crayfishes (i.e. Richman et al., 2015), these recent actions strongly support the formulation of a US strategy to guide future conservation efforts.

We propose here a strategy for conservation efforts for the US crayfish fauna. We arrive at this conservation strategy by first identifying knowledge gaps that hinder conservation efforts and offer insights on how to fill those gaps. As understanding the impacts of past actions is crucial for strategy formation, we then review ongoing or recent management actions for crayfish in response to major threats including impacts of invasive species and habitat loss or degradation. When common management actions for freshwater taxa or habitats have not been attempted for crayfish but were anticipated to be relevant, we review examples from other freshwater groups and propose avenues for research or implementation specific to crayfish. We conclude by listing specific strategy action areas. We do not conduct a thorough review of threats to crayfishes, as this has been conducted by Taylor et al. (2007) and Richman et al. (2015). We present this proposed strategy as a starting point and, as such, periodic review and revision is encouraged.

Knowledge gaps

Distribution, systematics, life history and ecology

The need for a comprehensive conservation strategy for imperiled crayfishes is amplified by the knowledge gaps facing stakeholders. These gaps span all areas of crayfish science, including distribution, evolution/taxonomy, ecology, and fisheries. Comprehensive species distribution data are among the most powerful data available for conserving imperiled aquatic fauna, because many policy and management decisions made by government agencies require current, taxon-specific range information (https://www.fws.gov/endangered/esa-library/pdf/listing.pdf; https://www.dnr.illinois.gov/ESPB/Documents/ET%20List%20Review%20and%20Revision/ESPBAuthorityToMakeChangesToTheList.pdf). Although the amount of peer-reviewed distribution information for crayfishes has increased in the past 15 years (review in Loughman & Fetzner, 2015), these efforts have been mostly restricted to the southeastern US. Crayfish biodiversity and distribution in vast regions of the central, western, and northeastern US have received only cursory efforts (Larson & Olden, 2011), been reported in the gray literature (Sheldon, 1989; Hubert,

2010) or are dated (Riegel, 1959; Crocker, 1979). A recent survey of natural resource agencies in all US states (Stratton & DiStefano, unpublished data) found that 59% of states that engage in crayfish work reported that basic information on native crayfish ranges in their jurisdictions would be most beneficial for effective crayfish conservation and management. The benefits of basic surveying for crayfishes have been demonstrated as such work has resulted in amended range estimates (Kilian et al., 2010; Taylor et al., 2011; Egly & Larson, 2018). These factors highlight the need for targeted sampling efforts in other regions of the US.

The taxonomy, and inferred evolutionary history of crayfishes in the US had, until recently, been stable. The generic and subgeneric assignment of crayfish species was traditionally based on secondary sex characteristics. However, phylogenies based on a handful of mitochondrial and nuclear DNA markers have been at odds with morphological-based taxonomy since 1996 (Crandall & De Grave, 2017). The incongruence between morphology and molecules leaves many unanswered questions about morphological convergence and species versus gene evolution in US crayfishes. Rapidly evolving molecular technologies (Fuentes-Pardo & Ruzzante, 2017) and decreasing costs (https://www.genome.gov/27541954/dna-sequencing-costs-data/) have placed whole-genome sequencing within reach for many laboratories and researchers. This trend should continue and these sequencing methods should be used by astacologists to provide insights on evolutionary relationships and species limits within crayfishes.

Understanding life history and ecological requirements is fundamental for species conservation, and conservation planning for crayfishes is hampered most by incomplete information for those two biological aspects. Stratton and DiStefano (unpublished data) support this contention by reporting that 55% of states monitoring crayfish identified the lack of life history or ecological information as a primary impediment to their ability to manage native crayfish populations. Moore et al. (2013) noted that life history studies were reported in the literature for only 12% of US and Canadian crayfish species, and were usually limited to species that are invasive or those of commercial importance. Our review of the literature does suggest an increase in biological information in peer-reviewed journals over the past decade. However, detailed species-specific life history papers since Moore et al. (2013) move the needle by only 20 species, or another 5% of the total US fauna. Most of these papers deal with only one to two aspects of crayfish life history attributes identified by Moore et al. (2013). Our knowledge gap is also increasing due to the description of new crayfish taxa. From 2013 to 2018, 15 new species were described, with most lacking detailed information on habitat requirements, diet, reproductive biology, trophic ecology, and population size and demography. Further complicating the issue is the increasing realization that at deeper levels of divergence, not all crayfish lineages have similar ecological characteristics (Thomas & Taylor, 2013; Larson et al., 2016), a belief that was historically prevalent (Stites et al., 2017).

Given their secretive lifestyles and specialized habitats, our understanding of ecological requirements of most burrowing and cave-dwelling crayfish is particularly stark. Habitat needs for some burrowers have been reported and they vary widely among species. Some seemingly thrive in human modified or managed environments such as roadside ditches, pastures, industrial, and urban environments (Taylor & Anton, 1999; Loughman et al., 2012; Rhoden et al., 2016a). Others are more specialized and are associated with pitcher plant bogs, forested seeps, and open-canopied grasslands and have undoubtedly lost habitat with land use change (Welch & Eversole, 2006; Welch et al., 2008; Simmons & Fraley, 2010). Terrestrial characteristics such as soil particle size, moisture, distance to surface water, and vegetation type all associated with habitat quality for a few burrowing crayfish (Grow, 1982; Welch & Eversole, 2006; Loughman et al., 2012; Helms et al., 2013a, b; Rhoden et al., 2016b). However, little to no information is available regarding groundwater quality tolerances or preferences, diet, and reproductive biology of burrowers and cave dwellers.

More attention to the biology of understudied crayfishes is clearly needed to advance the chances of successful conservation (Moore et al., 2013). While obvious, this call to action is difficult to adequately address considering the wide range of biological aspects available for study within species (i.e. fecundity, habitat requirements, allopatric species interactions, diet), the high level of species richness across the US, and competition for limited funding available for studying the broad taxonomic spectrum of protected species. Recognition of these challenges resulted in the formation of a working group of southeastern US astacologists in 2013 to identify and test low cost and repeatable sampling methods to shrink life history knowledge gaps for southeastern crayfishes (Stoeckel et al., 2015). An additional strategy may be to conduct detailed studies of one or two species within clades of closely related species that superficially show similar biological traits. Results of these studies could reasonably be used as surrogates for the remaining species. For example, at least 10 *Procambarus* species in the former subgenera *Ortmannicus* and *Leconticambarus* are burrowers known to occur in the same habitat type across the extreme southern Gulf Coastal Plain. All are found in ephemerally flooded lowland habitats and dig simple shallow burrows in ditches and pond banks and museum data document a similar annual timing pattern for the presence of juveniles and reproductively mature males. A detailed study of one of these species might provide useful estimates of life history parameters for all members of the larger clade of closely related and morphologically similar species. Many such clades exist across the eastern US (Hobbs, 1981, 1989; Schuster et al., in press).

Impacts of climate change

The impacts of climate change on freshwater biodiversity have been predicted in several works (i.e. Xenopoulos et al., 2005; Heino et al., 2009; Knouft and Ficklin, 2017), with one global analysis that suggests 15% (87 species) of global crayfish have high vulnerability to climate change per IUCN's trait-based assessment protocol (Hossain et al., 2018). However, the predicted impacts specific to crayfishes in the US has only recently been examined (Dyer et al. 2013; Krause et al., 2019). Using species distribution modeling methods to predict future distributions, the potential impacts to 14 US crayfish species (4% of US fauna) were assessed by Dyer et al. (2013) and Krause et al., (2019). Results were variable across species and suggest that flow, elevation, and geologic conditions may be more important than temperature for predicting range shifts. Dyer et al. (2013) also found both predicted range increases and decreases in their four study species. However, predicting the impacts of climate change on crayfishes is severely hampered by the lack of accurate distributional, ecological, and physiological data for many crayfishes (discussed herein). The cumulative effect of climate change and biotic interactions, such as those with invasive crayfishes (Capinha et al., 2013; Gallardo & Aldridge, 2013), has so far been neglected in the US. It is imperative that this receive attention given some climate scenarios may facilitate the spread of invasive crayfishes in the US (Martinez, 2012).

Understanding health and physiological requirements

The high diversity of US crayfishes, wide range of habitats (surface waters, terrestrial burrows, caves) and physiological changes during different stages of the molt cycle pose major challenges to determining optimal conditions and environmental tolerances of crayfish. A better understanding of how these factors impact their survival is required if we are to conserve imperiled crayfishes. General crayfish physiology has been previously described (Holdich, 2002) with special emphases on physiological regulation of the molt cycle (Chang & Mykles, 2011). Various review papers provide insight into major stressors such as low-ion environments (Wheatly & Gannon, 1995), thermal regimes (Westhoff & Rosenberger, 2016), heavy metals (Kouba et al., 2010; Sneddon & Richert, 2011), low calcium in acidic environments (Cairns & Yan, 2009), diseases, parasites, and pathogens (Edgerton, 2002; Longshaw, 2011), and shifting effects of symbiotic organisms on crayfish growth and survivorship with changing environmental conditions (Skelton et al., 2013). Despite these valuable resources, we lack comprehensive sets of species-specific information for even the most basic stressors. For example, studies reporting temperature tolerances, preferences, or optimal growth are published for $< 10\%$ of extant species worldwide (Westhoff & Rosenberger, 2016). Similarly, studies of disease agents, parasites, and symbionts focus on a relatively small number of commercially important species. Viral infections are particularly understudied in the Americas. There is also emerging evidence that physiological condition and molt stage may render previously identified pathogens such as crayfish plague (*Aphanomyces astaci* Schikora) more harmful to North American species than previously assumed (Aydin et al., 2014; Longshaw, 2016).

As these data gaps are filled, crayfish conservation would greatly benefit from use of a guiding framework to integrate results from diverse studies. For example, use of an adverse outcome pathway (AOP) allows for the integration and prediction of responses across biological organization levels from cells to individuals to populations to communities (Ankley et al., 2010; Kramer et al., 2011). Comparison and synthesis of published information are greatly facilitated by standardized approaches and endpoints (e.g., Westhoff & Rosenberger, 2016), like those developed and accepted by the freshwater unionid conservation community (ASTM, 2013). Guiding frameworks are also facilitated with the use of a common currency, such as energy, that can be traced through multiple levels of biological organization. Ecotoxicologists and population biologists are increasingly using dynamic energy budgets (DEB) (Nisbet et al., 2000; Sousa et al., 2010; Martin et al., 2012) and other closely related approaches for a wide array of taxa from fish (Gatti et al., 2017) to unionid mussels (Rosland et al., 2009). These models can be combined with AOPs (Groh et al., 2015; Goodchild et al., 2018) to relate effects of stressors on energetics to effects on individual growth and reproduction. Impacts on individuals can then be used to predict population level effects. Although the DEB approach has yet to be formally applied to crayfish, the importance of energetic budgets in understanding crayfish growth, population, and community dynamics has long been recognized for commercial and non-commercial species (e.g., Mormot, 1984; Villarreal, 1991; Frontera et al., 2011). Linkages between thermal stress at the cellular and individual levels were recently demonstrated explicitly for crayfish (Simcic et al., 2014). Use of energetic approaches within AOP frameworks hold much promise for conservation of the diverse array of crayfishes.

Assessing when stressors are present and/or at harmful levels is another major challenge. Many pollutants occur in short-term pulses and may require automated sampling systems for adequate characterization (e.g., Stoeckel et al., 2012). Furthermore, combinations of physiochemical stressors may induce synergistic or antagonistic effects not predicted by studies of individual stressors. One approach is to use biological early warning systems (BEWS) to monitor effects of ambient stressors under natural or artificial conditions. Physiological responses of organisms are integrated into automated water-monitoring systems and used to assess industrial and natural water quality in real-time (for full reviews see Kuklina et al., 2013; Bae & Park, 2014). Crayfish heartbeat, ventilation rates, and arterial flows are sensitive to environmental stressors and stress response can be quantified in real time using electrocardiography (Bierbower & Cooper, 2009), infra-red sensors coupled with fiber optics (Aagaard et al., 1991; Bini & Chelazzi, 2006), and electrical field potentials (Shuranova et al., 2003) (Fig. 3). Using these techniques, crayfish can be biomonitored for many stressors including metals (Styrishave & Depledge, 1996), ammonia (Bloxham et al., 1999), chloride (Kozák et al., 2009), hypoxia (Reiber & McMahon, 1998), and acidification (Udalova et al., 2012). Advances in other technologies may allow for on-site evaluation of crayfish health and stress using hand-held meters (e.g. Bonvillain et al. 2013). Such tools are useful for determining whether suspected stressors are relatively benign or require immediate action, and could be incorporated into management plans for critical habitats containing crayfish species of conservation concern.

Potential overexploitation

Overexploitation of wild crayfish populations via commercial and recreational fishing can be concerning in some situations. Most concerns involve species that are larger, long-lived and slow to maturity and are harvested before they can reproduce (Horwitz, 1991; Geddes & Jones, 1997; Jones et al., 2007). Crayfish

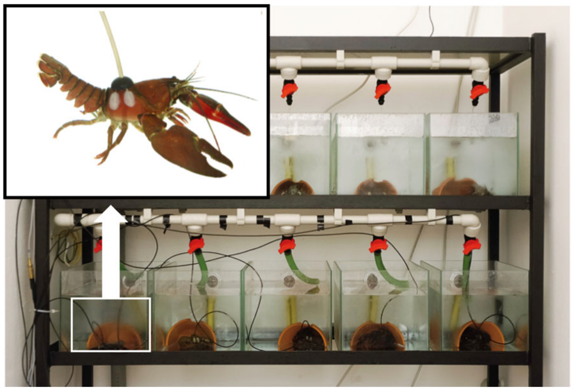

Fig. 3 Research on the physiological tolerance limits of crayfishes has been limited to a handful of species and a handful of potential stessors. An array of technologies such as the pictured fiber-optic sensors used to monitor cardiac activity in crayfish can be applied to crayfish physiology Images courtesy of P. Kozák and F. Lozek

have been exploited in Europe for >700 years and overfishing has been problematic in several countries (Köksal, 1988; Skurdal & Taugbøl, 1994). In Madagascar, subsistence and commercial fisheries exploit multiple long-lived species, and at least one (*Astacoides betsileoensis* Petit 1923) is vulnerable to overfishing (Jones et al., 2007). Countries have typically addressed overexploitation by setting fishing seasons, regulating capture methods and length limits to protect breeding age classes (sizes), and occasionally with fishing bans (Skurdal & Taugbøl, 1994; ADEE, 2017).

Crayfish exploitation in the US has a long history. They were utilized by Native Americans, with records dating from 5000 BC to the early 1700s (Comeaux, 1975; Stafford et al., 2000a, b; Huner, 2002). Initial use of crayfish among European colonists was attributed to French and Scandinavian settlers in Louisiana and Wisconsin and major markets for commercially exploited wild stocks arose in multiple areas of the country in the 1880s (California, Louisiana, Maryland, Oregon, Washington, Wisconsin; Comeaux, 1975). Wild crayfish are still exploited in the US for food (Fig. 4a, b), recreational and commercial fishing bait, educational and scientific study specimens, and the pet industry (Huner, 1978; DiStefano et al., 2016). Several states commercially (e.g., Louisiana, Oregon, California, etc.) or recreationally (e.g., Missouri, Wisconsin) harvest crayfish for food, but bait fisheries, both commercial and recreational, exist in many more states (Huner, 1978; Nielsen & Orth, 1988; DiStefano et al., 2009; Litvan et al., 2010). No economic data are available for crayfishes exploited in the pet, educational, or scientific fields. Estimated values of crayfish harvested for human consumption are \$172 million in the southeastern US and approximately \$300,000 in the Pacific Northwest (Larson and Olden, 2011, https://www.dfw.state.or.us/fish/commercial/landing_stats/2017/index.asp, R. Romaire, Louisiana State University, pers. com.). Primary harvested species have included *Pacifastacus leniusculus* (Dana 1852) in the Pacific Northwest (Lewis, 2002), *Procambarus clarkii* (Girard 1852) and *P. zonangulus* Hobbs and Hobbs 1990 in Louisiana and other southeastern states (Huner, 2002), and *Faxonius rusticus* (Girard 1852) and *F. virilis* (Hagen 1870) in the upper Midwest (Threinen, 1958; Hamr, 2002).

Fig. 4 The commercial and recreational harvest (**a**) of crayfish for food has long occurred in several regions of the US. Thousands of pounds are harvested annually (**b**) and the impact on natural populations is poorly monitored in some of those regions Image of harvesting (**a**) courtesy of S. Irwin; image of sacks of live, harvested crayfish (**b**) courtesy of R. P. Romaire

Overharvest of wild crayfish populations in the US strictly in terms of a reduction in the total numbers of individuals or a decrease to below the age of reproductive maturity has not been documented and has generally not been considered a serious threat (Momot, 1984, 1991, 1993). The current potential for crayfish overharvest is poorly understood. Many states collect little, if any, of the quantitative exploitation or biological data typically required to manage stocks through harvest regulation (Nielsen, 1993; Huner, 2002). Our review of websites for those states where crayfish are most actively harvested indicated that only some employ regulations designed to avoid overexploitation. A few states have minimum harvest size restrictions for some species and/or prohibit taking females carrying external eggs (e.g., California, Idaho, Minnesota, Oregon, Washington), or have harvest seasons (e.g., Minnesota [and boundary waters with Wisconsin], Mississippi, Oregon, Washington). Few regulate harvest quantity, and limits are generally liberal (Minnesota, Missouri, Oregon, Washington). The lack of harvest regulations in the southeastern states where crayfish harvest is the largest is most alarming and portends the need for increased attention.

Conservation actions to date

Managing impacts of invasive species

The introduction of non-native crayfishes to new drainages or regions has occurred through several different vectors and poses one of the most severe threats to the conservation of native crayfishes (Lodge et al., 2000; Taylor et al., 2007; Richman et al., 2015). Strategies for conserving native crayfishes from the impacts of invasives must be a primary component of any overarching conservation blueprint. The field of invasion biology has arrived at consensus that prevention of new biological invasions is preferable to, and more cost effective than, attempting to manage established invaders (Lodge et al., 2016). Prevention of biological invasions routinely takes the form of either regulation and enforcement of prohibited species, or education and outreach to stakeholders to prevent the release of legally permitted species that may still become invasive in the future. Within the US, invasive species regulations are generally blacklists of prohibited species at either the state or federal level. DiStefano et al. (2016) documents one such regulatory process and its outcomes for crayfish in Missouri, and many other state management agencies publish prohibited or permitted species lists in their fishing regulations or online. At the federal level, prohibition of injurious wildlife occurs under the Lacey Act, where one non-native crayfish species (*Cherax destructor* Clark 1936) was listed in 2016 (US Fish and Wildlife Service, 2016). Listing of species as prohibited or injurious in the US should follow a risk assessment process that is transparent and open to peer review, have a logical framework that includes factors considered important in the invasion process such as biological traits of species and environmental matches, and be repeatable regardless of user (National Science and Technology Council, 1999; Larson & Olden, 2012).

Strategies for managing invasive crayfish vary across the stages of the invasion process (Lodge et al., 2016). For many organisms, early detection at low-population abundances or densities has been found to be critical for successful control or eradication of biological invasions (Vander Zanden et al., 2010; Lodge et al., 2016). Surveillance for invasive crayfishes may include identification of new invasions from conventional government agency monitoring programs, but could also use emerging technologies like environmental DNA (Larson et al., 2017) or citizen science programs that report natural history observations through smart phone applications (Crall et al., 2015). Once a new invasive crayfish population is identified, several control or eradication options might be pursued, including physical removal of crayfish by trapping (Hansen et al., 2013) or electrofishing (Rogowski et al., 2013), and chemical treatment of invaded habitats (Recsetar & Bonar, 2015). In a review of management options for invasive crayfishes, Gherardi et al. (2011) reported that most invasive crayfish control or eradication efforts from Europe had failed. We are aware of exceptions; for example, Hein et al. (2006) combined trapping removal and predatory fish management to reduce the relative abundance of invasive Rusty Crayfish *F. rusticus* in a small, temperate lake in Wisconsin (Fig. 5a, b). However, Hansen et al. (2013) noted that this success was facilitated by drought conditions that stranded preferred *F. rusticus* habitat (i.e., cobble) above the waterline for several years. Similar control or eradication success may not be feasible for many ecosystems, as well as for agency budgets or timelines.

If most invasive crayfish populations are not easily eradicated, what management options exist for conserving impacted native crayfishes? First, some native crayfishes coexist with invasive crayfishes through habitat partitioning (Olden et al., 2011a; Peters & Lodge, 2013), and identifying habitats that may serve as refugia for native crayfishes is an urgent need. The spread of invasive crayfish into isolated habitats harboring native crayfish populations may also be prevented or slowed by managing the connectivity of waters. This can be done through maintaining natural barriers such as waterfalls or man-made barriers such as dams or water diversions, or constructing crayfish-specific barriers (Fausch et al., 2009) (Fig. 5c). For example, Frings et al. (2013) demonstrated the design of a barrier proposed as impassable to invasive Signal

Fig. 5 Prevention of new invasions is preferred over managing or eradicating established non-native crayfish populations, but some control efforts have been successful using a combination of trapping removal (**a**) and regulations to promote predatory fish populations (**b**). Managers have also sought to prevent the spread of established non-native crayfish populations by using natural and constructed dispersal barriers (**c**) with mixed success; effectiveness of these barriers may be limited by the potential overland movement of some crayfish species (**d**) Images courtesy of G. J. A. Hansen (**a**), E. R. Larson (**b**, **c**), and J. Monroe (**d**)

Crayfish *P. leniusculus*, while still allowing fish passage in compliance with the European Water Framework Directive. In California, multiple barriers have been designed and installed to prevent the spread of *P. leniusculus* into the few remaining habitats occupied by the ESA-listed Shasta Crayfish *Pacifastacus fortis* (Faxon 1914) (Cowart et al., 2018). Unfortunately, *P. leniusculus* either invaded these habitats during or after barrier construction. Overland dispersal (Fig. 5d) may be a challenge in designing such barriers, although Tréguier et al. (2018) suggest that successful establishment via overland dispersal for invasive crayfishes like the Red Swamp Crawfish *P. clarkii* is rare. As a potential measure of last resort, native crayfishes might be translocated to previously unoccupied habitats, isolated from invasive species (Fischer & Lindenmayer, 2000; Olden et al., 2011b). Such "ark sites" are commonly used to conserve native European crayfishes (e.g., Kozák et al., 2011), but to our knowledge have been attempted for only *P. fortis* in the US, with ambiguous outcomes to date (Cowart et al., 2018). Such translocation of native crayfishes carries risks of these species becoming invasive elsewhere, and remains a contentious area of policy debate (Olden et al. 2011b; James et al., 2015).

Habitat management

Like many freshwater taxa, crayfish are imperiled by habitat loss and degradation, including impacts of agricultural and urban land use, forestry, and energy production or mining (Richman et al., 2015). Although crayfish are often perceived as broad or indiscriminate generalists, many species have narrow habitat specializations, including rocky or coarse substrates for some stream-dwelling crayfish (e.g., Flinders & Magoulick, 2005) or perched water tables on uplands for some burrowing crayfish (Welch & Eversole, 2006). Such habitats are vulnerable to physical and chemical impairment from human land use and habitat conversion, and these impacts to habitat have contributed to the recent listing of two crayfishes under the ESA (US Department of Interior, 2016). Considerable research and management attention has been directed at maintaining or improving physical habitat in freshwater systems (Fig. 6a) (Zedler, 2000; Bernhardt et al., 2005), but we know of few efforts specifically designed to benefit native crayfish. As such, we identify here opportunities for crayfish habitat management inspired by practices for other taxa and freshwater ecosystems generally, and provide crayfish examples when available.

Among the most common practices in freshwater habitat management is the addition of substrates such as gravel or large wood that are needed for some life history aspect of target species but have been lost through anthropogenic changes in lotic and lentic ecosystems (Beechie et al., 2010). Effectiveness of such habitat additions has been equivocal for many targeted taxa (e.g., Riley & Fausch, 1995; Sass et al., 2012; Nilsson et al., 2017). Some restoration ecologists propose that habitat addition often fails because it treats the symptoms rather than causes of habitat impairment (Beechie et al., 2010). Alternatively, these approaches may serve as stopgaps that benefit target taxa temporarily while desired ecosystem processes are restored over larger spatial and longer temporal scales (Beechie et al., 2010). This could be relevant to crayfish conservation and management in some landscapes. For example, Adams (2014) documented many adult crayfish in degraded, habitat-poor coastal plain streams of Mississippi using trash (e.g., abandoned televisions, toilets, car parts) as habitat in absence of natural structure like wood. This suggests a potential management role by deliberate addition of woody debris in such streams, while seeking more process-based fixes to channelization and land use change (e.g., reforestation of watersheds or riparian corridors) over longer time scales. The preference of some crayfishes for coarse, cobble substrate as shelter (e.g., Peters & Lodge, 2013) could similarly be a target for habitat addition or supplementation in some contexts where this substrate was lost to sedimentation or gravel mining (e.g., Brown et al. 1998).

Fig. 6 Although billions of dollars have been spent on freshwater habitat management practices like stream restoration (**a**) in the US, crayfish have seldom been considered in these efforts. One major exception is the Comprehensive Everglades Restoration Plan (**b**), which has sought to manage hydrologic conditions to restore crayfish populations as forage for wading birds Images courtesy of D. J. Lawrence (**a**), N. Dorn (**b**)

Many freshwater management practitioners have moved towards prioritizing the restoration of processes that create and maintain lotic and lentic habitats, rather than constructing or installing desired habitats (Beechie et al., 2010). This process-based restoration often seeks to restore the longitudinal, lateral, and vertical connectivity of freshwater habitats to their watersheds, floodplains, and hyporheic zones by actions like removing barriers for migrating organisms or managing water releases from dams to better mimic natural flow regimes (Poff et al., 1997; Galat et al., 1998). For example, flow regime alteration is a leading driver of extirpations for native fishes in southeastern and southwestern US rivers (Kominoski et al., 2018), but effectively no studies have investigated the role of flow regime alteration or management on crayfish (but see Lynch et al., 2018). Similarly, we know of only one example where crayfish are the focus of a major freshwater management and restoration initiative in the US. The Comprehensive Everglades Restoration Plan seeks to recover wading bird populations by restoring hydrologic conditions (i.e., the timing and volume of water delivery) that support their preferred prey items at high abundances, particularly small fish and two native crayfishes (DeAngelis et al., 1998; Trexler & Goss, 2009; Boyle et al., 2014) (Fig. 6b). This novel restoration effort targets crayfish for their central role in ecosystems as high-value prey for organisms of conservation need, and represents the potential value of managing habitat specifically for crayfish in other freshwaters where they offer similar ecosystem benefits (e.g., Wolff et al., 2015).

There is considerable need to maintain remaining, intact ecosystems through mechanisms such as environmental regulations and the creation of freshwater-protected areas (Abell et al., 2007). Crayfish have factored minimally in policy to protect freshwater habitats, but have undoubtedly benefited from actions like mandatory riparian buffer strips in forestry landscapes (Lee et al., 2004) or the protection of streams and rivers in the US by the Wild and Scenic Rivers Act (Benke, 1990). Decisions about where on the landscape to prioritize for the protection of freshwater habitats through regulatory or legal methods are increasingly guided by decision-support tools that seek to optimize spatial representation of priority taxa while accounting for factors like land costs and threats to biodiversity (Groves & Game, 2016). Crayfishes have been incorporated into some efforts to identify priority freshwater regions of the US (Abell et al., 2000; Sowa et al., 2007; Elkins et al., 2016). Similar prioritization efforts are needed for other US regions with high numbers of data-deficient and imperiled crayfish species.

Ex situ conservation activities

Ex situ conservation actions have been applied to protect populations of imperiled freshwater organisms from ongoing or imminent threats or to re-establish extirpated or even new populations. These include moving population members out of the wild and either maintaining them in artificial conditions or immediately reintroducing them to places within their historical range, or less frequently introducing them to areas outside their native range (Primack, 2006). These methods can be highly effective and can serve as the "last resort" to prevent extirpation. However, they have potential problems such as being too narrowly focused, often fail, and should be applied carefully and holistically (Reading et al., 2002). *Ex situ* methods are common with endangered fish and mussels in the US (Carlson & Muth, 1993; George et al., 2009; Haag, 2012), but not with crayfish. Application of these practices to crayfish is more common in other countries where several crayfishes are highly endangered. For example, the recovery plan for Australia's threatened Giant Freshwater Crayfish (*Astacopsis gouldi* Clark 1936) includes proposed reintroductions (ADEE, 2017) and captive propagation efforts (Forteath, 1985; Kempton, 2017). Crayfish reintroduction efforts and captive propagation are considered standard practices in Europe (Souty-Grosset & Reynolds, 2009; Kozák et al., 2011) and have been initiated with several species in at least seven and five European countries, respectively (Kozák et al., 2011). The use of isolated reintroduction ark sites is considered a necessity in Europe where natives are threatened by invasive crayfishes and disease (Peay, 2009).

Ex situ methods in US crayfish conservation have been minimal, likely related to the existence of only six ESA-listed species. The USFWS is evaluating feasibility of translocations of endangered Nashville Crayfish (*F. shoupi* Hobbs 1959) to man-made holding ponds within their historical range (USFWS, 2017) to temporarily protect them from degraded water quality. The evolving USFWS Recovery Plan for endangered Shasta Crayfish (*P. fortis*) (USFWS, 1998; USFWS, 2009) listed translocations as a possible strategy to protect the species from encroachment of the invasive *P. leniusculus*. In 2013 and 2014, 42 *P. fortis* were translocated to an isolated pond to establish a new population, but success remains undetermined (Cowert et al., 2018). The newly formed Recovery Team for the Big Sandy Crayfish (*C. callainus*) and Guyandotte River Crayfish (*C. veteranus*) is developing captive propagation techniques for these species for eventual reintroduction efforts (Z. Loughman, West Liberty University, pers. com.). Propagation, augmentation, and reintroduction methods for crayfishes hold promise, but should be carefully planned, because they are susceptible to undesirable effects on both the relocated animals (e.g., physiological stress) and receiving native communities (e.g., reduced genetic diversity, introductions of disease/parasites, etc.) (Metcalf et al. 2012; McMurray & Roe, 2017; Roznere et al., 2017).

Proposed strategy for future US conservation efforts

We invite those concerned with the conservation of the US's unique crayfish fauna to use the following proposed strategy as a starting point for collaborative thought, discussion, and action. This would include those in academia, all levels of government natural resource agencies, non-governmental conservation organizations, and private citizens. Proposed action items are not listed in order of priority.

Allocate resources to assessing ecology, systematics, and distribution of crayfishes

Lobbying of government agencies to increase attention and funding for ecological, systematic, and distributional research is needed. All three biological aspects are fundamental to conservation, relatively inexpensive, and will greatly improve our ability to identify at-risk species. We acknowledge the limited available financial resources for freshwater conservation efforts in the US. The study and use of surrogate species within clades whose other members are rare, or display similar habitat requirements may be one option for dealing with this limitation.

Improve understanding of crayfish tolerance values

There is a need to understand environmental and chemical tolerances of crayfish and how these tolerances differ among taxa. To facilitate comparisons among studies, we recommend development of ASTM International standard guide(s) similar to those developed for freshwater unionids. Guides should discuss frameworks to link effects of stressors at the cellular, individual, population, and community levels. Special attention should be given to development of methodologies specific to surface waters, terrestrial burrows, and caves, and development of alternate study designs for rare species when number of available individuals is limited.

Increased attention to crayfish harvest and overexploitation

The lack of species or size-specific crayfish harvest regulations and quotas in most states creates the potential for overharvest and subsequent undetected population declines for some species, particularly those that display low fecundities or are late maturing (Momot, 1984). A critical review and continuing assessment of existing wild population harvest regulations and the collection of ecological data for commercially harvested species are needed at the state and tribal level.

Develop and enforce policies and regulations to prevent introduction of invasive crayfish

Given the critical role of prevention in managing biological invasions (Lodge et al., 2016), we recommend that states continue to develop and update lists of prohibited crayfish species and use current risk assessment tools. These lists should be synchronized among states within shared watersheds to avoid "weak links" problems (Peters & Lodge, 2009). Risk assessment tools should identify species most likely to become invasive in the future (Larson & Olden, 2010; Zeng et al., 2015), identify where invaders might establish and how they might spread (Larson & Olden, 2012), and prioritize prevention and outreach at locations where impacts of invasive species may be most severe (Olden et al. 2011a) (Fig. 4b). We also urge more active implementation and enforcement of laws that restrict live crayfish trade, either as food, bait or pets.

Research and test factors that will limit invasive crayfish spread

Given that control and eradication of established invasive crayfish populations is often costly and routinely ineffective, preventing secondary spread of such populations may be our best hope for conserving the native crayfish populations they threaten. More research is needed on patterns and mechanisms of spread of invasive crayfishes through natural dispersal or human-linked transport, and how this spread is affected by natural and anthropogenic barriers. The success of dispersal-limiting mechanisms should be evaluated within a multi-faceted pest-management framework rather than simply as a stand-alone approach.

Make crayfish the focus of habitat management and restoration

Crayfishes have been woefully absent as target species for habitat management and restoration activities. We propose that native crayfish receive increased focus of current and future activities in freshwater ecosystems and monitoring to evaluate their responses. Given the documented spread of invasive crayfishes, managers could face the dual challenge of managing habitat to reduce the abundance and spread of invasives while maintaining and restoring populations of rare species. As such, crayfish community responses to habitat and restoration activities need to be explored.

Incorporate crayfish into conservation planning for protected areas

Preventing degradation or loss of existing high-quality habitat is more likely to conserve species than attempting to restore impaired habitat, particularly in freshwater ecosystems. The location of protected areas or conservation easements is routinely guided by decision-support tools that use factors like costs of different conservation activities, threats to biodiversity, and the distribution of focal biodiversity (Groves & Game, 2016). Inclusion of crayfish in systematic conservation planning is needed, but dependent on reducing data deficiencies for rare native crayfish species, and disseminating this information to freshwater scientists and policy planners.

Study and develop criteria for crayfish propagation, augmentation, and reintroduction (PAR) methods

As highlighted by George et al. (2009) for fishes, all three PAR methods should be evaluated concurrently to determine both biological and cost-effectiveness. Research needs specific to crayfish include, but are not limited to: examination of methods, facilities and equipment for *ex situ* culture, the use of propagated individuals of rare species for *ex situ* environmental and chemical tolerance testing, genetic stock assessments, methods for reintroduction of site assessments, identification of commensal organisms/pathogens potentially present on reintroduced crayfishes, life history requirements of propagated species and timing of reintroductions, transportation and *in situ* reintroduction equipment and methods, and the development of post-introduction monitoring methods.

Increase communication and outreach

We feel that the value of crayfishes to ecosystems has been undersold to those outside of academia and public resource management agencies. To reach that audience and expand the pool of stakeholders, those aspects of crayfish biology that will be most recognized should be highlighted in outreach efforts. For example, the critical importance of crayfishes to the viability of recreationally and economically important sportfish populations (DiStefano, 2005) should resonate with professionals and the general public alike. Social media, combining text and attractive graphics, is an underutilized but potentially valuable tool in distributing these messages beyond the small circles of managers and researchers.

Conclusions

We review here gaps in information that limit our ability to effectively conserve the US's globally unique crayfish fauna. In addition, we review the limited number of conservation and management actions that have been directed at crayfishes and those utilized on other freshwater taxa that have relevance for crayfishes. We feel that both reviews are necessary to provide needed background before proposing specific action items in a conservation strategy. Our proposed strategy contains suggested action areas to: address our knowledge gaps; minimize the impacts of invasive species; integrate crayfishes into habitat and community management decisions; and improve the visibility of crayfishes. Whereas the implementation of one or few of these action items will benefit US crayfishes, we hope that crayfish stakeholders will implement and test conservation measures that integrate multiple items concurrently.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

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