The critically endangered hairy marron, *Cherax tenuimanus* Smith, 1912: A review of current knowledge and actions required to prevent extinction of a species

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The hairy marron, *Cherax tenuimanus* Smith, 1912, is a freshwater crayfish endemic to the Margaret River catchment in the south-west of Western Australia (Southwestern Province). Once abundant throughout its native range, *C. tenuimanus* is being rapidly replaced by the more widespread smooth marron, *Cherax cainii* Austin, 2002; to the extent that *C. tenuimanus* is now critically endangered. To enable policy makers to formulate a suitable recovery plan, there are key questions that need to be answered surrounding the biology and ecology of both species, particularly where the range extension of *C. cainii* has resulted in the two species existing in sympatry. The paucity of knowledge is further confounded by considerable historical confusion surrounding their morphological differentiation, nomenclature, and indeed their taxonomic classification as separate species. As a prelude to management planning, we provide a review of *C. tenuimanus* taxonomy, drawing particular attention to areas of confusion and disagreement in published literature. This review also highlights gaps in our understanding of the mechanism behind the decline of hairy marron and provides direction for future research and actions required to enhance the conservation of this critically endangered species.

KEYWORDS: conservation, *Cherax cainii*, freshwater crayfish, Margaret River, endemic, Western Australia, south-west, smooth marron

INTRODUCTION

Marron are large freshwater crayfish endemic to the south-west of Western Australia, of which two species are currently recognised. The most widespread species, the smooth marron, *Cherax cainii* Austin, 2002, occurs over much of the south-west of Western Australia where it forms the basis of a popular recreational fishery and aquaculture industry (Morrissy 1978). In contrast, a second protected and critically endangered species, the hairy marron, *C. tenuimanus* Smith, 1912, has a range restricted to the Margaret River catchment (Austin & Ryan 2002).

The Margaret River from of marron was identified as vulnerable in 1990 (Horwitz 1990a). Following reclassification as a distinct species, *C. tenuimanus* was identified as imminently threatened with extinction (Molony 2002). Consequently the species was listed as critically endangered at the state level under the Western Australian *Wildlife Conservation Act 1950* in 2005 and at the national level under the *Commonwealth of Australia Environment Protection and Biodiversity Conservation Act 1999* in 2006. Most recently *C. tenuimanus* has received international recognition and has been listed as critically endangered by the IUCN, a category that identifies it as facing a very high risk of extinction in the wild (Austin & Bunn 2010; IUCN 2001).

A draft plan to direct recovery actions for *C. tenuimanus* was developed by the Western Australian Department of Fisheries. The plan outlined ongoing or future recovery actions, however, there remain a number of key knowledge gaps that have hindered the implementation of conservation measures for the species.

This review summarises current knowledge on the ecology, taxonomy and conservation challenges of *C. tenuimanus* in order to inform a science-based approach to future management activities aimed at preventing any further decline of the species. Specifically, it will clarify historical work on the taxonomy based on morphology, and genetic analysis, and how it has contributed to the current taxonomic status of the species. It also addresses difficulties in differentiating between the two species and their hybrids in the field, and places quantitative data on distribution and abundance in the appropriate context, while providing a synthesis of *C. tenuimanus* population biology and ecology; discussing real and potential threats in the context of data derived from both captive and wild stocks; and propose conservation actions required to conserve *C. tenuimanus*.

Taxonomic recognition of *Cherax tenuimanus* and *Cherax cainii* as distinct species – an historical perspective

The history of the type material and designation of type specimens is controversial; the classification of marron as two separate species has been challenged (de Graaf *et al.* 2009) and the change to the accustomed usage of the name *C. tenuimanus* from the widespread form to the restricted form has been questioned (Molony *et al.* 2006). This review is undertaken in accordance with the designation of two species and the specific naming proposed by Austin and Ryan (2002).

Common names have been less controversial and were formally assigned at the "Scientific Workshop on the Margaret River Marron" (Koenders 2002); the Margaret River form was designated as the "hairy marron". The other form, which is endemic to the Southwestern Province and has been translocated within Western Australia, as well as across Australia and throughout the world (Shipway 1951; Morrissy 1978; Horwitz 1990b), received the common name "smooth marron".

Morphological evidence for recognition of distinct species

A single species of marron, *Cherax tenuimanus*, was originally described in 1912 (Smith 1912). Three subsequent studies of *Cherax* taxonomy also referred to only a single species (McCulloch 1914; Clark 1936; Riek 1967). In 1986, marron were split into two sub-species based on differences in electrophoretic and morphological characteristics between animals from Margaret River and the widespread form (Austin 1986). The form endemic to Margaret River was named *C. tenuimanus tenuimanus* and was distinguished by; clusters of long setae on the cephalothorax and sometimes the abdomen, a strongly raised median carina extending to the cervical groove, and a thorax without numerous tubercles (Austin 1986). The widespread form was designated as requiring a new sub-specific epithet and was identifiable by an absence of distinct long setae and the presence of numerous distinct tubercles on the thorax (Austin 1986). Subspecies classification was maintained in subsequent marron classifications (Horwitz 1995b; Austin & Knott 1996).

In 2002, the Margaret River form was elevated from sub-species to species based on a review of allozyme data collected intermittently during a 20-year period from 1979 to 1998, and the morphology of each species (Austin & Ryan 2002). The Margaret River form was designated as *C. tenuimanus*, and the widespread smooth form was assigned the new name *Cherax cainii* (Austin & Ryan 2002). Justification for this was based on the first published reference to marron listing the locality for *C. tenuimanus* as Margaret River (Smith 1912).

Confusion and controversy surrounding morphology and taxonomy

Smith (1912) examined more than one specimen of marron provided to him by Mr Woodward, the then Director of the Western Australian Museum and Art Gallery, as well as specimens in the British Museum. No specimen numbers were provided by Smith (1912) and the only other information regarding the origin of materials examined was his listing of the locality as Margaret River (Table 1). The initial description and drawings (Smith 1912) are not typical of the Margaret River form of marron described in 2002 (Austin & Ryan 2002) as only inconspicuous hairs are mentioned and no setation is present in the 1912 illustrative plate. However, the illustration does appear to have a median carina extending to the cervical groove; a trait of the Margaret River form of marron (Table 1) (Horwitz 1995b; Austin & Ryan 2002).

Subsequent taxonomic descriptions of marron failed to provide specimen numbers for the material examined (Table 1) (McCulloch 1914; Clark 1936). Samples examined by McCulloch (1914) were provided by Mr Woodward of the Western Australian Museum and Art Gallery and included specimens from outside of the Margaret River. The 1914 illustration of *C. tenuimanus* (*sensu stricto C. cainii*) (McCulloch, 1914) is typical of *C. cainii* as described in Austin and Ryan (2002) (Table 1), although the description mentions the median carina may run back to the cervical groove, a trait of *C. tenuimanus* (Horwitz 1995b; Austin & Ryan 2002). In contrast, a 1936 publication on Australian crayfish, which also examined marron specimens from outside the Margaret River, described *C. tenuimanus* as having a "densely hirsute carapace and abdomen", characteristics that are clearly those of the Margaret River form (Table 1) (Clark 1936).

The absence of specimen numbers prevents subsequent researchers identifying the material examined. A search of collections in the Natural History Museum (London) and the Western Australian Museum, was unsuccessful in locating any record of a holotype collected by Smith (Molony *et al.* 2006). In the absence of a designated type specimen, a lectotype was assigned in 1969 after examination of a marron of "about 11 inches" in the British Museum, which was assumed to be part of the materials examined by Smith (1912) based on size (Riek 1969). In contrast to the historic publications, the work that resulted in splitting *C. tenuimanus* into two species clearly stated which specimens were examined (Austin & Ryan 2002). The specimens examined included WAM C 127 (= WAM 4131), which was assumed by Austin and Ryan (2002) to be the holotype for *C. tenuimanus*; despite Smith (1912) not designating a holotype. In accordance with the International Code of Zoological Nomenclature (ICZN 2000) both a lectotype and a holotype cannot exist, however we do not attempt to address this situation with this manuscript.

The species nomenclature designated by Austin and Ryan (2002) was considered to conflict with the accustomed usage of *C. tenuimanus* referring to the widespread smooth species, and a reversal of the species names was proposed (Molony *et al*. 2006). The proposal did not mention the existence of the lectotype, and based on the evidence provided, it was not upheld by the International Commission on Zoological Nomenclature (ICZN) (ICZN 2008). Therefore the specific names and type specimens remained as those designated by Austin and Ryan (2002): type specimens for *C. cainii* (WAM C 28348) and for *C. tenuimanus* (WAM C 127) (ICZN 2008).

Genetic evidence for recognition of distinct species

An initial electrophoretic comparison of marron from Margaret River with those of Inlet River found the two populations to be conspecific (Austin 1979). However, all following studies of genetic relationships between marron from separate river systems provide strong support for the differentiation of the Margaret River form of marron from all other types. An analysis of allozyme variation in marron found that the Margaret River population was electrophoretically distinct at three loci (Austin & Knott 1996). Examination of three di-nucleotide microsatellite loci across 88 animals to determine genetic distance between five subpopulations, also found Margaret River animals to be distinct from all

Table 1 Summary of the taxonomic studies of marron. N/A= not applicable.

	Smith 1912	**McCulloch 1914**	**Clark 1936**	**Riek 1967**	**Riek 1969**	**Austin & Ryan 2002**	
Species listed	*C. tenuimanus*	*C. tenuimanus*	*C. tenuimanus*	*C. tenuimanus*	*C. tenuimanus*	*C. tenuimanus*	*C. cainii*
Type specimen or materials examined clearly given?	No	No	No	Yes "*Type*.–In the British Museum (Natural History), London."	Yes "*Type*.–The only specimen of the type series located in BM is the one of "about 11 inches". This male specimen, No.1968:221, cephalothorax length 125mm (overall body length 280mm), is selected as the lectoholotype." BM = "British Museum (Natural History), London."	Yes "*Holotype*. ♂ 62.7 mm OCL, Margaret R., Western Australia, 2.iii.1911, coll. B. Lipfert, WAM C 127 (WAM 4131)."	Yes "*Holotype*.♂, 84.8mm OCL, from Scott R., Brennan Bridge, Scott R. Road, 12 km north-east of Augusta, south-western Western Australia, coll. C. Austin 14.xii 1998, Western Australian Museum (WAM) C 28348"
If no to above, what information is provided?	"The largest specimen measures 6 ½ inches. Specimens in British Museum about 11 inches."	"Of the series examined the greater number were obtained in the Harvey River, seven miles above Harvey; one is from Korijekup, Harvey River; one from Margaret River; One from Balingup Brook; and three from the Warren River"	"With the exception of seven species the types or paratypes of each species have been examined" pg5. As no type locality is given for *C. tenuimanus* specimens, it is assumed that this is one of the seven species for which the type was not examined.	N/A	N/A	N/A	N/A
Type locality clearly given?	No	No	No	Yes "*Type Locality*.–Margaret River, Western Australia."	Yes "*Type locality*.–Margaret R., W.A."	"Margaret R., Western Australia"	"Scott R., Brennan Bridge, Scott R. Road, 12 km north-east of Augusta, south-western Western Australia"

Table 1 (cont.)

	Smith 1912	**McCulloch 1914**	**Clark 1936**	**Riek 1967**	**Riek 1969**	**Austin & Ryan 2002**	
Species listed	*C. tenuimanus*	*C. tenuimanus*	*C. tenuimanus*	*C. tenuimanus*	*C. tenuimanus*	*C. tenuimanus*	*C. cainii*
If no, what information is provided?	"*Locality*.– Margaret River, Western Australia" is listed, but this is not clearly stated as the type locality.	"Of the series examined the greater number were obtained in the Harvey River, seven miles above Harvey; one is from Korijekup, Harvey River; one from Margaret River; One from Balingup Brook; and three from the Warren River"	"*Habitat.– Western Australia:* Margaret River (Miss H. Alexander, 1936) ; Harvey River; Korjekup; Kojonup; Balingup Brook; Warren River; Blackwood River; Katanning."	N/A	N/A	N/A	N/A
Origin of biological specimens clearly stated?	No	Yes – most material was received in January 1912 from Mr. Bernard H. Woodward, Director of the Western Australian Museum"	No	"The illustrations are based on a specimen from Kalgan", colour is based on "specimens from Beedelup Falls, near Pemberton"	No – refers to Riek (1967).	Yes – all material from Western Australia Museum	Yes – all material from Western Australia Museum
If no, what information is provided?	Specimens from WA provided by Mr. Woodward of Perth	N/A	"*Habitat.– Western Australia:* Margaret River (Miss H. Alexander, 1936) ; Harvey River; Korjekup; Kojonup; Balingup Brook; Warren River; Blackwood River; Katanning." These locations largely correlate with those listed by McCulloch 1914 whose specimens originated from the Western Australian Museum.	N/A	N/A	N/A	N/A
Quantity of specimens examined clearly given?	No	Yes, "A well graduated series of forty specimens, ranging from 57-296mm."	Yes – "12 specimens examined".	No	No – refers to Riek (1967).	Yes – 31	Yes – 62
If no, what information is provided?	"The largest specimen measures 6 ½ inches. Specimens in British Museum about 11 inches". Therefore more than one examined.	N/A	N/A	"Illustrations are based on a specimen from Kalgan", colour is based on "specimens from Beedelup Falls, near Pemberton". Therefore more than one. examined.	N/A	N/A	N/A

Species assignment based on description*	Unclear	Unclear	*C. tenuimanus*	Unclear	Unclear	*C. tenuimanus*	*C. cainii*
Justification for above*	Smith describes "numerous groups of short inconspicuous hairs". Austin and Ryan (2002) describe *C. cainii* as having "short inconspicuous setae". Preserved specimens of *C. tenuimanus* also have short inconspicuous setae (Senior author, pers. obs.). Smith describes "a few small tubercles on the branchiostegites". Austin and Ryan describe *C. tenuimanus* as having small-moderately sized tubercles" as opposed to the "large conspicuous tubercles" of *C. cainii.*	The majority of specimens originated outside Margaret River, therefore *C. cainii.* Median carina "may run back to the cervical groove" typical of *C. tenuimanus,* however, the median carina may also "terminate well before that point", typical of *C. cainii*.	"Entire carapace densely hirsute" and "entire abdomen more or less densely hirsute."	Diagnostic features that would enable discrimination between the two species are not mentioned.	Diagnostic features that would enable discrimination between the two species are not mentioned.	Diagnostic paper on morphology of *C. tenuimanus*	Diagnostic paper on morphology of *C. cainii*
Species assignment based on illustration*	Unclear	*C. cainii*	Unclear	*C. cainii*	No Illustration	*C. tenuimanus*	*C. cainii*
Justification for above*	Illustration in Smith 1912 (PL. XXII) shows a continuous median carina extending to the cervical groove, typical of *C. tenuimanus*. It lacks large conspicuous tubercles on the branchiostegites that are typical of *C. cainii.* No hairs are present in the illustration – diagnostic of *C. cainii.*	Illustration in McCulloch 1914 (Plate XXXIV) shows no setae. Branchiostegites possess large conspicuous tubercles and the abdomen has moderate-large tubercles typical of *C. cainii*.	Plate (IV) is a line drawing of the cephalon only.	No hairs are present. Tubercles on areola dorsally present, although reduced as specimen appears to be a sub-adult.	N/A	Diagnostic paper on morphology of *C. tenuimanus*	Diagnostic paper on morphology of *C. cainii*

*Using characteristics defined by Austin & Ryan (2002) as different between the *C. tenuimanus* and *C. cainii.*

other marron populations and deserving of conservation (Imgrund *et al.* 1997; Imgrund 1998). Further studies comparing 12s mitochondrial DNA sequence resulted in population subdivisions that were entirely consistent with those found in 1996 (Nguyen *et al.* 2002). Two haplotypes were present, one haplotype was exclusive to marron from the Margaret River and a second haplotype was associated with all other locations (Nguyen *et al.* 2002). Subsequent analysis of four mitochondrial DNA loci (12s, 16s, Cyt *b*, and CO1) further confirmed *C. tenuimanus* from the Margaret River system to be phylogenetically distinct from all other locations (Munasinghe *et al*. 2003).

The argument for classification of *C. tenuimanus* and *C. cainii* as separate species was based on testing of the hypothesis that if the taxonomic conclusions of Austin and Knott (1996) were correct and the two marron forms were sub-species, then allozyme data should reveal a high degree of genetic mixing and substantial introgression of alleles (Austin & Ryan 2002). Although hybrids were present, their abundance was not representative of that expected from random mating, suggesting hybrids either had reduced viability, or the marron forms showed assortative mating behaviours, thus providing justification for the description of two separate species (Austin & Ryan 2002). This argument has been challenged by subsequent studies that have found higher proportions of hybrids (Bunn 2004, de Graaf *et al.* 2009), however no empirical testing has been attempted.

Identification of *Cherax tenuimanus* and *Cherax cainii* in practice

Marron are easily distinguished from all other *Cherax* species in the south-west of WA because they are considerably larger and possess spines on the telson (Horwitz 1995b). A combination of morphological characteristics can be used to differentiate the two marron forms (Austin & Knott 1996) and a formal description of each species is provided by Austin and Ryan (2002). The most distinctive of the differences are: the presence of a median carina that extends continuously, without depression, to the cervical groove; prominent tufts of long recumbent setae; and the absence of tuberculation on the areola on *C. tenuimanus* (Austin & Ryan 2002).

Field identification of the two marron species in Margaret River based on morphological differences is confounded by the presence of hybrid/backcrossed animals displaying a range of characteristics from each of the species (Lawrence 2002), and inconsistent variations in morphology due to sex, maturity, and size (Bunn *et al.* 2008). An attempt to improve the accuracy of field identification of pure and hybrid animals was made utilising the morphology of the median carina, and presence or absence of clusters of setae (Bunn *et al.* 2008). Using these characters, approximately 90% of *C. cainii* and *C. tenuimanus* could be identified correctly; however, correct identification of hybrids was more difficult, with an accuracy of only approximately 70% (Bunn *et al.* 2008). The difficulty associated with identification has obvious implications for the accuracy of population data and breeding studies where morphology has been used to identify the species. This is the same data that has underpinned management decisions to date and an improved method of identification is required to enhance on ground conservation actions (Bunn *et al.* 2008).

Current biological and ecological knowledge of *Cherax tenuimanus*

Wild population data and captive breeding work may suffer from difficulties in identification of hybrids. All previous studies have used the best characteristics for identification of hairy marron based on knowledge at the time of undertaking their work. However, without definitive genetic testing being undertaken, a level of incorrect identification may have occurred across all those studies.

Distribution and abundance

Prior to 1980, only *C. tenuimanus* was present in the Margaret River (Austin & Ryan 2002). Introduction of *C. cainii* into Margaret River is thought to have occurred in the early 1980s (Austin & Knott 1996). It is not known if the introduction of *C. cainii* was from a single event, multiple events, or even if it is ongoing. In less than 20 years, *C. tenuimanus* has been wholly replaced at the site where *C. cainii* was first located within the Margaret River (Austin & Ryan 2002). The upstream spread of *C. cainii* has been rapid, and by 2002, *C. tenuimanus* had been replaced in the middle reaches of the river (Bunn 2004; de Graaf *et al.* 2009). Marron populations in the upper reaches were wholly *C. tenuimanus* in 1995, however, by 2002 they contributed only 30% of the marron population in this stretch of river (Bunn 2004). Estimates of the population of *C. tenuimanus* have continued to decline and now range between 5 to 25% of marron in the upper Margaret River (DoF unpublished data).

Growth and survival

Growth rate of *C. tenuimanus* in the wild has not been thoroughly investigated and the only data on growth comes from a single pool located in the upper reaches of the Margaret River, Canebrake Pool (Bunn 2004). Within this pool, both *C. tenuimanus* and *C. cainii* reached a similar size, although *C. cainii* grew at twice the rate of *C. tenuimanus* (0.063 vs. 0.033 $mm.day^{-1}$, respectively) (Bunn 2004). These results are based on a very small number of individuals and are skewed by the inclusion of animals recaptured in the same sampling period in the analysis (Bunn 2004). Attempts to estimate growth based on modal peaks from consecutive cohorts, are likely to be inaccurate given the small sample size and lack of clear cohorts (Bunn 2004), therefore these growth values are not discussed herein. No information on comparative survival of *C. tenuimanus* in the wild is available and both growth and survival of wild populations thus requires further investigation.

Data on growth rate in captivity is more abundant. Juvenile *C. tenuimanus* grew quickly and at the time of stocking into grow-out ponds, were larger than offspring of *C. cainii* from five different rivers (Lawrence *et al.* 2007a). At the end of the two years of grow-out, survival did not differ and *C. tenuimanus* were of similar size to the *C. cainii* from the Kent, Shannon, Donnelly, and Warren Rivers (Lawrence *et al.* 2007a). Growth rate of *C. tenuimanus* in captivity was approximately four fold that calculated for wild *C. tenuimanus* (0.11 vs. 0.033 mm.day^{-1}) and double that for wild *C. cainii* in Margaret River (Bunn 2004; Lawrence *et al.* 2007a); most likely a result of diet supplementation of captive animals with high quality feed pellets (C. Lawrence pers. comm.). Unlike the wild population, captive male *C. tenuimanus* were significantly larger than females (82.70g S.E. ± 1.65g vs. 55.87g S.E. ± 3.97g after 2 years of grow-out (n=30)) (Lawrence *et al.* 2007a). Survival of *C. tenuimanus* in captivity was similar to that of *C. cainii* from various rivers, even when all were grown communally, demonstrating an equal ability to compete (Lawrence *et al.* 2007c).

Reproduction

Despite concerns about the conservation status of this species in 2002 (Koenders 2002), the ongoing captive breeding of the species, and the production of a draft recovery plan in 2008, knowledge of the reproductive biology of *C. tenuimanus* has progressed little. There is some evidence of a difference in the timing of reproduction for each species based on differences in the timing of reduced catchability linked with reproduction (Bunn 2004) and of the possibility of later gonadal maturation in female *C. tenuimanus* (J Bunn pers. comm.; DoF unpublished data). This is an area requiring further investigation as it has numerous implications for conservation actions.

Nothing is known about reproductive success of wild *C. tenuimanus*. The only data comes from captive breeding (Morrissy & Cassells 1990; Henryon 1995; Lawrence *et al.* 2007a). Both Lawrence *et al.* (2007a) and Henryon (1995) selected animals that possessed hairs and a continuous median carina (C. Bird pers. comm.; M. Henryon pers. comm.) in an attempt to breed only *C. tenuimanus*. Lawrence *et al.* (2007a) further tried to reduce the chance of using hybrids by only collecting animals from the upper reaches where the *C. tenuimanus* population was in the highest proportion, and by sourcing *C. tenuimanus* from an isolated population transferred from the Margaret River onto a private property in the 1970's. Early attempts at breeding marron from Margaret River resulted in very low rates of breeding, 2–8% (Morrissy & Cassells 1990; Henryon 1995) compared to 68.5% for long term domesticated stock of *C. cainii* (Morrissy & Cassells 1990). Despite best efforts, it is possible that hybrids with *C. tenuimanus* characteristics may have been included (Horwitz 1994). Greater success was later had by Lawrence *et al.* (2007a) where 53% of females captured from the Margaret River were mated successfully. Captive breeding found an inverse correlation between the percentage of berried *C. tenuimanus* females and weight, indicating a decrease in breeding frequency with size, a trait similar to *C. cainii* from various rivers (Lawrence *et al.* 2007a). All marron produced equal sex ratios of juveniles (Lawrence *et al.* 2007a).

Hybridisation

There is clear evidence of hybridisation between *C. tenuimanus* and *C. cainii* in the Margaret River (Imgrund *et al.* 1997; Austin & Ryan 2002; Nguyen *et al.* 2002) and in captivity (Henryon 1995; Lawrence *et al.* 2007b). Breeding experiments crossing *C. tenuimanus* with *C. cainii* have shown that the river of origin and the sex of the parent from that river, impacted the rates of successful reproduction (Lawrence *et al.* 2007b).

Fertile hybrids have been produced in captivity (Lawrence *et al.* 2007b) and electrophoresis techniques used to identify *C. tenuimanus*, *C. cainii*, and hybrid marron in the Margaret River have also identified the presence of F2 back crosses in the wild, demonstrating the fertility of hybrids in the wild (Bunn *et al.* 2008). Growth comparisons of hybrids in captivity found that, with the exception of one instance where Margaret River hybrids (Margaret River *C. tenuimanus* females, and Kent river *C. cainii* males) grew 32% faster than its parents, hybrid offspring typically grow 30–63% slower than the parents (Lawrence *et al.* 2007b).

Behaviour

The two species of marron show some slight variations in behaviour. A laboratory investigation of agonistic interactions between *C. tenuimanus* and *C. cainii* from the Warren River found size was the main factor determining dominance for males (Jenour *et al.* 2007). When animals were the same size, both marron types showed a similar frequency of agonistic interactions (Jenour *et al.* 2007). Female *C. tenuimanus* were less aggressive than *C. cainii* when of equal size or smaller (Jenour *et al.* 2007). When female *C. tenuimanus* had the advantage of size, aggressive interactions were equal, a pattern not seen in males (Jenour *et al.* 2007) nor in studies on crayfish of other species (Bovbjerg 1956; Lowe 1956; Vorburger & Ribi 1999).

Use of shelter for both *C. tenuimanus* and *C. cainii* was minimal when each animal was housed individually and didn't change for males when held in sympatry regardless of relative size (Jenour *et al.* 2007). Female *C. tenuimanus* and *C. cainii* showed a high preference for shelter when kept separately and when housed together with limited shelter, shelter occupancy was higher for marron with a size advantage (Jenour *et al.* 2007).

Conservation of *Cherax tenuimanus*

Summary of known threats

Investigations into the biological characteristics of *C. tenuimanus* in the wild have been confounded by small sample sizes and discontinuous data. In addition, given the error associated with identifying hybrids (see Bunn *et al.* 2008), all studies that have not used genetically tested animals risked the inclusion of hybrids in their research. Despite these caveats, previous work provides valuable insight on the mechanisms behind the decline in *C. tenuimanus* numbers.

Hybridisation is considered one of the major factors causing a decline in the *C. tenuimanus* population (Horwitz 1995a; de Graaf *et al.* 2009), however, other authors have found fewer hybrids than would be expected from random mating (Austin & Ryan 2002). Captive breeding and genetic studies have demonstrated that fertile hybrids can occur, but success of *C. tenuimanus* and *C. cainii* crosses in producing hybrids depends on the river of origin of *C. cainii* and its sex (Lawrence *et al.* 2007b). Where *C. tenuimanus* have been wholly replaced, the population lacks any hybrids at all (Bunn 2004).

Therefore the production of hybrids itself may not be causing the decline, rather reproductive interference may be the mechanism impacting the *C. tenuimanus* population. Parental heritage of hybrids should be examined to elucidate the role of hybridisation. Differences in reproductive potential may also factor in the decline of *C. tenuimanus*. If the low rate of breeding of wild *C. tenuimanus* compared to wild *C. cainii* held in captivity is reflective of a pattern in the wild, this may play a significant role in the decline of *C. tenuimanus*. All aspects of reproductive biology of *C. tenuimanus* and *C. cainii* in sympatry require further investigation in wild populations.

Direct competition is unlikely to be a driver of the decline as both species have demonstrated an equal ability to compete when raised communally (Lawrence *et al.* 2007c). However, an investigation of female interspecific intrasexual competition has shown *C. cainii* to be more aggressive (Jenour *et al.* 2007). Replication of these behaviours in the wild could impact female *C. tenuimanus* directly through losing competitive interactions around shelter acquisition, and/or it could potentially result in the exclusion of *C. tenuimanus* females from food resources or mates.

An environmental replacement mechanism was proposed by Bunn (2004) that suggested the correlation between the presence of farmland bordering the Margaret River and the absence of *C. tenuimanus* in that stretch of river. Bordering land use may have an impact, although *C. tenuimanus* were found throughout Margaret River, prior to the introduction of *C. cainii*, whilst still influenced by the current land use regimes. In addition, the spatial distribution of *C. cainii* was also consistent with a pattern of upstream spread from the point of initial introduction recorded by Austin and Knott (1996).

Knowledge gaps and conservation actions

There are still many aspects of marron ecology in the Margaret River where no conclusions can be drawn due to a paucity of data, e.g. timing of breeding, growth rates, and movement. Without this knowledge, it is difficult to determine the mechanism behind the replacement of *C. tenuimanus* by *C. cainii* and in turn, any recovery actions are likely to be met with limited success.

Development and implementation of an effective, science-based, well-resourced recovery plan is essential for preventing extinction of the critically endangered *C. tenuimanus.* The following key principles have been identified as actions that are achievable with current knowledge and their chance of success is not necessarily linked to understanding the replacement mechanism. Once completed, these actions will form the platform for future actions that will aim to enhance the wild *C. tenuimanus* population, e.g. restocking or investigations into methods for reduction of the *C. cainii* population.

Development of improved field identification techniques to support practical management strategies

The success of practical intervention strategies relies on rapid and accurate field identification of genetically 'pure' *C. tenuimanus*. Field identification based on morphological differences however, has been confounded by the presence of hybrid and backcrossed animals displaying a range of characteristics from each of the species (Lawrence 2002), and possible variations in morphology due to sex, maturity, and size (Bunn *et al.* 2008). The primary and most confronting problem in *C. tenuimanus* conservation is thus the absence of an appropriate method of accurate differentiation between *C. tenuimanus*, *C. cainii,* and the resulting hybrids and back-crosses. Initial classification of *C. tenuimanus* and *C. cainii* into two separate species was based on allozymes; however this technique is not well suited to providing identification in the field. An attempt to generate a key for identification used a small number of characteristics and achieved reasonable success, although it highlighted the need for further improvement (Bunn *et al.* 2008). An urgent need therefore exists for the development of a validated, practical, accurate, and quantifiable method of field identification.

Development of an improved understanding of the genetic purity of remaining *Cherax tenuimanus* population

Given the prolonged period of sympatry of *C. tenuimanus* and *C. cainii* populations within the Margaret River, genetic introgression between the species may have occurred. Therefore a strategy to determine the level of "purity" of remaining *C. tenuimanus* is required before any attempt to establish a breeding population for restocking can begin. Genetic studies involving microsatellites are currently underway to identify the extent of genetic introgression between sympatric *C. tenuimanus* and *C. cainii* populations with the aim of identifying individuals most suited to a captive breeding program (Kennington *et al.* 2013).

Establishment of a captive breeding population of *Cherax tenuimanus*

The recent and rapid decline of *C. tenuimanus* demonstrates that the establishment of a captive breeding population is essential. Some progress has been made in this regard with successful breeding from a population of genetically identified broodstock animals in the Department of Fisheries hatchery facility at Pemberton. Further work is required to ensure the purity of this population. In addition, establishing a captive breeding population of *C. tenuimanus* has to date proved more challenging than for their *C. cainii* counterparts for reasons largely unknown. Overcoming these limitations will be essential to producing animals in sufficient numbers to restock natural waterbodies where the species might be able to become self-sustaining once again.

CONCLUSIONS

Cherax tenuimanus have been rapidly replaced by *C. cainii* within the Margaret River to such an extent that they are now critically endangered (de Graaf *et al.* 2009; Austin & Bunn 2010). A lack of knowledge was highlighted at the *Scientific Workshop on the Margaret River Marron* (Koenders 2002) in 2002 and more than 10 years later many of the same knowledge gaps still exist. Much of what is known is derived from a small number of wild individuals, studies of marron in captivity, or assumed to be similar to *C. cainii*. The paucity of knowledge combined with confusion regarding taxonomy and identification has hampered the effective management of *C. tenuimanus* resulting in the continued decline in both its numbers and its range.

In order to provide an effective way forward to prevent extinction of *C. tenuimanus*, the draft hairy marron recovery plan needs to be revised and completed to include actions with measurable outcomes. With the dwindling numbers of *C. tenuimanus* in Margaret River, the first actions of the recovery plan should be improved methods of identification, determination of the purity of the remaining *C. tenuimanus* populations, and the establishment of a captive breeding population of pure *C. tenuimanus*. Subsequent actions need to address knowledge gaps in basic biology and determine the mechanism of decline, whilst at the same time enhancing the *C. tenuimanus* population and reducing the *C. cainii* population.

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