Chapter thirty-one

Introduction and spread of crayfish (Parastacidae) in Western Australia and their potential to displace indigenous species

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INTRODUCTION

On a global scale, crayfish have been translocated extensively beyond their natural range, both within and between continents, due largely to demand for their commercial culture (Holdich 1987, Horwitz 1990, Elvey *et al.* 1996, Gherardi and Holdich 1999). Deleterious impacts on the receiving environment typically include predation on and competition with indigenous species (Holdich 1987, Horwitz 1990, Elvey *et al.* 1996, Gherardi and Holdich 1999, Chapter 28), alteration to food webs resulting in changes to nutrient and energy flow (e.g. Holdich 1987, Nyström *et al.* 1999, Chapter 28), and the introduction of diseases (e.g. Horwitz 1990, Gherardi and Holdich 1999, Vogt 1999, Chapter 28). The potential for a non-indigenous crayfish species (NICS) to replace an indigenous species has been recognized by, for example, Capelli and Munjal (1982), Butler and Stein (1985), Momot and Leering (1986), Söderbäck (1991), and Vorburger and Ribi (1999), with competitive exclusion being cited as the mechanism for such species replacements (Bovbjerg 1952, 1970, Aiken

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1965, Capelli 1982). Under competitive exclusion two, geographically sympatric, non-interbreeding populations sharing ecological attributes cannot coexist indefinitely; eventually, the population with the superior competitive ability will displace the other (Cole 1960, Hardin 1960). In the case of typically aggressive crayfish, this may occur through interference competition when one species is able to inhibit another's access to a common limiting resource through territoriality or aggression (Jaeger 1974).

In contrast to the evidence from Europe, currently there are no reports in Australia of displacement neither of indigenous crayfish by an NICS nor of introductions of crayfish non-indigenous to the continent. However, there has been widespread translocation of crayfish within Western Australia (WA), and the yabby, introduced from Victoria, currently is expanding its distribution within the State. This is of particular concern given the conservation significance of the WA crayfish fauna (Whiting *et al.* 2000). Due to the ancient separation of freshwater systems of this region from the rest of Australia, the crayfish fauna has remained effectively isolated, resulting in an endemic biota (Figgis 1993, Myers *et al.* 2000) that now is threatened by displacement and/or replacement by non-indigenous species.

This paper summarizes the current situation of NICS in WA and specifically discusses the potential for the deleterious impact of yabbies to indigenous crayfish species and to the ecology of local natural freshwater ecosystems generally.

LEGISLATION

Australia has a long history of introductions of animals and plants that have had a deleterious effect on indigenous fauna. This has lead, in part, to the development of legislation to prevent unauthorized introductions of non-indigenous species (NIS); however, movement of species within the continent is not so well regulated.

Within Australia there are two levels of jurisdiction governing the importation and exportation of fauna. At the Commonwealth level, the Wildlife Protection (Regulation of Exports and Imports) Act (1982) regulates imports of plants and goods that may have an ''adverse effect on, or on the habits of, native Australian animals'' (Part 1: 3E). If an NICS were imported into Australia and became established, it then could be included in the List of Key Threatening Processes under section 183 of the Environment Protection and Biodiversity Conservation (EPBC) Act (1999). NICS currently do not appear in the list since none have been imported from overseas to date (see www.deh.gov.au/cgi-bin/sprat/public/publicgetkeythreats.pl).

Regulations for the importation and exportation of crayfish within Australia are State-specific. In general terms, the exportation of crayfish from each State or territory is not regulated (with the exception of Tasmania); movement within the State is not regulated (except in the Northern Territory), but importations are regulated (Horwitz 1990). It is acknowledged, however, that it is very difficult to prevent unregulated transport of crayfish, particularly given the interest in establishing populations for aquaculture and recreational fisheries.

CRAYFISH IN WA

The crayfish fauna of WA is represented by two genera (Family Parastacidae), *Cherax* Clark and *Engaewa* Riek. In discussing *Cherax* spp. in the State, it is easier to use the commonly expressed vernacular terms to avoid confusion over which scientific names formally are correct. The indigenous peoples of south-western Australia recognized three forms of crayfish that now are classified within the genus *Cherax*: marron, gilgies, and koonacs. Translocations have occurred both within WA and into WA from other States (Table 1). Whilst this paper focuses principally on the likely impacts of increases in geographical ranges of the marron, redclaw, and the yabby, the potential for extinction of one or more of the five currently recognised species of *Engaewa* (Horwitz and Adams 2000) caused by the yabby also should be anticipated. *Engaewa* spp. have very restricted coastal distributions in the extreme south-western corner of the State.

Marron

Nicholl and Horwitz (2000) have recognized the marron as a flagship species for river conservation within WA. Since these large crayfish are much sought after for human consumption, considerable effort has been expended in their aquaculture, locally, interstate, and overseas (Morrissy *et al.* 1990). It comes as a surprise to many that the current distribution of marron in WA represents a geographical range significantly increased post-European colonization of the State. Morrissy (1978), based on historical accounts and the State Fisheries Department records, concluded that the pre-European distribution of marron was south of Mandurah in coastal lakes, creeks, and rivers from the Harvey to the Kent rivers (Fig. 1). The restricted distribution of marron resulted from their habitat requirement of permanent pools and their limited powers of dispersal (Shipway 1951, Morrissy 1978, Morrissy and Fellows 1990).

Whilst it is not known if the historical expansion of marron into rivers and permanent wetlands north of Mandurah have had deleterious impacts on the indigenous crayfish and other stream fauna of this new range, the movement of marron by humans within the south-west corner of the State may not have been without casualty. Recent data indicate that the widespread smooth marron morph is having a markedly negative impact on the 'hairy' marron morph! *Cherax tenuimanus* (Smith), the 'hairy' marron, was described on specimens from Margaret River but marron from other rivers beyond this catchment recently have been separated into a second species, *Cherax cainii* Austin, the 'smooth' marron (Austin and Ryan 2002). The more ubiquitous *C. cainii*, which

Table 1 Species of *Cherax* spp. in WA, together with their indigenous and non-indigenous distributions.

Species name	Common name	Indigenous distribution	Non-indigenous distribution
Cherax cainii	Smooth marron	The high rainfall region between just west of Albany and just south of Perth (Riek 1967, Morrissy 1978).	Hutt River in the north to Esperance in the east (Lawrence and Morrissy 2000).
Cherax destructor	Yabby	Over 2 million km^2, from South Australia and southern Northern Territory in the west, to south-west Victoria and the extreme south-east of SA in the east (Riek 1967).	WA – Hutt River in the north to Esperance in the south-east (Morrissy and Cassells 1992, Horwitz and Knott 1995). Isolated populations inland at Cue and Leonora. Tasmania–Midlands
Cherax preissii	Koonac	Widespread throughout much of the south-west and Wheatbelt, from north of Perth to east of Albany, mainly inland	
Cherax quadricarinatus	Redclaw	Far northern Queensland and northern and eastern parts of the Northern Territory (Riek 1969, Curtis and Jones 1995). Known only from limited area, in exorheic drainage systems from Daly River, NT, to Normanby River, NE QLD.	WA – Kimberley Drainage Division in Western Australia. QLD – populations in lake systems in northern and south-eastern Queensland.
Cherax quinquecarinatus	Gilgie	North of Perth to west of Albany, mainly coastal	
Cherax tenuimanus	Hairy marron	Restricted to the Margaret River	

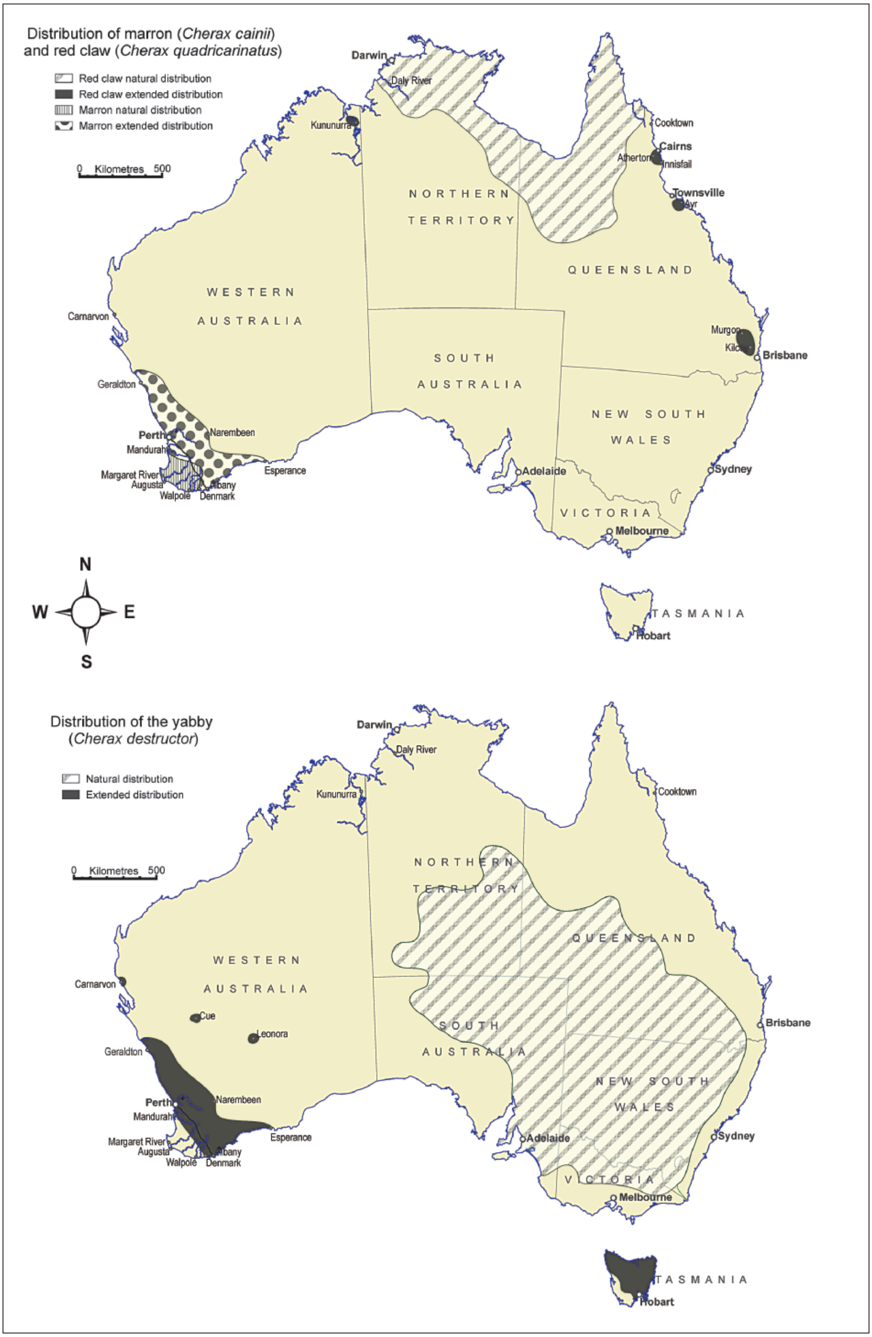

Fig. 1 Map showing the current known distributions of yabbies and redclaw in Western Australia. Distributions are not necessarily continuous and represent best current information. There are likely to be other occurrences which have not yet been discovered.

is the subject of most marron research, is the species widely used in aquaculture, including within the Margaret River catchment itself where smooth marron escapees have bred with hairy marron. Consequently, the distribution of the hairy marron phenotype has been restricted predominantly to forested headwater reaches of the Margaret River, and is now formally gazetted under the WA Wildlife Conservation Act 1950, following IUCN Red List Categories and Criteria version 3.1, as critically endangered (Bunn 2004). The potential for species replacement through competitive exclusion or reproductive interference are yet to be evaluated. There is, however, some evidence that *C. cainii* has a greater growth rate and earlier spawning (Bunn 2004). A management plan to enhance recovery of the 'hairy' morph within the Margaret River system will rely heavily on local community involvement to be effective (Bunn 2004).

The biological impacts of the northern spread of marron into areas with drier, warmer climate and different geological conditions from those wetter, cooler conditions characteristic of their 'pre-European' range have not been evaluated, although there is clear evidence of phenotypic plasticity. Individual biomass, corrected for body length, shows statistically significant reduction on a south to north axis (M. Bennet-Chambers 2007, unpublished data). Given this significant gradient, it is appropriate to raise the question of whether aquaculture of marron in the northern areas where evaporation substantially exceeds rainfall constitutes the wisest use of a limited groundwater resource. It is unlikely that the ecological costs of growing marron depending on groundwater have ever been included in calculating the full costs of production.

Redclaw, *Cherax quadricarinatus*

The redclaw *Cherax quadricarinatus* von Martens is endemic to ephemeral catchments of the Gulf of Carpentaria of northern Australia (Riek 1969, Curtis and Jones 1995, Jones *et al.* 2000). Because of its attraction for aquaculture, the species has been translocated widely within northern Australia and overseas (Horwitz 1990, Curtis and Jones 1995), and not always legally. Redclaw is classed as a restricted fish species for importation into WA (Anonymous 1997). Even so, the potential for aquaculture in the Ord Valley in the East Kimberley of the 'Walkamin' strain was assessed under quarantine (Doupé *et al.* 2004). A limited number of aquaculture licenses subsequently were issued, and shortly after wild populations of redclaw were found established in Lake Kununurra, a Ramsar wetland formed through impoundment of the Ord River (Fig. 1) within the Kimberley Drainage Division of Western Australia (Morgan *et al.* 2004). Since redclaw used in Ord River aquaculture are a genetically different strain to those now found in Lake Kununurra, the source of their introduction is unknown. Doupé *et al.* (2004), however, suggest it is the result of illegal translocations by recreational fishermen. Redclaw has subsequently spread downstream from Lake Kununurra into the lower Ord River, where local recreational anglers have reported redclaw in the stomach of barramundi [*Lates calcarifer* (Bloch)] and catfish (*Arius* spp.). It is quite likely that the species will soon reach Parry Lagoon on the Ord River floodplain, another Ramsar wetland.

The implications for the ecology of these systems are unknown; however, three indigenous species of *Macrobrachium* prawns [*Macrobrachium australiense* Holthuis, *M. bullatum* Fincham, and *M. rosenbergii* (de Man)] and three species of atyiid shrimp (*Caridina* cf *longirostris*, *C. ?nilotica*, and *C. serratirostris* de Man) may all come under competitive pressure. Given their rapid growth rate and tolerance of a wide range of environmental conditions (Jones and Ruscoe 2001), redclaw are likely to thrive in fresh waters of northern WA and rapidly expand their range into the many aquatic systems in this region. Recently, the State Department of Fisheries provided funding to elucidate both the genetic origins and extent of redclaw throughout the Ord River and the reproductive biology, parasitology, and trophic interactions of this with other decapod species.

The yabby, *Cherax destructor*

Since being introduced in 1932 into WA, from a farm dam in western Victoria, the yabby, *Cherax destructor* Clark, has spread into natural river systems within the south-west of WA where it now co-occurs with indigenous crayfish species. Although morphologically distinguishable from the white yabby, *Cherax albidus* Clark, also from eastern Australia, allozyme evidence provides little support for genetic separation between the two species and it has been suggested that the two species should be synonymized (Austin 1986, Campbell *et al.* 1994). *Cherax destructor* is the senior synonym by virtue of page priority; hence, zoologists in WA use the species epithet *destructor*, for example, as used here, but for essentially commercial reasons, fisheries personnel use the epithet *albidus* (e.g. Morrissy and assells 1992). Austin (1985) reported little allozyme diversity from yabbies in the State, but recent studies now indicate considerable variation in WA yabby populations. This perhaps reflects the expansion of yabby aquaculture in the 1990s with farmers introducing multiple strains from eastern Australia.

Although introduced initially to a farm dam at Narembeen, 280 km east of Perth, into a landscape that would not have facilitated easily the natural spread of the crayfish, its hardiness and ability to grow even in stagnant farm dams, together with the human interest in crayfish as a food item, meant that crayfish were spread quickly and widely. Many farmers actually thought they were culturing the indigenous koonac [*Cherax preissii* (Erichson)]. By 1985, most known yabby sites were still east of the Albany Highway (i.e. east of the typical range of indigenous WA crayfish; Austin 1985). Yabby populations were first reported in natural waterbodies west of the 'yabby exclusion zone' by Lynas *et al.* (2004). They have since then shown a continuing strong spread northwards, to the north-east and south-east, with their current distribution being from the Hutt River in the north to Esperance in the south-east (Morrissy and Cassells 1992, Horwitz and Knott 1995). They have also colonized cave streams *via* temporary, short streams on coastal sand-plain (Jasinska *et al.* 1993), occur in coastal plain rivers to the west of the Darling Scarp, and occur in the arid northern Goldfields Region near Leonora (see Fig. 1). The spread of yabbies into natural habitats has generated potential for interactions with other WA indigenous fauna. For example, the spread of yabbies into the Swan-Avon catchment has led to their potential interaction with the critically endangered western swamp tortoise, *Pseudemydura umbrina* Siebenrock, near the Ellen Brook Nature Reserve proclaimed for preservation of the tortoise (Bradsell *et al.* 2002). Yabbies showed strongly aggressive and predatory behaviour toward tortoise hatchlings in a laboratory study using hatchlings of a non-endangered species of tortoise (Bradsell *et al.* 2002).

It seems reasonable to suggest, given the extent of their range expansion to date and apparent capacity to colonize a wide diversity of waterbodies, that yabbies will continue to progress into larger river systems of the Swan Coastal Plain, making their move further into the south-west relatively simple, as has occurred with other invasive species, such as the mosquitofish *Gambusia holbrooki* Girard.

The extensive spread of yabbies appears facilitated by their biology. They are an *r*-selected species with a short life cycle, multiple spawning events, a high spawning frequency, fast growth rates and high fecundity (Lawrence and Jones 2002, Beatty *et al.* 2005). Under suitable conditions, yabbies are able to breed year-round (Morrissy *et al.* 1984). Such life-history traits would allow the successful colonization of disturbed habitats and areas which have undergone anthropogenic modification, such as many of the rivers of south-western Australia. This effectively enables yabbies to become the most abundant crayfish species in many of the freshwater systems throughout its translocated range in south-western Australia (Beatty *et al.* 2005). In addition, yabbies are burrowing crayfish adapted to long-term population survival in the fluctuating environments of relatively impermanent and often highly eutrophic still waters (Morrissy *et al.* 1984). They are also more tolerant than indigenous species of extremes in temperature (Morrissy 1990), hypoxia (Morrissy *et al.* 1984, Holdich and Lowery 1988), and salinity (Department of Fisheries website http://www.wa.gov.au/westfish/aqua/broc/aqwa/marron/).

Human activity has also aided their spread through misguided information and recreational carelessness. Typically, the extent of the problem has gone largely unnoticed due to the common misnaming of this crayfish as the koonac. Yabbies are commonly used as bait for redfin perch and trout fishing in the large government irrigation dams to the south of Perth, with unused live bait often being discarded directly into these waters (Morrissy and Cassells 1992).

Impacts to marron and gilgies

Despite their range expansion and suitability as colonisers, little research has been undertaken, until recently, to ascertain the possible ecological impacts of the invasive yabby in WA. Consequently, studies were undertaken to examine

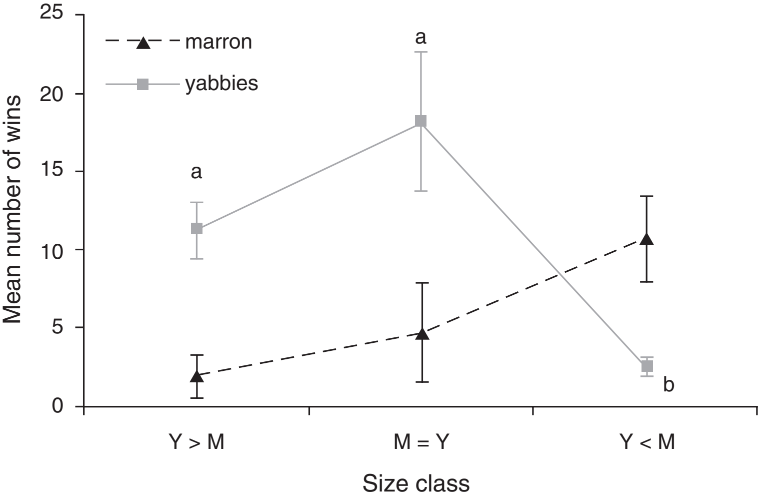

Fig. 2 The interaction between species and size in relation to the mean number of tension contacts 'won' (±SE) by marron and yabbies (n = 28). Letters denote equal means determined using the least significant range test.

the potential for competitive exclusion of two indigenous species, the smooth marron, *C. cainii* and the gilgie, *Cherax quinquecarinatus* (Gray).

In aggressive behaviour trials designed to predict the likely outcomes of competitive interactions in natural systems, aggressive dominance was found to be strongly influenced by size (Lynas 2002). When yabbies were larger or equal in body mass to marron they 'won' a significantly higher number of tension contacts (Fig. 2). Alternatively, when yabbies were of smaller body mass than marron, the marron 'won' a significantly higher number of contacts (Fig. 2; Lynas 2002). Given the small size of gilgies, aggressive experiments with yabbies utilised only individuals of similar body mass. In such interactions, yabbies were found to be equal in aggression to gilgies (Lynas 2002). The importance of size in establishing aggressive dominance is well reported in studies of crustaceans generally (e.g. Hartnoll 1974, Stein 1976), as well as crayfish (Bovbjerg 1956, Lowe 1956, Horwitz 1980, Momot and Leering 1986, Vorburger and Ribi 1999).

Laboratory-based competition experiments were also conducted with sediment as the limiting resource. Sediment was chosen because of its documented significance in influencing crayfish distributions (Bovbjerg 1952, 1970, Suter and Richardson 1977, Grow 1981, Capelli and Magnuson 1983), and its necessity for protection from predators and cannibalism. In these trials, both indigenous species demonstrated a preference for clay substrate, perhaps because they were able to bury themselves in this sediment (Fig. 3; Lynas *et al.* 2006). In the presence of yabbies, however, the number of both gilgies and

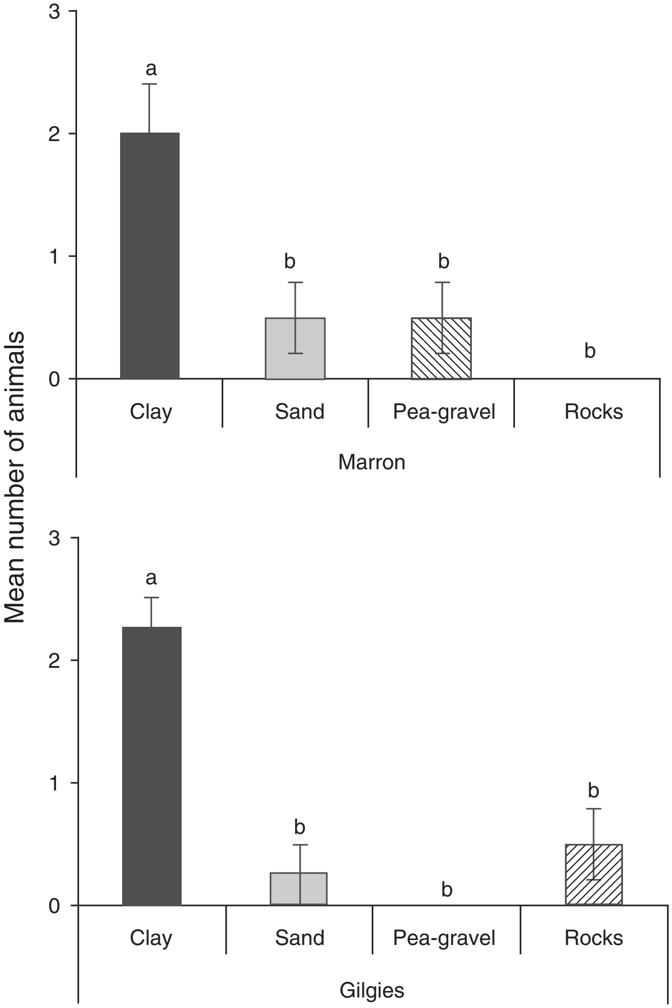

Fig. 3 Mean number (±SE) of marron (above) or gilgies (below) on each sediment when alone, i.e. not in the presence of yabbies. Letters denote equal means determined using the least significant range test.

marron found on the clay was significantly reduced (Fig. 4; Lynas *et al*. 2006). Agonistic behaviour in the form of tension contacts (fight, strike, threat, and avoidance) was common during the trials, with interspecific contests being most commonly recorded on the clay substrate in both marron and gilgie trials (Lynas *et al*. 2006). Therefore, it seems that yabbies used agonistic behaviour to control access to the limiting resource and effectively excluded marron and gilgies from clay substrates in the laboratory (Lynas *et al*. 2006).

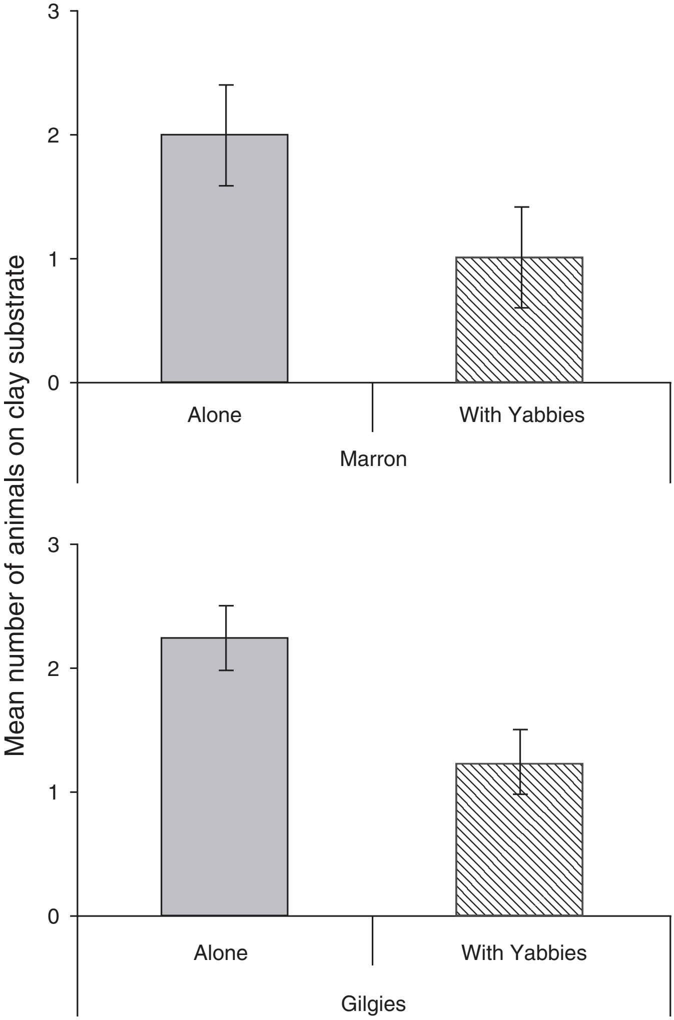

Fig. 4 Mean number (±SE) of marron (above) or gilgies (below) on the "preferred" clay substrate when alone and when in trial with yabbies.

Results from both aggressive behaviour and sediment competition trials indicate that, in habitats of co-occurrence where there is substantial overlap in resource use, the potential for exclusion of marron and/or gilgies by the invasive yabby is high (Lynas 2002, Lynas *et al.* 2006). The experiments demonstrated that aggressive behaviour could be used to procure a limiting resource. Superior competitive ability manifested itself through interference, with the displacement of subordinate species from preferred substrates

(Lynas *et al.* 2006). Yabbies were found to be capable of evicting both marron and gilgies from suitable substrates, thereby indicating the exclusion of these species from the use of a limiting resource under laboratory situations (Lynas *et al.* 2006).

It is suggested that in natural environments marron are likely at a disadvantage. Marron have a life-history strategy between a typical *r*- (summer brooder) and K-selected (winter brooder) species (Beatty 2005). Traits analogous to a winter brooder include synchrony of breeding period, long life cycle, and reliance on permanent aquatic systems (Morrissy 1975, 1983, Beatty *et al.* 2003, Beatty 2005). Traits of a summer brooder include a relatively short brooding period during summer, high egg number per brood, and a rapid growth rate (Beatty *et al.* 2003, Beatty 2005). Although capable of attaining a larger size than yabbies, 2 kg *vs.* 90–100 g (Lawrence and Jones 2002) and having a similar growth rate (Beatty *et al.* 2005), marron mature later and at a much larger size than yabbies (Beatty *et al.* 2003). In a study of marron established in the Hutt River (outside its natural range), Beatty (2005) reported release of juveniles earlier than that previously noted by Morrissy (1975) for the more southerly Warren River populations. Plasticity in biological parameters was considered due to environmental conditions, namely temperature and photoperiod (Beatty *et al.* 2003, Beatty 2005).

There is considerable asynchrony in the biological cycles of these species, with yabbies reaching maturity and releasing juveniles earlier than marron. Therefore, yabbies would have the size advantage when members of both species come into contact in natural systems. In summer, the diet of both marron and yabbies in the Hutt River is dominated by *G. holbrooki,* but yabbies show a dietary shift towards herbivory in winter (Beatty 2007). Consequently, when yabbies and marron co-occur in sympatry in natural habitats, yabbies may dominate food resources and suitable shelter sites over marron juveniles. Marron would have little likelihood of successfully establishing stable populations where yabbies already exist. Predicting the outcome of which species would ‘win’ when yabbies invade a river system with a stable marron population already in occupation is much more difficult and probably depends upon the initial conditions. Larger marron may dominate access to limiting resources over smaller yabbies. Nevertheless, yabbies would persist due to their high fecundity and ability to withstand environmental fluctuations resulting in a more unpredictable future. The survival of marron populations would be subject to increased uncertainty since their juveniles would be unable to compete successfully with yabbies. Furthermore, given the importance of size in determining the outcome of aggressive interactions, we predict that in natural environments where yabbies attain a much larger size than gilgies (≤ 30 g in biomass), yabbies generally would have a size advantage, thereby controlling access to limiting resources such as food and suitable shelter sites when the two species occur in sympatry. Beatty (2007) further suggested the dietary switch reported in yabbies from the Hutt River leads to the potential for competition with the smaller gilgies in unproductive freshwater systems common to the south-west.

As well as competition from NIS, indigenous WA crayfish are at risk from infection from the microsporidian *Thelohania parastaci* Moodie known to be carried by the yabby (Horwitz 1990, Moodie *et al.* 2003). WA crayfish species had not been exposed previously to the disease and therefore are likely to be susceptible. *Thelohania* was found in WA farm dam populations of yabbies in the 1990s (Jones and Lawrence 2002), and has since been reported in yabby populations in the Hutt River (Beatty 2005). This microsporidian could be transmitted to indigenous species by sympatric yabbies. Infection of crayfish by this parasite leads to the destruction of striated and cardiac muscle tissue, resulting in reduced locomotor activity (Henneguy and Thélohan 1892, Cossins and Bowler 1974, Quilter 1976). Survival time of infected individuals has been reported to range from a few months (in the New Zealand *Paranephrops zealandicus* White in Quilter 1976) to two years (in the astacid *Austropotamobius pallipes* Lereboullet in Brown and Bowler 1977), although whether death is always inevitable for infected individuals has yet to be ascertained (Moodie *et al.* 2003). *Thelohania,* therefore, may increase the risk of predation of infected crayfish and reduce their ability to compete with healthy individuals.

Impacts to koonacs

Koonacs, the third main indigenous crayfish species in south-western Australia, have suffered a reduction in distribution post European settlement due to fragmentation and loss of swamps feeding into the headwater streams. The potential impact of the yabby on the endemic koonac, *C. preissii*, is currently unknown; although, Horwitz (1980) noted the importance of size in aggressive interactions between gilgies and koonacs. Juvenile gilgies were found to be dominant over juvenile koonacs but no aggressive differences were detected in the adults of these species (Horwitz 1980). Since yabbies are strong burrowers, they likely would be able to invade swamps inhabited by koonacs. The indigenous species breed in spring within capped burrows and unplug them at the end of the dry season to forage within the waterbody. Given the importance of size in aggressive and competitive interactions, juvenile koonacs are likely to be out-competed by larger yabbies when they emerge from burrows.

Impacts to *Engaewa*

Finally, the importance for conservation of the five currently recognised species of *Engaewa* (Horwitz and Adams 2000) cannot be ignored. The small, strongly burrowing forms of *Engaewa*, with typical burrowing characteristics *sensu* Holdich (2002), have a very restricted coastal distribution in permanently moist acid peat swamps from Dunsborough to Albany; such swamp habitats are more continuous along the south coast from Walpole to Augusta, but become much more fragmented between Augusta and Dunsborough (Burnham 2005). Initially thought to be closely related to the genus *Engaeus* from south-eastern Australia, the study on a region of the 16S mitochondrial gene by Crandall *et al.* (1999) concluded that the genus represents a major, distinctive clade within the Parastacidae. Such relict forms, with ancestry dating from Gondwanic origins, are particularly susceptible to increasing pressures from human activities, including habitat fragmentation and loss (Burnham 2005). Whilst *Engaewa* spp. and indigenous *Cherax* species currently coexist in various levels of sympatry throughout the geographic range of *Engaewa*, it will be important to evaluate the impact on *Engaewa* spp. of the further spread of the yabby into the south-western corner of the State, should it occur. Potential impacts are likely from changes to the structure and function of the ecosystem, including habitat alteration, changes to food web dynamics, and the introduction of disease.

THE FUTURE UNDER A DRYING CLIMATE AND GLOBAL WARMING

Current climatic trends in the south-west of WA likely afford a further advantage to the invasive yabby, particularly over marron. With an increasing drying climate and reduced rainfall across the south-west of WA, groundwater levels are decreasing (Allan and Haylock 1993, Anonymous 2002). There are likely to be numerous ecological consequences. Wetlands and streams driven by groundwater inputs may become ephemeral or permanently dry. Those crayfish able to burrow to the water table may survive dry periods (Bovbjerg 1952, 1970, Taylor 1983). The yabby is a strong burrower (Morrissy *et al.* 1984) and has been recorded alive from burrows beneath lake beds that have been dry for eight years (Holdich and Lowery 1988). Marron, however, inhabit permanent freshwater systems and are not strong burrowers but show a preference for sheltering under logs or stones in the bed of streams (Shipway 1951). Indeed, Riek (1969) suggested the poor development of chelae muscles in marron restricted their burrowing ability. Further, marron do not burrow to escape drought (Maguire *et al.* 1999, Lawrence and Jones 2002). However, in a laboratory trial designed to determine the response of crayfish to lowering groundwater, a single marron did construct an angular pit (j-shaped burrow) approximately 30 cm deep when water levels were artificially lowered (Lynas 2002). This refutes the suggestion that marron are physiologically unable to construct burrows. The experiment further highlights the plasticity of marron and suggests that further investigation on the drought-response mechanisms of WA crayfish and effects of lowering groundwater are required. Gilgies and koonacs are both strong burrowers and able to survive in temporary environments. Therefore, marron would likely be more severely impacted by lowering groundwater levels, with yabbies having a considerable advantage.

With an increase in water temperatures associated with global warming, yabbies would again be at an advantage. The maximum growth of yabbies is at 28 °C (Holdich and Lowery 1988), but for smooth marron, maximum growth is at 24 °C. No research has been undertaken on temperature responses of koonacs and gilgies, but an increasing temperature would likely reduce fitness given they are both indigenous to the colder waters of south-western WA.

CONCLUSIONS

Within the vast area of WA, crayfish occupied a comparatively small area within the reliably high rainfall zone of the south-western corner of the State, where they were widely disjunct from the crayfish of eastern Australia. Because of the interest for their consumption by humans, marron (*C. cainii*), redclaw (*C. quadricarinatus*), and yabbies (*C. destructor*) have been translocated, probably in many cases by recreational fishermen, but also by aquaculturalists, and without regulatory sanction. It is not known if the early spread of marron has affected the ecology of invaded aquatic systems. Similarly, the effects of the recent introduction of redclaw to the Ord River system are unknown. The spread of smooth marron into the Margaret River, however, is threatening the persistence of the endemic hairy marron, *C. tenuimanus*. The impact of the invasive yabby is likely to be much more detrimental to the indigenous crayfish of WA (marron, gilgies, and koonacs), particularly given the drying climate in the south-west, with burrowing crayfish more likely to survive periods of drought. Yabbies, too, have greater tolerance of increased salinity than indigenous crayfish, with dryland salinity being a major landuse and ecological problem in the southern half of WA. In all cases of interactions with indigenous crayfish, the aggressive yabby is likely to be competitively superior, particularly in the juvenile stages because of the earlier release of young into streams.

The spread of the yabby seems inexorable, given commercial interest, the current widespread distribution, the extent of unregulated movement (for example populations inland at Leonora and Cue), and developing climate change. It is difficult to foresee any effective control impeding the continuing spread of *C. destructor* in WA and consequent impacts on indigenous species.

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