

The geographic ranges of Tasmanian crayfish: extent and pattern

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ABSTRACT

The geographic ranges of the 34 native species of freshwater crayfish known from Tasmania are mapped and described from extensive museum collections. Extents of occurrence range from over 30,000 to about 5 km² and species in the open water genus *Astacopsis* have significantly greater ranges than the burrowing species in one of two undescribed genera within *Parastacoides*. Species living in Type 1 burrows associated with open water have significantly larger ranges than those found in Type 2, water table, burrows. Many species show mosaic distributions with either parapatric boundaries, or narrow zones of geographic overlap, or sympatric contact zones. In most cases, closely related species are also geographically close; exceptions to this trend may represent older clades, some members of which have suffered range contractions. The Tasmanian crayfish fauna presents a useful opportunity to examine questions about geographic ranges.

Key words: geographic range, Parastacidae, parapatry, Tasmania

I. INTRODUCTION

The variation in the extent of geographic ranges of animals and its control has attracted considerable attention in recent years (Brown *et al.* 1996; Gaston 2003). While attention has been particularly directed towards the effect of latitude and Rapoport's "Rule" (Gaston *et al.* 1998), other factors, such as body size, trophic group, dispersal ability and abundance, have been discussed, as well as the general problem of how best to define and represent geographic ranges on maps. The majority of studies to date have dealt with the large scale, making comparisons between ranges at the continental or greater scale.

At a smaller geographic scale the problems of the definition of ranges are exaggerated, as the life-time ranges of individual animals become larger relative to the overall range of the species. Thus the effect that records of vagrant animals have on the estimation of a species range may be substantial. Crayfish, particularly burrowing species, have significant advantages in this regard, since the animals' individual ranges are very small, dispersal rates are slow, and their

presence in an area is generally unambiguous. Few other land or freshwater animals are so sedentary.

A further problem for the accurate description of geographic ranges is disturbance by humans, in the form of local extinctions or translocations. In many places in the temperate zone it is now difficult to gain any clear idea of the natural ranges of species. The island of Tasmania offers an uncommon opportunity to record the natural ranges of a fairly diverse crayfish fauna. Some 40% of the island is reserved in national parks, and even in the areas developed for agriculture or forestry there are still sufficient remnant crayfish populations to reconstruct pre-european distributions.

The Tasmanian crayfish fauna comprises at least 34 species, only one of which (*Cherax destructor* Clark, 1936) is introduced. Table I summarises the fauna. Recent taxonomic studies (Hansen and Richardson in press) have subdivided the genus *Parastacoides* Clark 1936 into two new genera, referred to in what follows as *Parastacoides* new genus 1 and *Parastacoides* new genus 2, abbreviated below as *P.* new genus 1 and *P.* new genus 2. *Parastacoides* has been shown to be a junior synonym of *Geocharax* Clark, 1936, and so disappears. These two genera have 11 and 3 species respectively; they are described here using the codes in Hansen and Richardson (2002). Crayfish have been collected and studied in Tasmania for over a century, and substantial collections exist in museums and the University of Tasmania. Although much of the western half of the island is difficult to access, large-scale surveys, either to assess the impact of hydro-electric developments or to catalogue the values of the Western Tasmania World Heritage Area, have provided a good coverage of collections.

This contribution seeks to describe the patterns in the geographical ranges of the entire Tasmanian crayfish fauna and to relate them to latitude, ecology, the interactions between species, and phylogenetic relationships. As a result we hope to raise questions for further testing.

II. MATERIALS and METHODS

Distributional data were obtained from a variety of sources. The School of Zoology, University of Tasmania holds a databased collection of some 1500 specimens of *Parastacoides*, and further substantial collections of the other Tasmanian genera, including *Geocharax*. Horwitz (1990) published detailed distribution maps for *Engaeus* species, and these have been supplemented by more recent studies by the Threatened Species Unit (Nature Conservation Branch, Dept. of Primary Industry, Water and Environment, Hobart) to define the

distributions and status of *Engaeus* species listed under Tasmania's *Threatened Species Protection Act 1995*.

Hamr (1992) reviewed the genus *Astacopsis* and published distribution maps for the three species in that genus. The distributional information for the giant freshwater crayfish, *A. gouldi* Clark, 1936, has been improved by more recent surveys (Horwitz 1994; Blühdorn 1997).

The distributional data are all in the form of point records of collection localities, either as Australian Map Grid coordinates, or as raster images scanned from publications (Horwitz 1990; Hamr 1992). These were combined in the desktop mapping program MapInfo (ver. 5.5, MapInfo 1999) to produce maps on which polygons representing the distribution of each species could be overlaid. The area of each range was measured using the area function in MapInfo.

The least biased way to convert a set of point data to a range polygon is to draw the minimum convex polygon around those points. This was the basic approach used here to estimate ranges, and while this approach should be realistic when there are many point records for each species, it will inevitably result in an overestimate of range size. In some cases where there had been intensive efforts to define ranges (in the case of threatened species, for example) we were able to use reliable negative records to refine the distributions and draw concave polygons.

The other problem in converting point data to polygons is the relationship between the area of occurrence for each species and its area of occupancy. Clearly crayfish do not occupy every part of the landscape within a minimum convex polygon drawn around collection records, but it is difficult to decide at which point to represent the distribution as a series of disjunct areas. Only in two cases (apart from species occurring on off-shore islands), *Engaeus disjuncticus* Horwitz 1990 and *E. lengana* Horwitz 1990, did we choose to subdivide ranges into disjunct areas; this followed the interpretation of the main collector of these species (Horwitz 1990).

Statistical analyses were carried out using SPSS (Ver 11 for Macintosh).

III. RESULTS

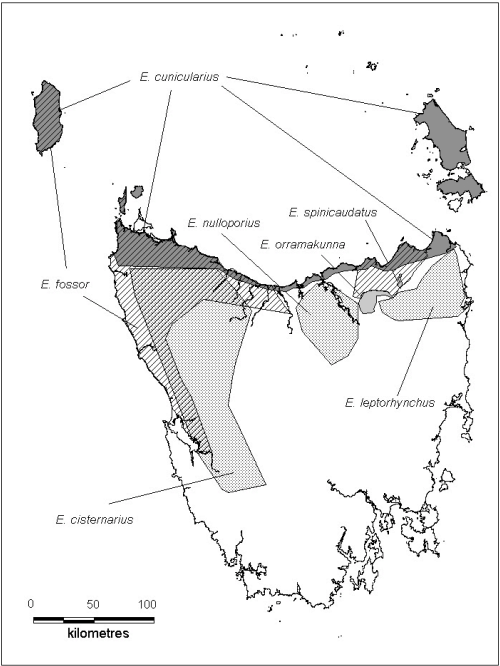
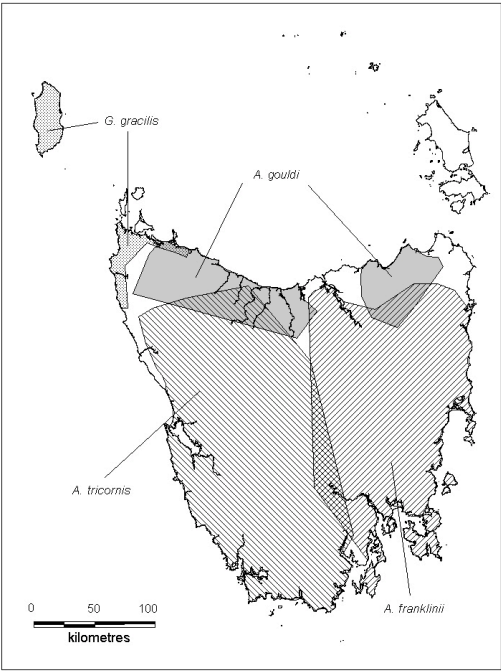
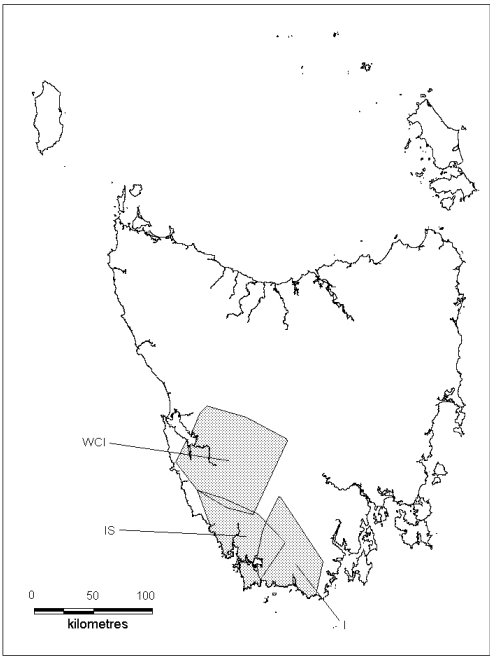
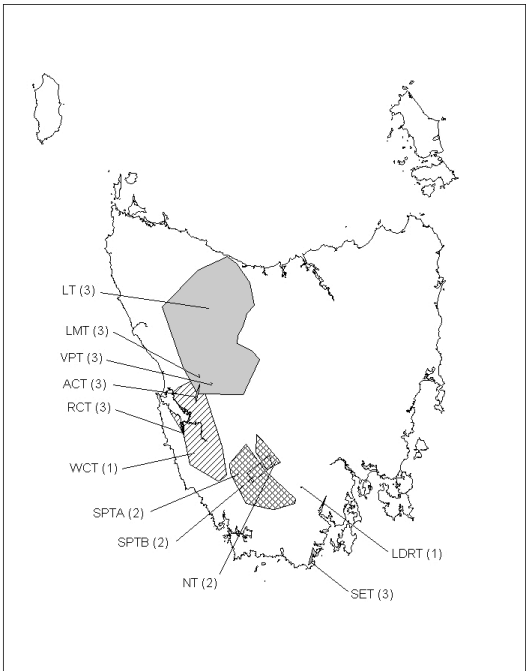
The ranges of Tasmanian crayfish in the native genera are shown in Figures 1-5. The burrowing species are mainly found in the west and north of the island, while the river-dwelling *Astacopsis* species are found throughout. Figure 6 shows that areas of high diversity can be seen in the north east (mostly *Engaeus* spp.) and the central west (*Engaeus* and *Parastacoides* spp.).

Figure 1. Polygons showing the extent of occurrence of 11 undescribed species in *Parastacoides* new genus 1.

Figure 2. Polygons showing the extent of occurrence of three undescribed species of *Parastacoides* new genus 2.

Figure 3. Polygons showing the extent of occurrence of three species of *Astacopsis* and *Geocharax gracilis* in Tasmania. Note that *G. gracilis* is also found in western Victoria and South Australia.

Figure 4. Polygons showing the extent of occurrence of seven species of *Engaeus* in Tasmania. Note that *E. cunicularius* is also found in southern Victoria.



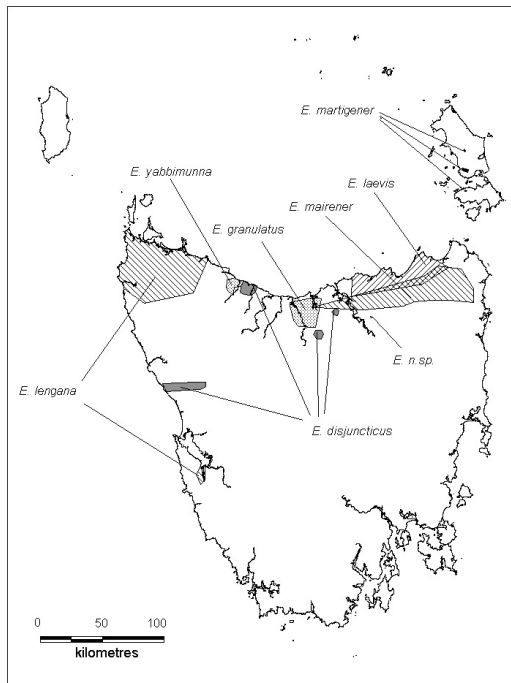


Figure 5. Polygons showing the extent of eight species of *Engaeus* in Tasmania. Note that *E. laevis* is also found in southern Victoria.

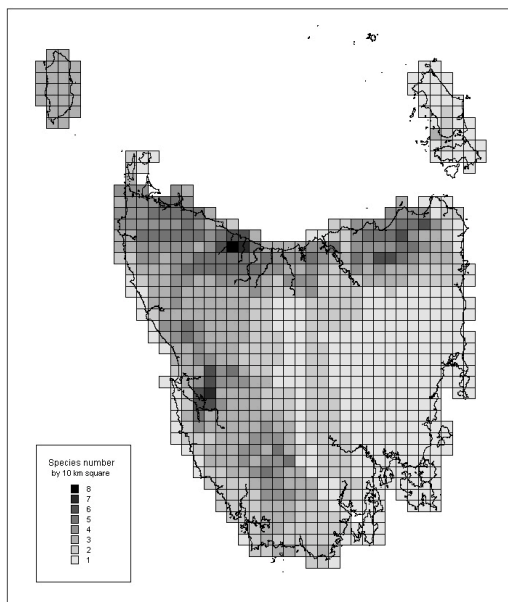


Figure 6. Numbers of native freshwater crayfish species in 10 km squares in Tasmania. No data are available for two of the offshore islands.

Table I. Native freshwater crayfish in Tasmania, showing their extents of occurrence (range) and the burrow type (Horwitz and Richardson 1987) in which they are usually found; decimal values indicate that the species is found in more than one burrow type.

Name	Burrow Type	Range (km⁻²)	Log Range
<i>Astacopsis franklinii</i>	1.0	23950	4.38
<i>Astacopsis gouldi</i>	1.0	9175	3.96
<i>Astacopsis tricornis</i>	1.0	30740	4.49
<i>Engaeus cisternarius</i>	2.5	11570	4.06
<i>Engaeus cunicularius</i>	1.5	6525	3.81
<i>Engaeus disjuncticus</i>	2.5	401	2.60
<i>Engaeus fossor</i>	2.0	10501	4.02
<i>Engaeus granulatus</i>	2.0	498	2.70
<i>Engaeus laevis</i>	1.0	1279	3.11
<i>Engaeus lengana</i>	1.0	2892	3.46
<i>Engaeus leptorhynchus</i>	2.5	2432	3.39
<i>Engaeus mairener</i>	2.5	2241	3.35
<i>Engaeus martigener</i>	2.0	15.1	1.18
<i>Engaeus nulloprius</i>	1.5	2499	3.40
<i>Engaeus orramakunna</i>	2.5	296	2.47
<i>Engaeus spinicaudatus</i>	2.0	27	1.43
<i>Engaeus tayatea</i>	2.0	1559	3.19
<i>Engaeus yabbimunna</i>	2.0	131.9	2.12
<i>Geocharax gracilis</i>	1.5	2266	3.36
<i>P. new genus 1 RCT</i>	2.0	39	1.59
<i>P. new genus 1 WCT</i>	2.0	2489	3.40
<i>P. new genus 1 NT</i>	2.0	321.4	2.51
<i>P. new genus 1 LDRT</i>	2.0	5	0.70
<i>P. new genus 1 SET</i>	2.0	37.8	1.58
<i>P. new genus 1 SPTA</i>	2.0	1752	3.24
<i>P. new genus 1 VPT</i>	2.0	5	0.70
<i>P. new genus 1 LT</i>	1.5	7468	3.87
<i>P. new genus 1 LMT</i>	2.0	5	0.70
<i>P. new genus 1 ACT</i>	2.0	18	1.26
<i>P. new genus 1 SPTB</i>	2.0	225.6	2.35
<i>P. new genus 2 WCI</i>	1.5	5560	3.75
<i>P. new genus 2 I</i>	1.5	2910	3.46
<i>P. new genus 2 IS</i>	2.0	2850	3.45

Table I lists the range areas, and when the ranges are ranked (Fig. 7) it is clear that they span several orders of magnitude, and that the species from each genus are not uniformly distributed across the whole span. An analysis of variance of range sizes by genera showed that there was a significant effect of genus ($F_{3,28} = 6.111$, $P = 0.0025$) and *post hoc* tests found that the mean range of *Astacopsis* spp. was significantly greater than that of *P. new genus 1*. While the mean ranges of *P. new genus 2* and *Engaeus* were indistinguishable, it is notable that variation in range sizes of the three species in *P. new genus 2* is much less than in all the other genera.

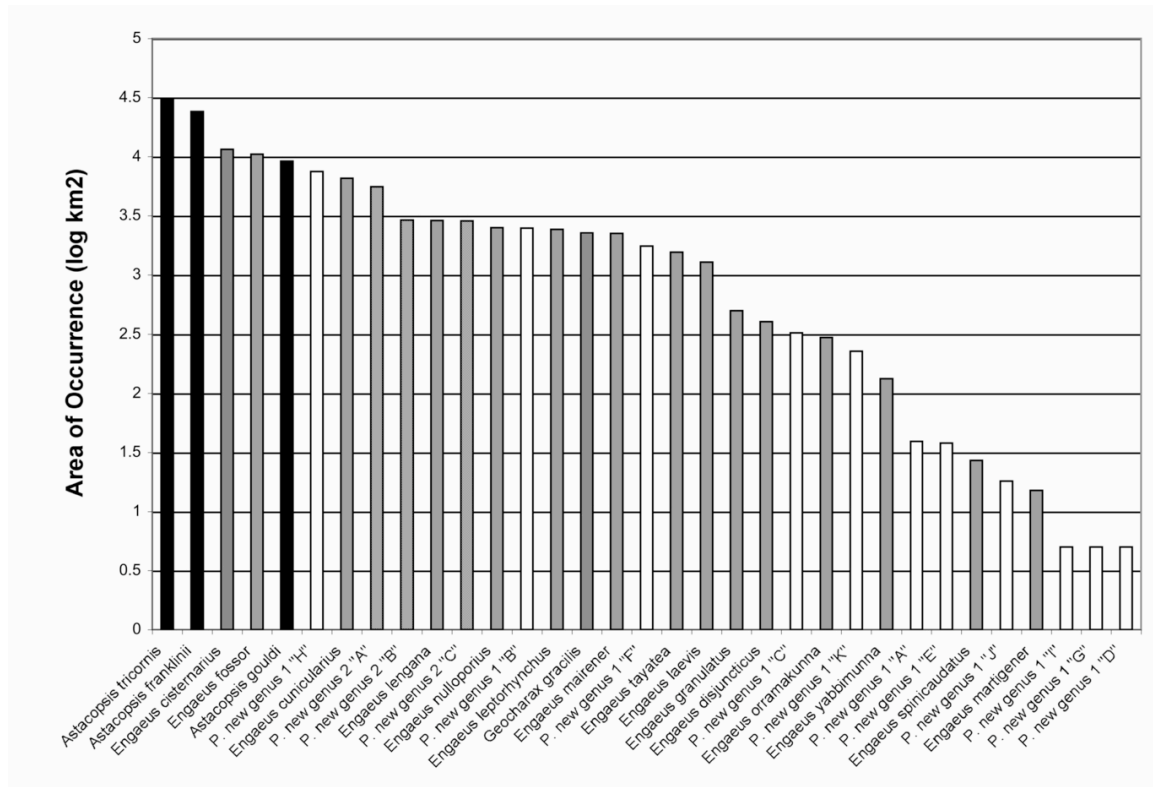


Figure 7. Areas of occurrence (log transformed) of Tasmanian freshwater crayfish, ranked by size. Column fills represent genera: black: *Astacopsis*; grey: *Engaeus*; white: *Parastacoides* new genus 1; diagonal hatch: *P. new genus 2*; horizontal hatch: *Geocharax*.

Table I includes a score describing the type of burrow that each species usually constructs. Horwitz and Richardson (1986) classified crayfish burrows on the basis of their relationship with surface or ground water, but it is common for a species to be found in more than one burrow type. Thus Table I includes categories “1.5” for species found in both Type 1 and Type 2 burrows and “2.5” for those found in both Type 2 and Type 3 burrows. When range sizes are plotted against burrow type (Fig. 8) it appears that more species fall into Type 2 than any other class and that the span of range sizes in this class is greater than the others. Analysis of variance confirms a significant effect of burrow type on range

size ($F_{3,28} = 7.631$, $P = 0.0007$) and *post hoc* tests show that the mean range size for species found in Type 2 burrows is significantly less than those found in Type 1 and 1.5.

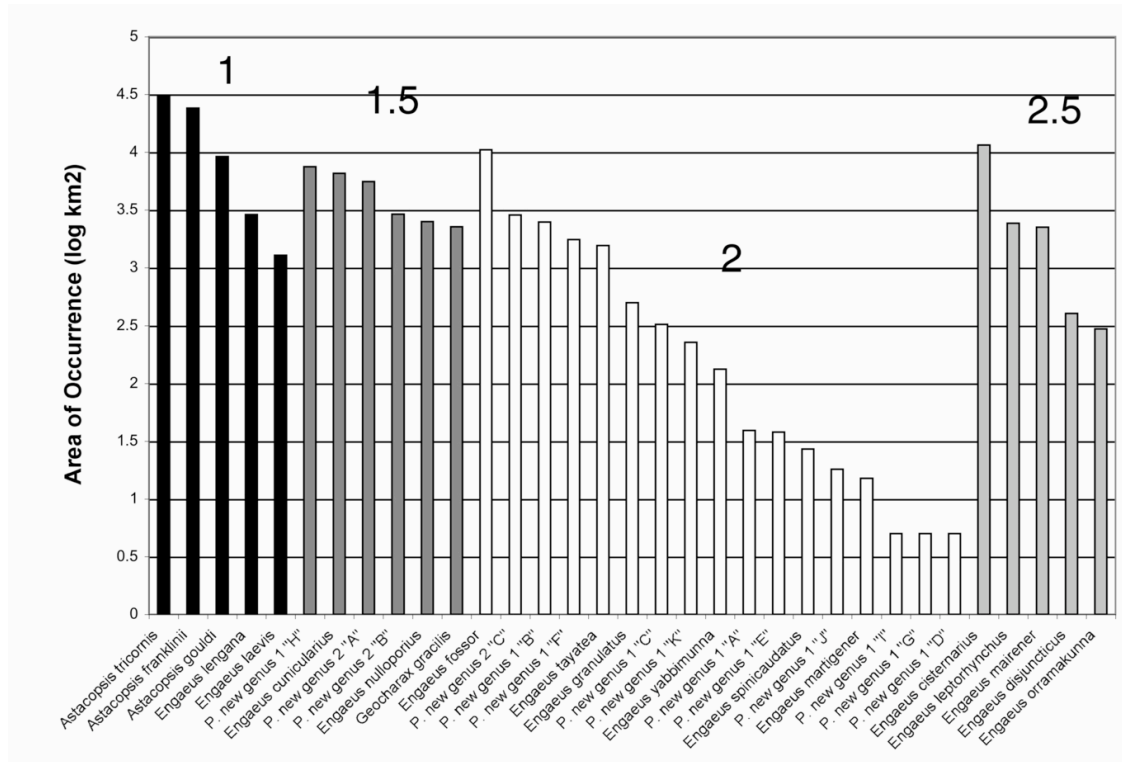


Figure 8. Areas of occurrence (log transformed) of Tasmanian freshwater crayfish, ranked by burrow type (Horwitz and Richardson 1986). Intermediate scores are used for those species commonly found in more than one burrow type (see text).

The relationships between the ranges of all 34 native species were examined and six possible states were recognised (Table II). Ranges separated by at least 5 km were said to be non-overlapping (Nlap); ranges that were contiguous along a significant length of their common boundary, or which overlapped by less than 5 km were said to be parapatric (Para). Several pairs of species showed partially overlapping ranges along a significant front; where these overlapped more than 5 km but less than 40% of the smaller range they were termed sympatric contact zones (SCZ), following Hansen and Richardson (2002). Figure 9 illustrates the differences between parapatric boundaries and sympatric contact zones in one area of the island. The remaining classes all described degrees of substantial overlap between ranges; if one range overlapped more than 40% of a smaller range this was described as “overlap” (Olap). The last two cases were where one range was entirely within the other; they were separated on whether the two species were found ecologically sympatric (IntS), or whether there was some form of habitat partitioning between them (IntA) (eg Richardson and Swain 1980; Horwitz *et al.* 1985; Richardson and Horwitz 1988).

Table II. Summary of geographical interactions between freshwater crayfish in Tasmania.

Interaction	Definition	Cases in <i>Parastacoides</i>	Cases in <i>Engaeus</i>	Cases in <i>Astacopsis</i>
Nlap	Ranges > 5 km apart	132	128	0
Para	Ranges < 5 km apart	10	36	0
Scz	Ranges overlapping > 5 km. But < 40% of smaller range	12	20	3
Olap	Ranges overlapping by > 40% of smaller range	18	18	0
IntS	One range internal; animals ecologically sympatric	4	6	0
IntA	One range internal; animals ecologically separated	6	2	0

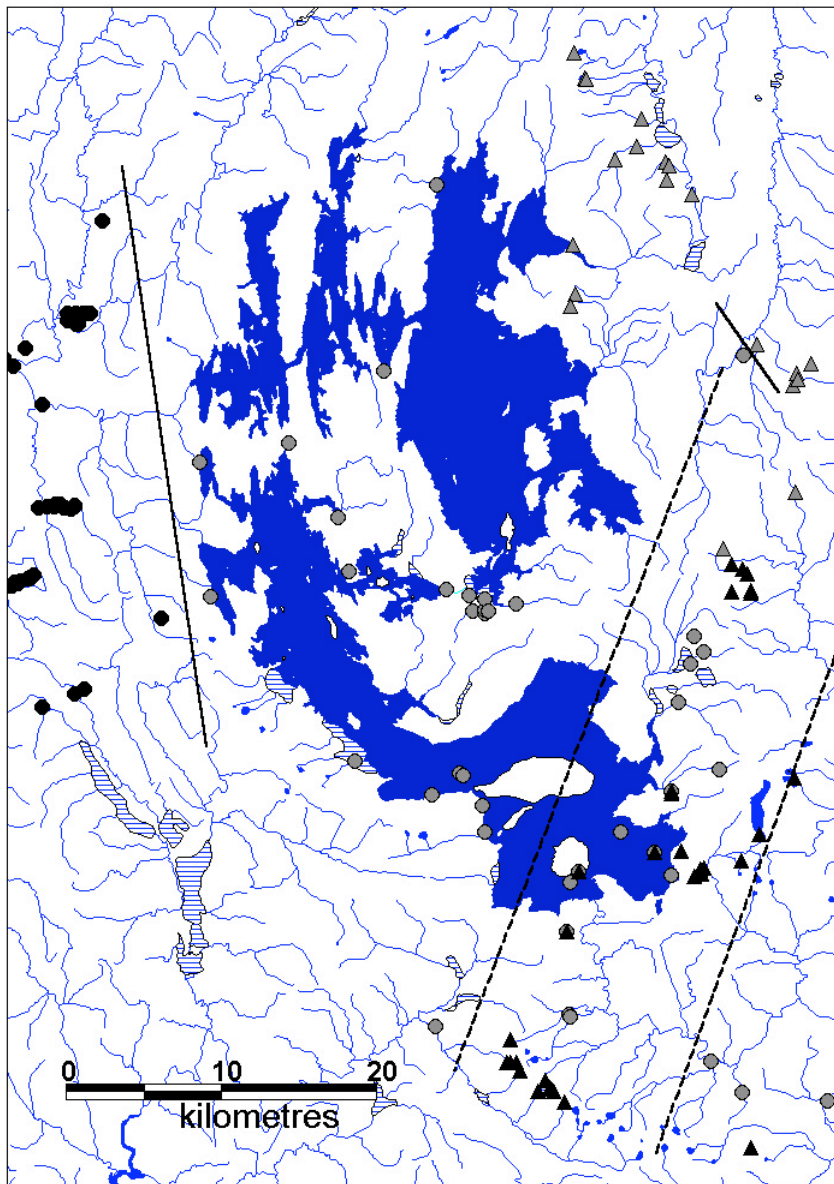


Figure 9. Distributions of burrowing crayfish around the Lakes Gordon and Pedder, south west Tasmania, to show parapatric boundaries (solid lines) and a sympatric contact zone (dashed lines). Solid circles: *Parastacoides* new genus 1 WCT; grey circles: *P.* new genus 1 SPTA; grey triangles: *P.* new genus 1 NT; black triangles: *P.* new genus 2 I.

The frequencies of the different types of range interactions can be compared between the genus *Engaeus* and the two closely related new genera derived from *Parastacoides* (Fig. 10). Frequency tests suggested that parapatric boundaries and sympatric contact zones were more commonly found between

Engaeus spp. The relationships between the three *Astacopsis* species appear to be sympatric contact zones from Figure 3; however, the overlaps between *A. gouldi* and the other two species are largely due to two doubtful records and if these are eliminated, the interactions would be defined as parapatric. The boundaries between *A. franklinii* and *A. tricornis* also appear parapatric in the areas of their range that have been closely, studied (Hamr 1992).

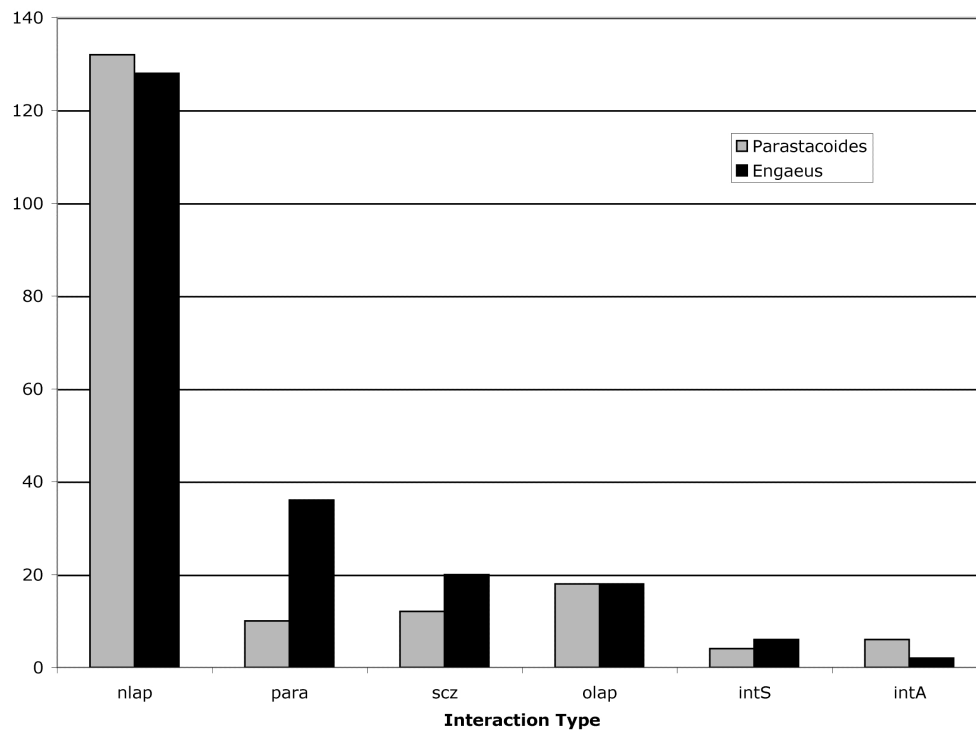


Figure 10. Frequencies of various types of interactions between species of *Engaeus* and undescribed species of *Parastacoides*. nlap: no overlap; para: parapatric boundary; scz: sympatric contact zone; olap: overlapping; intS: one distribution internal and ecologically sympatric; intA: one distribution internal and ecological separate (for fuller explanation, see text).

Finally, the spatial relationships between species ranges were compared in terms of what is known of the phylogenetic relationships between the species. Horwitz (1990) did not present a full phylogeny of *Engaeus* spp., but suggested some groupings of related species, which show substantial geographical concurrence (Fig. 11). The situation is a little more complex in *P.* new genera 1 and 2 (Fig. 12); some clades (*P.* new genus 1 NT, SPTA and SPTB; ACT, WCT and LMT; *P.* new genus 2 WCI, I and IS) are geographically congruent, but the members of one apparently closely-related pair, *P.* new genus 1 WCT and LDRT, are widely geographically separated. *P.* new genus 1 LDRT is also strongly separated from the rest of its clade.

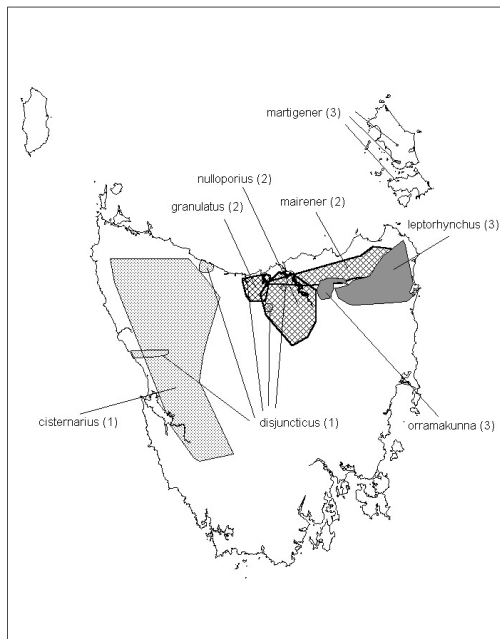


Figure 11. Extents of occurrence of *Engaeus* species suggested by Horwitz (1990) to be phylogenetically related. Numbers in brackets refer to phylogenetic groupings.

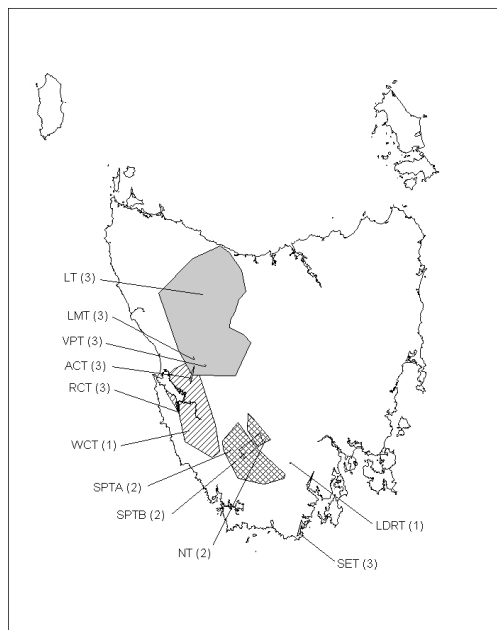


Figure 12. Extents of occurrence of undescribed species in *Parastacoides* new genus 1 suggested by Hansen and Richardson (2002) to be phylogenetically related. Numbers in brackets refer to phylogenetic groupings.

IV. DISCUSSION

The local diversity of crayfish in Tasmania is relatively high in the context of the Australian fauna (Whiting *et al.* 2000), but no detailed analyses of regional Australian crayfish faunas have been carried out. Species densities of crayfish in parts of North America are undoubtedly higher, but once again there are no comparable regional analyses (but see Crandall 1998). France (1992) examined the latitudinal (as opposed to geographic) ranges of North American crayfish at a continental scale too great to be comparable with the two to three degrees of latitude spanned by Tasmania.

Range size is clearly related to broad scale habitat, and it is unsurprising that the river-dwelling *Astacopsis* species have ranges that exceed those of most of the burrowing species, because of the opportunities for dispersal through drainage systems and their relative independence of wet soils to burrow in. However, two burrowing species, *Engaeus cisternarius* and *E. fossor*, have ranges of similar size (in fact greater than that of *Astacopsis gouldi*). This probably reflects their distribution in the western half of Tasmania, where the climate is wet and seasonality is low (Jackson 1999), providing large, continuous areas of suitable habitat. Both species are also often associated with drainage channels, *E. fossor* on the floodplain of the stream and *E. cisternarius* on gully sides (Suter and Richardson 1977), once again giving them access to avenues of dispersal. Most of the rest of the species with above average range sizes are found in the wetter, western parts of the island.

The smaller range sizes are dominated by species from *P.* new genus 1. Like all species in this genus (and *P.* new genus 2) they are found in the western half of Tasmania. There are no obvious ecological reasons for their restricted ranges, either in terms of climate, soil or vegetation, or interactions with other species (they are not involved in parapatric or sympatric contact zones), suggesting that the causes are historical.

The relationship between range sizes and the type of burrow that species construct reflects the pattern of habitat discussed above to some extent. The largest average ranges are found amongst species constructing Type 1 burrows in at least some situations, but interestingly the group of species that live in Type 2 burrows has the smallest average range, less than that of the predominantly Type 3-burrowing group. While the classification of species by burrow type is difficult (because many species can be found in more than one type of burrow), this may suggest that the Type 2 burrow restricts the dispersal of species more than either burrows constructed either in or at the side of open water, or Type 3 burrows, the most terrestrial type. The ability to construct a Type 3 burrow and

thus remain independent of the ground water table may allow dispersing animals to persist in situations where an animal in a Type 2 burrow would not survive a summer dry period.

The mosaic distributions and parapatric contact zones between ranges suggest strong interactions of some kind between the species involved. These may include direct competition for resources, genetic effects such as reinforcement or stepped clines (Littlejohn and Watson 1985), or more subtle interference between mating systems (Bull 1991). At present there is little direct evidence to choose between these possibilities. Some of the narrow interactions zones are between closely-related species (eg *Astacopsis* spp., *P. new genus 2* spp., *P. new genus 1* SPTA and NT), while others are between species in the two new *Parastacoides* genera. No small-scale genetic studies have yet been done that might indicate the presence of hybrid zones between any of these pairs.

In ecological terms, local habitat partitioning has been recognised between several species (Richardson and Swain 1980 Horwitz *et al.* 1985; Richardson and Horwitz 1988), but it remains unknown whether the same mechanisms apply to any geographical separations.

In most cases, phylogenetically close species were also geographically close, but the exceptions are of interest. *P. new genus 1* WCT and LDRT are more closely related than any other pair of *P. new genus* species and yet their distributions are highly disjunct. Their clade, however, is deeply separated from the remaining species in *P. genus 1*, and this suggests that they may represent the relictual evidence of what were once more widespread species. Since *P. new genus 1* WCT has the larger range and is closer to the centre of the genus range, while *P. new genus 1* LDRT has a minute range at the very eastern edge of the genus' range, we suggest that it is *P. genus 1* LDRT, or its ancestors, that have suffered major range reduction. The same argument could be applied to *P. new genus 1* SET and its phylogenetic and geographical relationship with the rest its clade.

The objective of this study was principally to describe the patterns of distribution in the Tasmanian crayfish fauna, taking advantage of the relatively diverse fauna and relatively undisturbed landscape. The description of the patterns has been straightforward, but a considerable amount of work remains to be done to provide convincing explanations for them.

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REFERENCES

- Blühdorn, D.R. (1997) Recovery plan for the Tasmanian Giant Freshwater Lobster, *Astacopsis gouldi* Clark Inland Fisheries Commission, Hobart.
- Brown, J.H., Stevens, G.C., and Kaufman, D.M. (1996) The geographic range: size, shape, boundaries, and internal structure. *Annual Review of Ecology and Systematics* **27**, 597-623.
- Bull, C.M. (1991) Ecology of parapatric distributions. *Annual Review of Ecology and Systematics* **22**, 19-36.
- Crandall, K.A. (1998) Conservation phylogenetics of Ozark crayfish: assigning priorities for aquatic protection. *Biological Conservation* **84**, 107-118.
- France, R. (1992) The North American latitudinal gradient in species richness and geographical range of freshwater crayfish and amphipods. *American Naturalist* **139**, 342-354.
- Gaston, K.J. (2003) *The structure and dynamics of geographic ranges*. Oxford University Press, Oxford.
- Gaston, K.J., Blackburn, T.M., and Spicer, J.I. (1998) Rapoport's Rule: time for an epitaph? *Trends in Ecology and Evolution* **13**, 70-74.
- Hamr, P. (1992) A revision of the Tasmanian freshwater crayfish genus *Astacopsis* Huxley (Decapoda: Parastacidae). *Papers and Proceedings of the Royal Society of Tasmania* **126**, 91-94.
- Hansen, B. and Richardson, A.M.M. (2002) Geographic ranges, sympatry and the influence of environmental factors on the distribution of species of an endemic Tasmanian freshwater crayfish. *Invertebrate Systematics* **16**, 621-629.
- Horwitz, P.H.J. (1990) A taxonomic revision of species in the freshwater crayfish genus *Engaeus* Erichson (Decapoda: Parastacidae). *Invertebrate Taxonomy* **4**, 427-614.
- Horwitz, P.H.J. (1994) Distribution and conservation status of the Tasmanian giant freshwater lobster *Astacopsis gouldi* (Decapoda: Parastacidae). *Biological Conservation* **69**, 199-206.
- Horwitz, P.H.J. and Richardson, A.M.M. (1986) An ecological classification of the burrows of Australian freshwater crayfish. *Australian Journal of Marine and Freshwater Research* **37**, 237-242.
- Horwitz, P.H.J., Richardson, A.M.M., and Boulton, A. (1985) The burrow habitat of two sympatric species of land crayfish, *Engaeus urostrictus* and *E. tuberculatus* (Decapoda: Parastacidae). *Victorian Naturalist* **102**, 188-197.
- Jackson, W.D. (1999). The Tasmanian environment. In *Vegetation of Tasmania* (eds J.B. Reid, R.S. Hill, M.J. Brown and M.J. Hovenden), pp. 11-38. Australian Biological Resources Study, Canberra.
- Littlejohn, M.J. and Watson, G.F. (1985) Hybrid zones and homogamy in Australian frogs. *Annual Review of Ecology and Systematics* **16**, 85-112.
- Richardson, A.M.M. and Horwitz, P.H.J. (1988). Habitat partitioning in parastacid crayfish. *Freshwater Crayfish* **7**, 91-97.

- Richardson, A.M.M. and Swain, R. (1980) Habitat requirements and geographical distribution of three subspecies of *Parastacoides tasmanicus*, and *Engaeus cisternarius* (Crustacea; Decapoda: Parastacidae), burrowing crayfish from south west Tasmania. *Australian Journal of Marine and Freshwater Research* **31**, 475-484.
- Suter, P.J. and Richardson, A.M.M. (1977) The biology of two species of *Engaeus* (Decapoda: Parastacidae) in Tasmania. III. Habitat, food, associated fauna and distribution. *Australian Journal of Marine and Freshwater Research* **28**, 95-103.
- Whiting, A.S., Lawler, S.H., Horwitz, P., and Crandall, K.A. (2000) Biogeographic regionalization of Australia: assigning conservation priorities based on endemic freshwater crayfish phylogenetics. *Animal Conservation* **3**, 155-163.