Freshwater Biology (2007) **52**, 1820–1833 doi:10.1111/j.1365-2427.2007.01766.x

APPLIED ISSUES

The ecology and conservation status of Madagascar's endemic freshwater crayfish (Parastacidae; *Astacoides*)

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SUMMARY

1. Freshwater crayfish of the genus *Astacoides* are endemic to the highlands of eastern Madagascar. Very little is known about their ecology and how this affects their vulnerability to threats. Working in the Fianarantsoa forest corridor, we used a combination of ecological research (>29 000 crayfish caught and released) and interviews (>130 interviews in 38 villages) to investigate the ecology and status of four of the seven described species.
2. *Astacoides* species studied showed very slow growth, with growth rates of *Astacoides granulimanus* and *Astacoides crosnieri* among the slowest known in any species of crayfish. We found individuals of all three species for which we had growth data which we estimate at more than 20-years old. The size at which females became ovigerous varied among species. *Astacoides betsileoensis* withheld reproduction until a large size (only 30% of females were gravid at 60-mm carapace length, compared with 90% for *A. granulimanus*). This is likely to make *A. betsileoensis* particularly vulnerable to overexploitation and we found that only 10% of individuals measured in a market ($n = 909$) would have reproduced before being caught compared with 35% of the more common *A. granulimanus* ($n = 30\ 561$).
3. Habitat loss is a serious threat to the genus; even *A. granulimanus*, the most widespread species, was only found in rivers or streams flanked by natural vegetation. *Astacoides caldwelli*, the rarest species in this study, was found only at low altitudes (<800 m) in rivers draining forested catchments. Habitat loss is particularly rapid in low elevation forest. *A. crosnieri* was restricted to swampy land that is rapidly being converted to rice fields. Introduced Asian snakehead fish (*Channa maculata*) may pose a hitherto unrecognised threat to some species, particularly *A. betsileoensis*.
4. Madagascar's freshwater habitats have great significance for global biodiversity yet conservation effort, as in much of the world, has focused on terrestrial ecosystems. Until recently almost nothing was known about the ecology of *Astacoides* crayfish, a diverse and economically important genus. Here, we show that members of the genus vary markedly in their reproductive biology, growth rates, habitat requirements and the threats they face. We suggest that habitat loss is an urgent threat, especially to *A. caldwelli* and *A. crosnieri*,

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while overharvesting is probably the most immediate threat to the larger *A. betsileoensis*. We call for more attention to be paid to Madagascar's exceptional, yet understudied, freshwater biodiversity.

Keywords: biodiversity, habitat, harvesting, introduced, Madagascar

Introduction

Globally, freshwater crayfish are a highly threatened group. Between one-third and one-half of the world's crayfish species are in decline or threatened with extinction (Taylor, 2002) and species in North America may be going extinct at a rate of 4% per decade (Ricciardi & Rasmussen, 1999). The most serious threat to many species is the introduction of non-native crayfish species and the diseases they carry (Soderback, 1995; Lodge *et al.*, 2000). Habitat loss and overharvesting also threaten some populations (Horwitz, 1994; Whitmore & Huryn, 1999). Because of their keystone role in stream and river communities (Nyström, Bronmark & Graneli, 1996; Parkyn, Collier & Hicks, 2002; Usio & Townsend, 2004), changes in crayfish fauna can have knock-on effects on stream biota. Despite the urgency of the situation, we lack basic information on the ecology of many crayfish species and the threats they face.

Madagascar's freshwater crayfish (Parastacidae: *Astacoides*), the only uniquely tropical crayfish genus, contains a great diversity of forms. The 'excessively spiny' *Astacoides betsileoensis* for example probably exhibits the most ornate appearance of any extant or extinct crayfish species (Hobbs, 1987). For more than 100 years zoogeographers have puzzled about how the progenitors of the genus *Astacoides* reached Madagascar and about their relationship with other crayfish taxa (Huxley, 1896; Reik, 1972; Hobbs, 1987; Crandall, Harris & Fetzner, 2000). There are no freshwater crayfish native to Africa or the Indian subcontinent and the isolated position of Madagascar with respect to other crayfish populations has led to interesting, if not satisfying, speculation (see Crandall, 2003 for a review).

Astacoides (see Table 1 for taxonomic authorities) are endemic to the eastern highlands of Madagascar where they are harvested by local people for subsistence use and small-scale trade (Jones *et al.*, 2006). Despite this economic importance, there is almost no published information available about the ecology of any species and the distribution of species within Madagascar is imperfectly known (Raberisoa, Elouard & Ramanankasina, 1996; Boyko *et al.*, 2005). Hobbs (1987) used morphology, particularly carapace ornamentation and cheliped shape, to infer the likely habitat of each species, extrapolating from his knowledge of morphological features and habitats among the North American crayfish family Cambaridae. The lack of ecological information makes it difficult to formally assess the conservation status of *Astacoides* species. However, a review of available information (Crandall, 2003) suggested that all six described species be considered as vulnerable or endangered under the World Conservation Union Red List criteria (IUCN, 2003) citing harvesting as the most important threat. Since then a seventh species has been described and the authors note its restricted distribution and likely need of conservation attention (Boyko *et al.*, 2005). Detailed work has recently been carried out on the population dynamics and vulnerability to harvesting of one species; *Astacoides granulimanus* (Jones *et al.*, 2005; Jones & Coulson, 2006) which suggests that this species may be less vulnerable to harvesting than previously thought. Preliminary work (Jones *et al.*, 2006) looking at the composition of the crayfish harvest suggests that the very large *A. betsileoensis* may be more threatened but no information is available on the ecology or threats faced by this species.

This paper results from the first in-depth study of the ecology of *Astacoides* species. We combine information on growth rates and reproductive biology, a broader study of habitat usage and information from interviews with local people. From this we draw conclusions about the ecology and conservation status of four of the seven described species of crayfish in Madagascar.

Methods

The detailed ecological study reported here was carried out in Ranomafana National Park between

Table 1 The main habitats where each taxon of *Astacoides* was recorded

Taxon (number captured)	Forest streams (>1000 m.a.s.l.)	Forest streams (<1000 m.a.s.l.)	Slow-flowing rivers (>1000 m.a.s.l.)	Slow-flowing rivers (<800 m.a.s.l.)*	Swampy areas within forest	Rice fields/canals	CPUE max., mean ± SD (n)
A. betsileoensis (Petit) red/green (n = 933)	†		‡			†	16, 11 ± 3 (n = 12)
A. betsileoensis (Petit) red (n = 20)	†		‡				N/A
A. caldwelli (Bate) (n = 132)		†		‡			9, 5 ± 3 (n = 4)
A. crosnieri E (Hobbs) (n = 1510)					‡	†	135, 63 ± 25 (n = 18)
A. crosnieri W (Hobbs) (n = 1027)	†				‡	†	46, 34 ± 9 (n = 9)
A. granulimanus (Monod & Petit) (n = 26 400)	‡	‡	‡	‡	†	†	85, 37 ± 20 (n = 82)

The number of crayfish of each taxon recorded during this study is given below the taxon name. Metres above sea level are indicated by 'm.a.s.l.' Catch per unit effort (CPUE) gives an approximate measure of abundance.

The unit of effort is two crayfish harvesters searching for 2 h. Maximum CPUE, mean ± SD and the number of 2-h search periods carried out is given for each species. N/A: data not available.

*Between 800 and 1000 m is the edge of the escarpment; there are therefore few slow flowing rivers between these altitudes.

†Occasionally found in this habitat.

‡major habitat type where this species was recorded.

April 2001 and November 2005. More than 29 000 crayfish were caught in a mark-and-recapture study (detailed analysis on the vulnerability of *A. granulimanus* to harvesting is presented in Jones *et al.*, 2005). To validate our findings from the Ranomafana area we also visited sites throughout the Fianarantsoa forest corridor (see Fig. 1) to look at habitat associations and distributions of the species (April–November 2005). During this broader study we caught and measured more than 500 crayfish from 28 locations. We also carried out 133 interviews in 38 communities to cross-check our observations about habitat associations and to investigate perceived trends in crayfish abundance.

Study area

The Fianarantsoa forest corridor is a 160-km continuous stretch of Malagasy eastern rainforest (Fig. 1) stretching south from Ranomafana National Park. It runs along a steep escarpment separating Madagascar's central plateau to the west (>1000 m) from the lowlands to the east (<800 m). The eastern rainforests are a highly biodiverse ecosystem under extreme pressure from land conversion for agriculture (Green & Sussman, 1990). The economy of the area is based on a mixture of irrigated rice production in the valleys and slash-and-burn on hill slopes. Many households also rely heavily on harvesting forest products such as crayfish for subsistence use or sale although local taboos prevent some villages from commercial crayfish harvesting (Jones *et al.*, 2006). Dependence on forest products is particularly high during the 'hungry season' when rice stocks run out and the new harvest is not yet in (Dostie, Haggblade & Randriamamonjy, 2002). The hungry season is earlier on the western than the eastern side of the corridor, but tends to fall between August and January (Hardenbergh, 1993).

Species present, habitat requirements and relative abundance

Working with local crayfish harvesters, we searched potentially suitable crayfish habitat (identified from local knowledge and Hobbs' (1987) suggestions based on the species' morphology). The crayfish were caught by hand, using the two methods used locally: turning rocks and feeling underneath for sheltering crayfish, or 'fishing' using a stick with worms tied on with plant fibres. Identification of crayfish followed

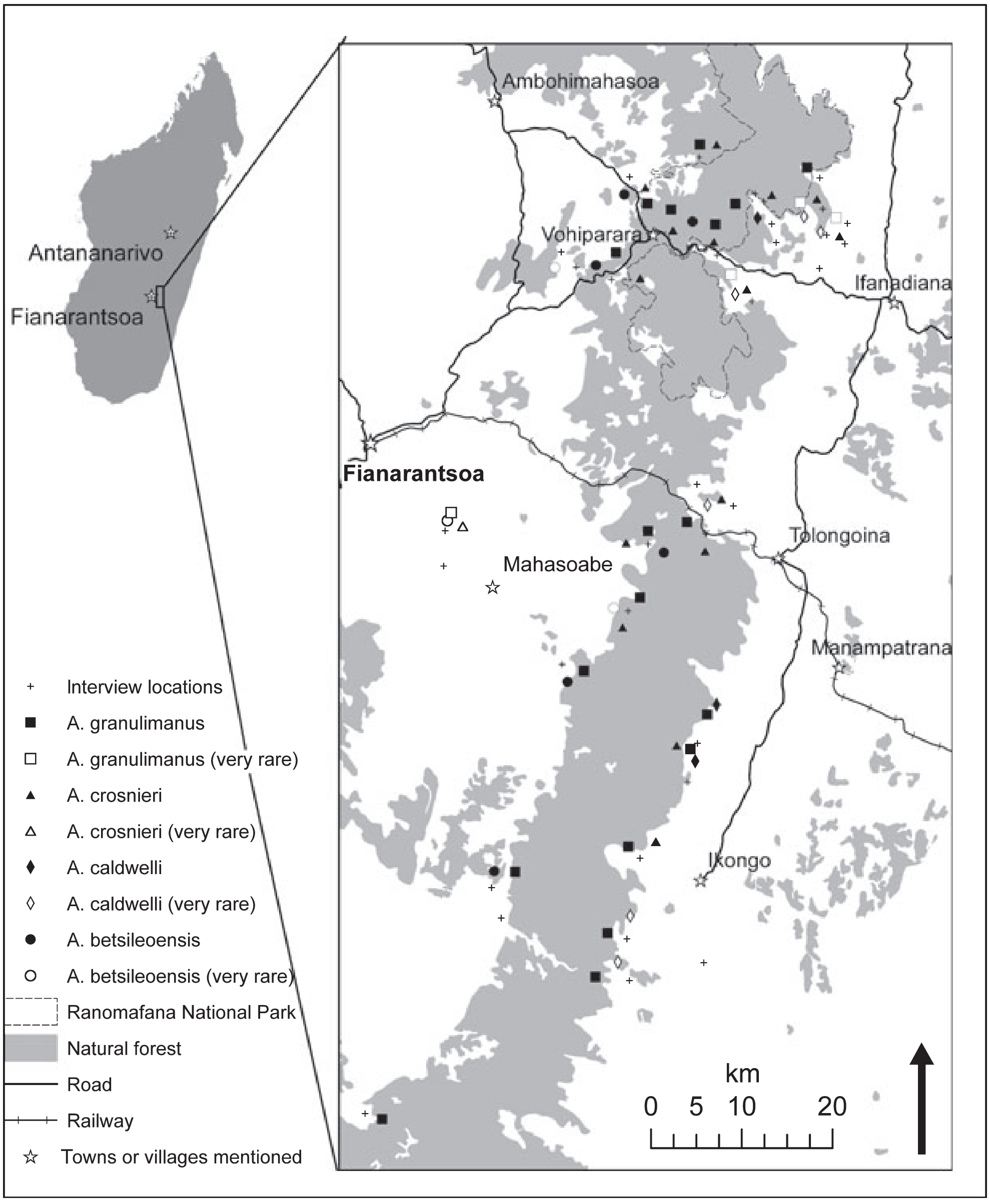

Fig. 1 The Fianarantsoa forest corridor showing the crayfish species found at each location visited in the study and the locations of interviews.

Hobbs (1987). Voucher specimens were deposited at Brigham Young University, U.S.A. and the University of Antananarivo, Madagascar. We recorded sampling locations with a Global Positioning System and made notes on habitat type including vegetation cover, stream width, depth, incline and substrate type. To investigate which species could tolerate disturbed habitat we also searched apparently less suitable habitat, such as rice fields, irrigation canals, heavily silted streams and rivers strongly influenced by human activities. At a sub-set of sites, all with apparently good habitat, we carried out timed searches (two crayfish harvesters searching for 2 h) to provide a relative measure of abundance in terms of catch per unit effort.

Reproductive biology

We investigated the reproductive biology of *Astacoides* species in the Ranomafana area by recording the species, sex and carapace length (CL) of all crayfish caught. We counted the number of eggs on each egg-bearing female caught. To investigate the relationship between size and fecundity and whether this relationship varied between taxa, we built a Generalized Linear Model (GLM) using egg number as the response variable, CL and CL^{-2} as covariates and taxon as a factor.

We investigated the proportion of females of each taxon bearing eggs each year using a GLM with binomial error structure and logit link function, with breeding or not breeding as the response variable. Carapace length was a covariate and taxon was a factor. Only females caught between July and November, the peak reproductive period, were included in this analysis. We used this relationship to investigate the proportion of harvested individuals of each species which would have reproduced prior to being caught. The data on the sizes of crayfish when caught came from a study of the crayfish harvesting village of Vohiparara (see Jones *et al.*, 2006). In total 32 000 harvested crayfish of the three species found in the area (*A. betsileoensis*, *Astacoides crosnieri* and *A. granulimanus*) were measured. Harvested crayfish were separated into 1-mm size classes (equivalent to measurement error) and the number of harvested crayfish in each class multiplied by the estimated proportion of that size class which reproduce in a given year (from the GLM). Errors were estimated by taking bootstrap samples with replacement of both market and reproduction data using R (R Core Development Team, 2006).

Growth

Previous research (Jones & Coulson, 2006) has described the growth of *A. granulimanus.* We investigated the growth of three other species; *A. betsileoensis*, *Astacoides caldwelli* and *A. crosnieri*. Crayfish were marked with individual marks (Visible Implant Elastomer, Northwest Marine Technology, Shaw Island, Washington, U.S.A.). Individuals were recaptured during opportunistic visits to the sites over a period of 4 years. Where repeated measures of the same individuals were available, we fitted the change in size and the time interval between measurements to the specialized Von Bertalanffy growth function (VBGF; Equation 1) using the programme FISAT II (FAO, 2004):

$$L = L_\infty - (L_\infty - L_0)\exp^{-(kt)} \qquad (1)$$

where L is length at time t, L_∞ is length at infinity and k is the rate at which L_∞ is reached. The VBGF has often been used to describe crustacean growth, including that of crayfish (Anastacio, Nielson & Marques, 1999). The standard errors in parameter estimates were used to estimate the 95% confidence intervals on the growth curves by bootstrapping in programme R (R Core Development Team, 2006). Previous work (Jones & Coulson, 2006) has found no difference in growth rate between the sexes in *A. granulimanus* so we combined both sexes to maximize samples sizes.

Trends in crayfish abundance and distribution over time

We carried out informal interviews to gain additional information on distribution, habitat requirements and perceived trends in abundance over time. Interviews were carried out in Malagasy (two of the non-Malagasy authors are fluent in the language). We interviewed crayfish harvesters and elders in forest frontier villages as well as interviewing elders in villages which have experienced extensive deforestation within living memory. Approximately, 133 interviews were carried out in 38 villages across the corridor region and involved more than 250 informants. Crayfish taxa in the area are easily distinguished and each have a unique vernacular name (see Jones *et al.*, 2006), although these may vary from place to place. At the end of each interview we confirmed which taxon was locally assigned to each vernacular name using a picture board and preserved specimens. In many villages, we employed our informants to help with the field work following the interview, giving us further opportunity to confirm the identification of local vernacular names. In all cases the informant's taxonomy agreed with ours and each taxon we recognized had a single and consistent local name.

Results

Species present

We identified the crayfish as belonging to six taxa, preliminarily identified as four species: *A. betsileoensis*, *A. caldwelli*, *A. crosnieri*, *A. granulimanus* (see Table 1). *Astacoides crosnieri* found to the east of the escarpment

(*A. crosnieri* E) were much smaller than those found to the west (*A. crosnieri* W; Jones, 2004) and slightly different in form with a particularly narrow areola. For the purpose of this study we treat the two populations separately, pending genetic analysis. Hobbs (1987) described two forms of *A. betsileoensis*; the red type and the red/green type. We found both types in Ranomafana National Park during this study, their distributions being apparently separated by a waterfall in the Nanaroa River west of Vohiparara. Throughout the rest of the study areas we recorded only the red/green type. Fig. 1 shows the locations visited in this study and the species recorded at each site.

Habitat use and relative abundance

The taxa of *Astacoides* in the corridor area were found in different, but overlapping, habitat types (Table 1). Both forms of *A. betsileoensis* were found mostly in deep, slow-flowing rivers above 1000 m, but occasionally in smaller tributaries where deep pools mimicked the habitat offered by a larger river. They were found mostly in areas of natural vegetation although a reproductive individual was recorded from an irrigation channel in a large rice field and a number were found in a pine plantation (though the river bank itself had natural vegetation). *Astacoides betsileoensis* was never found to be very abundant with a maximum of 16 individuals found during a 2 h of search (Table 1). *Astacoides betsileoensis* is a secondary or tertiary burrower (*sensu* Hobbs, 1942) and was found in burrows up to a metre long, with extensive galleries running parallel to the bank.

Astacoides caldwelli was only found in large rivers at low altitude (600–800 m) to the east of the escarpment. Deforestation has been extensive at these low elevations and many of the rivers were in areas long cleared of natural forest, however, this does not necessarily signal tolerance of habitat loss as in all cases the catchments cases remain forested. Nowhere was this species abundant. A maximum of nine individuals were found during a 2-h search (Table 1). *Astacoides caldwelli* is a tertiary burrower (*sensu* Hobbs, 1942) but tends to make simpler burrows than *A. betsileoensis*.

Astacoides crosnieri E and W were always found in swampy habitat with a soft substrate. *Astacoides crosnieri* E was found at lower altitudes (600–800 m). It was only recorded from natural swampy forest with standing water. We searched an area of suitable habitat which had been converted the year before to a rice field and an adjacent unconverted area. We found only a handful of crayfish in the cleared area during a 2-h period but found 90 in the adjacent uncleared area (Table 1). This suggests that *A. crosnieri* E is quickly extirpated following habitat conversion. *Astacoides crosnieri* W was found at higher altitudes (above 900 m) and appeared to be more tolerant of a range of habitat types. It was frequently recorded from abandoned rice fields and even occasionally in the canals of active rice fields. *Astacoides crosnieri* is a primary burrower (*sensu* Hobbs, 1942), building a complex burrow system that seldom communicates with open water. The burrows were between 0.5 and 1.5-m deep, depending on the depth of the water table.

Astacoides granulimanus was found throughout the study area, wherever there was forest. It was most common in small, clear, fast-flowing forest streams (up to 85 individuals were found during a 2-h search; Table 1) where it was often the only crayfish present. It was also abundant in larger, deep rivers (sympatric with *A. betsileoensis* in the west or *A. caldwelli* in the east). *Astacoides granulimanus* appeared susceptible to deforestation as it was found down to much lower altitudes in forested than in deforested streams and was almost never found in streams whose banks had been recently cleared for agriculture. However, it is tolerant of non-primary native forest as it was found in highly disturbed natural forest to the west of Ranomafana National Park. It was also found in forest dominated by pine and eucalyptus near Mahasoabe (though the banks of the rivers in the plantation retained natural vegetation). The lowest altitude at which we recorded it was 600 m and we found it regularly up to 1300 m, above which we did not survey. Its burrowing habit is similar to *A. caldwelli*.

Reproductive biology

Timing of reproduction All species in the study area bred just once a year and showed strong synchrony in reproduction with a clear peak in the proportion of females bearing eggs between July and October. Eggs were laid in June or July and carried for approximately 4 months, hatching in October or November. All juveniles were independent by the end of January (data not shown). The timing of reproduction was dependent on altitude with populations at lower altitudes carrying eggs and young a few weeks earlier than those at higher altitudes.

The relationship between size and fecundity There was a strong positive relationship between size and female fecundity for all taxa (Fig. 2a,b). There was a weakly significant interaction between CL^{-2} and taxon suggesting that this relationship differs between the taxa ($F_{6,486} = 2.44$, $P = 0.046$).

The relationship between size and the proportion breeding There was a positive relationship between size and the proportion of females breeding for all species (Fig. 2c). This relationship varied between taxa (there was a strongly significant interaction between size and taxon; $F_{5,7846} = 6.07$, $P < 0.001$). *Astacoides betsileoensis* withholds reproduction compared with *A. granulimanus*, a species which reaches a similar eventual size. The proportion of females of a given size bearing eggs in any 1 year therefore differed markedly among species. More than 90% of *A. granulimanus* females bear eggs at 60-mm CL; however, only 30% of *A. betsileoensis* bear eggs at this size. The size at which 50% of females would be reproductive can be compared among species; this size varies from 31-mm CL for *A. crosnieri* E to 65-mm CL for *A. betsileoensis* (Fig. 3).

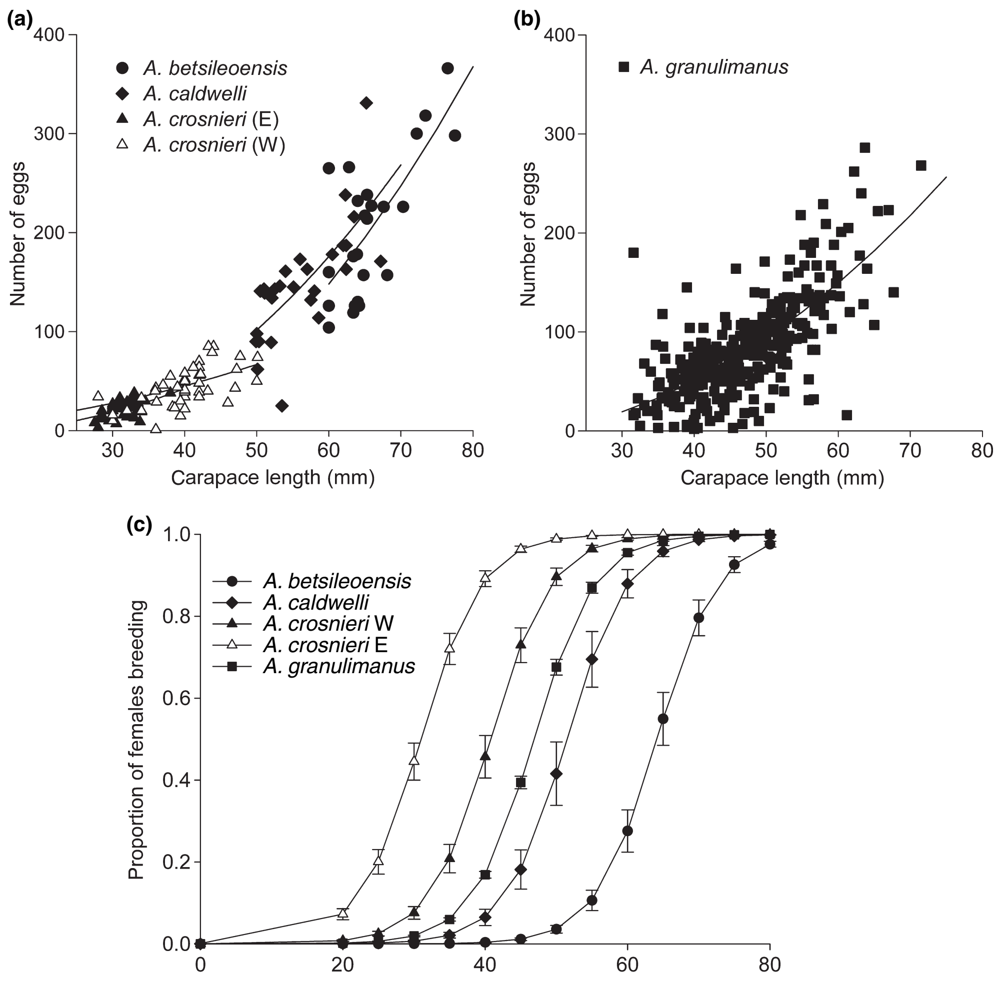

Fig. 2 (a) The relationship between size and fecundity of all the taxa except *Astacoides granulimanus* which is shown separately in (b) for clarity. The regression lines shown are predicted from the GLM described above (the minimal model described 71% of the variance). (c) The relationship between size and the proportion breeding for each *Astacoides* species studied, as predicted by a GLM with binomial error structure. Error bars show SEMs.

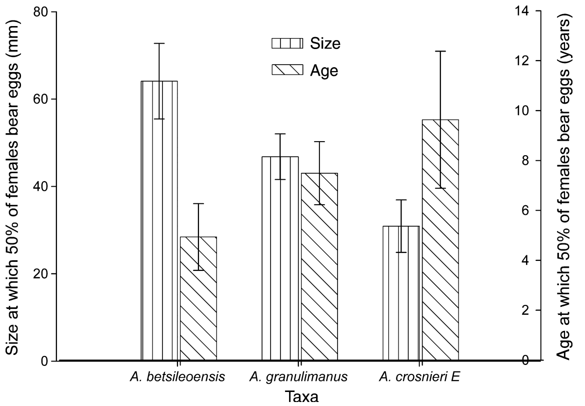

Fig. 3 The estimated size and age at which 50% of females bear eggs for *Astacoides betsileoensis*, *Astacoides granulimanus* and *Astacoides crosnieri* E. Error bars show 95% confidence intervals.

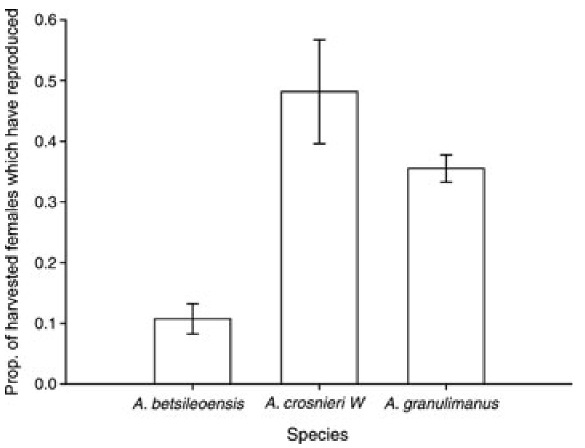

Fig. 4 The estimated proportion of *Astacoides granulimanus* (n = 30 561) *Astacoides betsileoensis* (n = 473) and *Astacoides crosnieri* W (n = 909) harvested by villagers in Vohiparara which would have reproduced prior to harvesting.

Using this information on the relationship between size and fecundity and data on the size distribution of harvested crayfish (Jones *et al*., 2006), we estimated that at least 35% of female *A. granulimanus* and 50% of *A. crosnieri* caught by harvesters would have reproduced before being harvested. However, this figure is only 10% for *A. betsileoensis* (see Fig. 4).

Growth

We had sufficient growth increments to construct growth curves for *A. betsileoensis*, *A. crosnieri* E and *A. granulimanus* (Fig. 5). *Astacoides betsileoensis*, which reaches the largest maximum size (79.8 mm), was the fastest growing (k = 0.33 ± 0.096). *Astacoides crosnieri* E reached the smallest maximum size (50.04 mm) and was the slowest growing (k = 0.1 ± 0.048). This faster rate of growth in *A. betsileoensis* means that although it withholds reproduction until a relatively large size, this size is reached more quickly than for the other taxa for which we have data (Fig. 3). All three taxa were very long lived with individuals living to more than 20 years (between 0.1% and 0.5% of each taxa caught were estimated as more than 20-years old).

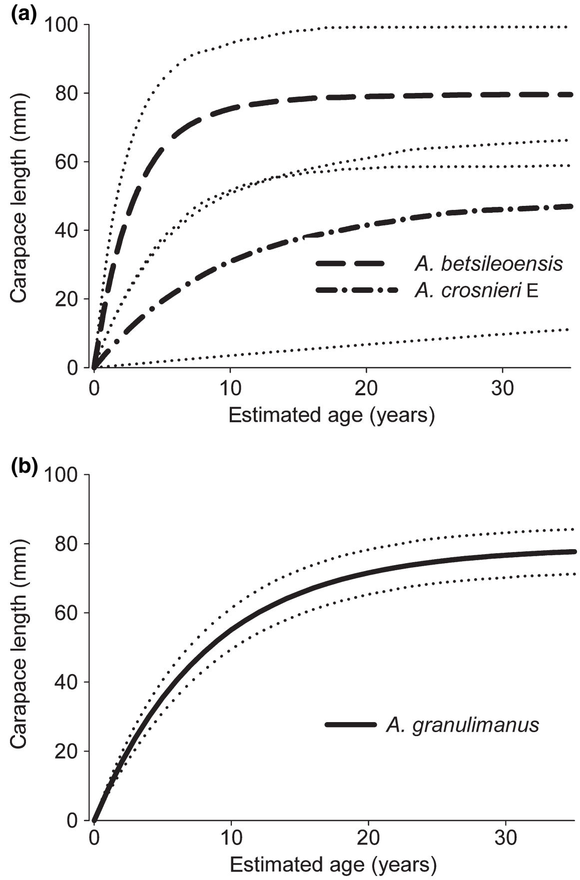

Fig. 5 The Von Bertalanffy growth function (VBGF) fitted to growth increments of (a) *Astacoides betsileoensis* (r^2 = 0.48) and *Astacoides crosnieri* E (r^2 = 0.50) and (b) *Astacoides granulimanus* (r^2 = 0.38). Error envelopes show 95% confidence intervals.

Trends in crayfish abundance over time and possible explanations

Informants commonly stated that crayfish populations (particularly *A. betsileoensis*, *A. caldwelli* and *A. crosnieri*) were declining in their local area. There

Table 2 The summarized results of 133 interviews with 250 informants from 38 villages and small towns from 15 communes surrounding the Fianarantsoa forest corridor

species	No. of interviews where species present	Harvested; C & S use	% interviews reporting a decline (no change)*	% of those reporting a decline blaming	
				Habitat loss†	Harvesting†
Astacoides granulimanus	116	Widely harvested (C & S)	47 (52)	25	33
Astacoides betsileoensis	58	Widely harvested (C & S)	91 (9)	6	91
Astacoides caldwelli	51	Harvested S where present (but found at low density)	98 (0)	24	22
Astacoides crosnieri	90	Seldom harvested (S only)	84 (13)	89	3

C, commercially; S, subsistence.
*The remainder were unsure whether a decline had occurred or not.
†Only three interviews did not suggest a reason for observed local declines in crayfish populations, those that did not suggest habitat or harvesting as the primary reason blamed a combination of these factors.

was less consensus about trends in populations of *A. granulimanus* with only 47% of interviews reporting a decline (see Table 2).

Overharvesting All villages where crayfish were present (35 out of the 38 visited) reported at least subsistence use of crayfish. In 20 of these villages some members of the community harvest crayfish commercially. Overharvesting was the main reason reported for the decline in *A. betsileoensis* and (to a lesser extent) *A. granulimanus* (see Table 2). The commercially harvesting villages were mostly at higher altitude, on the western side of the corridor and *A. granulimanus* and *A. betsileoensis* were the main target of commercial harvesting. Harvesting (subsistence only) was also mentioned by some as the reason for the decline in *A. caldwelli*.

Habitat loss Habitat loss was the main reason given for the decline of *A. crosnieri*. Informants told us that in the past these crayfish had been abundant in the many swampy, unimproved areas close to the forest frontier or within the forest. However, this type of land is most suitable for rice fields and is being rapidly converted. Two villages claimed *A. crosnieri* were no longer found anywhere within their territory as all natural swamps had been converted. Informants agreed that in new rice fields, crayfish could be found occasionally, but in rice fields more than 5- to 10-years-old crayfish were never found. Habitat loss was also reported as a major cause of the decline in *A. caldwelli*. Older informants in the deforested lowland areas to the east of the escarpment often mentioned that *A. caldwelli* had been very common in the large rivers in the valley bottoms between 20 and 40-years ago. All agreed that the populations are much reduced, with some elders even claiming that the species is now extinct (though interviews with younger people and our own sampling generally found them to be present but at very low density). Many people told us that this species needs cool water flowing through forests; as the forest is lost to slash and burn agriculture, so this species declines. Villages on the eastern side of the forest tended to blame the loss of forest on the slopes and river banks for the decline (or even local extinction) of *A. granulimanus*. However, villages in the west were more likely to record harvesting as a negative influence (or record no change in abundance).

Invasive species In Vohiparara, a village to the west of Ranomafana National Park, predation of young crayfish by the introduced fish *Channa maculata* (Asian snakehead or *fibata*), was given as a reason for this species' decline. We confirmed the presence of *C. maculata* in this area (photographs identified by Paul Loiselle) and that *C. maculata* do feed on crayfish (we found crayfish carapaces in the stomach of a captured *C. maculata*). Informants from all other areas (with the exception of Vohibato in Iazoara commune where *C. maculata* is present but not considered a threat to crayfish) told us that this fish was not yet found in their waterways.

Discussion

Our data suggest that Madagascar's crayfish are extremely slow growing. *Astacoides granulimanus* takes approximately 5 years to reach a size of 30-mm CL. This is comparable to estimates for *Parastacoides tasmanicus* (Hamr & Richardson, 1994) and *Paranephrops zealandicus*, previously described as the slowest growing crayfish ever recorded (Whitmore & Huryn, 1999). Despite the large error envelope, our data suggests that *A. crosnieri* is even slower growing, taking approximately 10 years to reach such a size whereas *A. betsileoensis* appears to be rather faster growing. We found individuals of all three species which we estimated as more than 20-years old. This life history, with long-lived, slow-growing individuals is likely to make *Astacoides*, particularly vulnerable to extinction (Purvis *et al.*, 2000; Fagan *et al.*, 2001.)

Benstead *et al.* (2003) highlighted three main threats to Madagascar's freshwater biodiversity: overexploitation, habitat loss or alteration and introduced species. All of these affect Madagascar's crayfish. Below we deal with each in turn and review all the current information on *Astacoides* ecology and the likely importance of each threat.

Vulnerability to overexploitation

Crayfish harvesting is common; every village we visited where crayfish were present reported at least subsistence harvesting. A recent study (Jones *et al.*, 2005 suggests that the harvest of *A. granulimanus* is potentially sustainable under current conditions in and around Ranomafana National Park. This is encouraging as these results suggest that at least one species of *Astacoides* can be sustainably harvested. However, the affect of harvesting on other species remains unquantified. We can use the ecological information presented here to draw conclusions about the relative vulnerability of other *Astacoides* species.

Differences in reproductive strategy influence a species' vulnerability to harvesting (Milner-Gulland & Mace, 1998; Kokko, Lindstrom & Ranta, 2001) and can give us useful information in the absence of direct studies. We found that taxa showed very different reproductive strategies with respect to the size at which they become reproductive with *A. betsileoensis* withholding reproduction until a particularly large size. By looking at the size distribution of crayfish harvested by one heavily harvesting village, we estimated that only 10% of *A. betsileoensis* would have reproduced prior to harvesting compared with three or five times as many of the harvested *A. granulimanus* and *A. crosnieri*, respectively. This suggests that *A. betsileoensis* is at serious risk of recruitment overfishing. The interviews supported the suggestion that *A. betsileoensis* may be particularly vulnerable to overharvesting with more than 90% of interviews reporting a decline in this species in their area and 90% of those attributing the decline to overharvesting. *Astacoides betsileoensis* had a very low abundance throughout the study site, as indicated by catch per unit effort (CPUE). However, this is at least partly because of the difficulty of catching crayfish from large, deep rivers in comparison with other habitats favoured by other species. *Astacoides caldwelli* is harvested opportunistically where present but it is not the target of heavy commercial harvesting. This is because it is mostly found at very low densities and to the east of the escarpment where many villages have local taboos preventing commercial harvesting (Jones *et al.*, 2006.

All crayfish taxa in the study area carry eggs from July or August with young becoming independent in December or January. The reproductive period of crayfish therefore coincides with the 'hungry period' of food scarcity (Hardenbergh, 1993). The coincidence of high-reproductive value of individuals with the time of highest harvesting pressure will make the promotion of management tools aiming to protect brood stock more difficult.

Despite the reassuring results that heavy harvesting of *A. granulimanus* may be sustainable (Jones *et al.*, 2005); we suggest that overharvesting of other species, particularly *A. betsileoensis*, may be a significant threat.

Habitat loss

Most of the limited work on the ecology of Madagascar's crayfish has taken place in the Ranomafana area (A. Deghan unpublished; H. Dixon unpublished; Jones *et al.*, 2005) where, thanks to intense conservation efforts, there is still good forest cover but where harvesting of crayfish is a common activity (Jones *et al.*, 2006). This has resulted in an emphasis in the literature stressing the importance of overexploitation as a threat relative to deforestation. For example, Crandall (2003) suggested that because slash-and-burn activities in Madagascar tend to be below 900 m and crayfish occur between 800 and 2000 m, the destruction of most of the lowland forests of Madagascar has had little impact on crayfish. This is misleading as although forest loss may be slower at higher elevations, much forest above 800 m has been, and continues to be, lost at an alarming rate (Gade, 1996; Freudenberger, 2003). In addition, we found crayfish down to 600-m altitude, with *A. caldwelli* and *A. crosnieri* E only recorded below 800 m. Habitat loss at these low altitudes is particularly rapid (Hawkins & Horning, 2001) suggesting that habitat loss is in fact a very serious threat to Madagascar's freshwater crayfish.

Astacoides crosnieri is dependent on swampy land; such land is a prime candidate for conversion to rice fields. This species vulnerability to habitat loss was supported by the interview data; 89% of interviews which concluded that *A. crosnieri* was in decline concluded that conversion of swampy land to agriculture was the primary cause. Many older people told us that when they were children they would collect this species from swampy land close to their village but that all such land is now converted and this species is no longer found.

Astacoides caldwelli is only found at low altitudes on the eastern side of the escarpment. The lowlands have been heavily deforested and although *A. caldwelli* is not currently found in forest, this is probably because forested rivers are not present at these low altitudes. This species was extremely rare throughout the study area, interviews with elders strongly suggested that this species has experienced a precipitous decline and that a combination of habitat loss and harvesting is to blame.

Previous limited work had suggested that *A. granulimanus* was tolerant of habitat alteration and eutrophication (H. Dixon unpublished). Our results, however, suggest that this species, currently extremely common in the Ranomafana area and found wherever there are clean streams running through forest, is in fact highly dependant on forest. Although we occasionally recorded individuals in deforested, eutrophic streams close to human habitation, they were infrequent and seldom ovigerous, suggesting these were sink populations. This dependence of *A. granulimanus* on forest habitat is reflected in one of its local names: the 'forest' crayfish (*Oran'ala*). It is interesting to note that we found healthy, reproductive populations of this species in some highly disturbed forest contiguous with intact forest and also in an area of pine and eucalyptus plantation. This suggests that the species can live and reproduce in non-native forest. However, we do not fully understand the factors which make this possible as other pine plantations visited did not have crayfish present. Our preliminary work suggests that the existence of native vegetation along the river banks may be a prerequisite and that vegetation history may also play an important role.

Introduced species

The vulnerability of freshwater ecosystems to invasion by exotics, and the damage that this can cause is increasingly recognized (Simon & Townsend, 2003; Dudgeon *et al.*, 2006). Ichthyologists are extremely concerned about the decimation of Madagascar's native freshwater fish fauna through competition and direct predation by introduced fish species with some species having been driven to extinction (Sparks & Stiassny, 2003). Villagers first alerted us to the possible threat that introduced fish pose to Madagascar's crayfish. Villages in Vohiparara blamed the Asian snakehead, *C. maculata* (local name: *fibata*) for the reduction in *A. betsileoensis* in their area. *Channa maculata* is a predatory fish, introduced to Madagascar in 1978, which is devastating native fish fauna throughout the country (Sparks & Stiassny, 2003). We confirmed the presence of *C. maculata* in the Namorona catchment (the main river draining Ranomafana National Park). Hitherto, the species had not been recorded from this catchment, the only known habitat of an undescribed endemic fish in the genus *Bedotia* (IUCN, 2004). The presence of *C. maculata* may represent a serious, as yet unrecognized threat to Madagascar's crayfish. *Astacoides betsileoensis* is likely to be particularly vulnerable to the threat from *C. maculata* as it is most commonly found in large rivers the habitat apparently preferred by *C. maculata*. Fortunately, most of the study area remains free from *C. maculata*. However, given this species' history of invasion and the fact it is still intentionally introduced to new waterways in Madagascar (P. Loiselle personal communication 2004), this threat may be increasing.

Introductions of exotic crayfish have decimated native crayfish populations in many parts of the world; both through direct competition and through the medium of crayfish plague (Vorburger & Ribi, 1999). Thankfully exotic crayfish species have not yet been introduced to Madagascar. Although it is not known whether *Astacoides* are susceptible to crayfish plague (caused by the fungus *Aphanomyces astaci*), other members of the family Parastacidae have been shown to be highly susceptible (Evans & Edgerton, 2002). Avoiding such introductions must be a priority for those concerned with crayfish conservation in Madagascar.

Note in proof: Unfortunately, since writing these words we have heard that a species of Procambarus (Cambaridae) has become established in rice fields around Antananarivo. This represents a serious new threat to Madagascar's freshwater biodiversity, particularly its crayfish fauna, and deserves urgent attention.

Conclusion

Until recently almost nothing was known about the ecology of *Astacoides* crayfish. Crandall (2003) reviewed the limited available information and concluded that harvesting was the major threat to the genus. Recent work has shown that harvesting is less of a threat to *A. granulimanus* than previously thought (Jones *et al*., 2005). However it is vitally important that conclusions about this common species are not extended blindly to other members of the genus. The data presented here suggests that, because of its large size at first reproduction, *A. betsileoensis* may be more vulnerable to overharvesting than *A. granulimanus* and interviews suggest that it is in decline. The importance of habitat loss as a threat to *Astacoides* species has not been previously highlighted. The pace of forest loss at low altitudes and conversion of swampy land to rice fields represents an urgent threat to *A. caldwelli* and *A. crosnieri*. Indeed, habitat loss is likely to be an important threat for all *Astacoides* as even *A. granulimanus*, the species with the broadest habitat requirements in this study, is seldom found far from natural vegetation. Introduced fish species, such as *C. maculata*, represent a new and growing threat.

Astacoides, with their mysterious biogeographical origins, wide diversity of forms (Hobbs, 1987) and economical importance (Jones *et al*., 2006) are one of the world's most fascinating, yet least studied, crayfish genera. We identify habitat loss and overharvesting as serious threats to this group. Madagascar's freshwater habitats have great significance for global biodiversity (Olson & Dinerstein, 1998; Benstead *et al*., 2003), yet conservation effort, as in so much of the world, has focused overwhelmingly on terrestrial ecosystems (Sparks & Stiassny, 2003; Andreone *et al*., 2005). Among the numerous challenges facing conservation in Madagascar, it is important that the country's exceptional freshwater biodiversity is not forgotten.

Acknowledgments

We thank the Association National pour la Gestion des Aires Protégées, the Direction des Eaux et Forêts and the villages where we worked for permission to carry out this research. We also thank Andrew Balmford, James Gibbons, Paul Loiselle, Andrea Manica and Gabrielle Rajoelison. Field work was funded by Rufford Maurice Laing Foundation, the Royal Geographical Society and the British Ecological Society.

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(Manuscript accepted 22 February 2007)