

***The sustainability of crayfish
harvesting in Ranomafana
National Park, Madagascar***

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Author's declaration

This dissertation is my own work and contains nothing which is the outcome of work done in collaboration with others, except as specified in the text and acknowledgements. The text does not exceed 300 pages and no part has been submitted for another degree or diploma.

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Abstract

Madagascar's freshwater crayfish, belonging to the endemic genus *Astacoides*, are harvested throughout their range in the eastern highlands of the country. They provide an important source of protein and revenue to local communities but there is concern that the harvest may be unsustainable. In this thesis I assess the sustainability of crayfish harvesting in and around Ranomafana National Park, an area well known for its reliance on crayfish harvesting.

Six taxa (belonging to four described species) are found in the Ranomafana area. Most families in villages with access to forest carry out some harvesting for subsistence use. Due to variation in local taboos (*fady*) and in access to forest, commercial crayfish harvesting is very important in only three of the 27 villages I visited. However, in these villages crayfish revenue is very important, particularly to poorer households. One species, *Astacoides granulimanus*, dominates the harvest: more than 95% of crayfish caught in the harvesting village of Vohiparara are of this species.

I used a mark-and-recapture study involving more than 26,000 *A. granulimanus* across 79 sites under a range of harvesting intensities to estimate demographic parameters (growth, fecundity and survival) and investigate density-dependent control of growth and fecundity. No evidence for density-dependent control of growth was found, but the density of large crayfish negatively influenced the proportion of females of a given size which reproduced.

I investigated the sustainability of the harvest of *A. granulimanus* using two approaches: I) comparing population structure and density under varying harvesting intensity and II) using population models to investigate the forest area necessary to provide the observed annual harvest from one harvesting village and comparing that with the area available. The conclusions are encouraging as they suggest that the *A. granulimanus* harvest in the Ranomafana area may be sustainable under current conditions. Preliminary work suggests habitat loss may be a more immediate threat, so scarce conservation resources should perhaps be concentrated on reducing habitat loss rather than enforcing a ban on harvesting.

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Chapter 1

Introduction

“[Sustainability] is a magical theory that purports to satisfy unlimited human populations and unlimited per capita consumption with limited resources; the miracle of the loaves and fishes has become an objective of policy.” (Ludwig, 1993)

“There is increasing evidence that, particularly where habitat loss is a critical threat to species, sustainable use may be the chief mechanism through which conservation is achieved.” (Hutton & Dickson 2001)



Crayfish for sale in a *hotely* in Ranomafana village

1 Introduction

1.1 Exploited species and sustainable use

Throughout the world, people harvest wildlife resources to provide food, medicine, building materials and for recreation. Harvesting of wildlife resources is particularly important in developing countries where millions of people meet their basic needs from the wild (Balick & Mendelsohn 1992; Pimentel *et al.* 1997; Bennett & Robinson 2000). However, despite their importance to human livelihoods, many exploited species are threatened by overuse. Numerous commercial and artisanal fisheries around the world are classified as overexploited (Cook *et al.* 1997; Casey & Myers 1998; MacKenzie 2002; Myers & Worm 2003; Odada *et al.* 2003). Half of endangered mammals and a third of endangered birds are threatened, at least in part, because of harvesting (Hilton-Taylor 2000; Mace & Reynolds 2001) and hunting poses the most potent current threat to the persistence of many animal species in tropical forest (Redford 1992). Overexploitation of wildlife resources is therefore a serious problem. However, there is considerable debate between those who warn that such overexploitation by humans is almost inevitable (Ludwig *et al.* 1993), and those who consider that under the right socio-economic conditions sustainable harvesting can make an important contribution to both conservation and development (Child 1996; Mahapatra & Mitchell 1997; Hutton & Dickson 2001).

During the last 25 years, sustainable development has become a central theme of environmental and development policy (IUCN/UNEP/WWF 1980; IUCN/UNEP/WWF 1991). Sustainable use of natural resources is one of the three objectives of the Convention of Biological Diversity, the biodiversity treaty now signed by nearly 190 countries (CBD/UNEP 2004). Although clearly a laudable aim (few would argue for unsustainable use) the term has become politicised and highly controversial (Adams & Hulme 2001; Sanderson 2001; Hutton & Leader-Williams 2003).

1.2 What is sustainable harvesting?

The word sustainable means very different things to different people (Sutherland & Gill 2001). To some stakeholders, sustainable profit margins are the aim, while others want to minimise the risk of extinction of the target species and still others are concerned with avoiding negative affects on all parts of the ecosystem (Mace & Reynolds 2001; Robinson 2001). The World Conservation Strategy (IUCN/UNEP/WWF 1980) defined sustainable resource harvesting as that which does not significantly affect the wild population. However a reduction in population density is necessary if harvesters are to benefit from density-dependent increases in productivity (Robinson & Redford 1994).

Bennett and Robinson (2000) offer a useful set of criteria by which sustainability can be defined:

- 1) Harvested populations cannot show a consistent decline in numbers. Following the onset of harvesting population density almost always declines but if the decline persists the harvest is greater than annual production and the harvest is not sustainable.
- 2) Harvested populations cannot be reduced to densities where they are vulnerable to local extinction from stochastic processes.
- 3) Harvested populations cannot be reduced to densities where the ecological role of the species is impaired.

Taken together these three criteria establish a lower limit for ecological sustainability. However, many people would argue that socio-economic sustainability is also an important component of sustainability and so populations should not be reduced to densities where they cease to be a significant resource for human users. The population density of a harvested species required to maintain socio-economic sustainability will sometimes be higher than that required to maintain ecological sustainability (Bennett & Robinson 2000).

1.3 What factors determine sustainability?

Theoretical interest in the management of biological resources began more than 50 years ago (Errington 1934; Schaefer 1954; Beverton & Holt 1957). For decades, management focused on the biological aspects of the resource without considering the interface with human actions (Seixas & Troutt 2003). However it is now widely recognised that both biological and socio-economic factors play important roles in determining whether a harvest is likely to be exploited sustainably (Ludwig *et al.* 1993; Levin 1999; Eagle & Thompson 2003).

1.3.1 Biological factors affecting the sustainability of a harvest

Differences in life histories (the suite of demographic characteristics such as growth rates, survival and reproduction) between species have a strong influence on their vulnerability to overexploitation (Kokko *et al.* 2001). A low rate of population productivity associated with a 'slow' life-history makes a species less able to withstand harvesting pressure (Mace & Reynolds 2001). This variability in vulnerability between species is clearly demonstrated by the phenomenon of 'fishing down the food web' (Pauly *et al.* 1998): harvests switch to smaller-bodied, more productive species as larger species become depleted through harvesting. Such a trend has been demonstrated in global fish catches (where the switch has been from large piscivorous species towards invertebrates and planktivores; Pauly *et al.* 1998) and in bushmeat markets (where primates and carnivores are becoming replaced by rodent and bird species; Fa *et al.* 2000). Differences in the form and strength of density-dependent regulation between species also result in large differences in how much can be harvested sustainably (Kokko & Lindstrom 1998). Other aspects of a species' biology, such as mating system, can also influence vulnerability. Species which aggregate for reproduction, such as the Nassau grouper (Sala *et al.* 2001) or the Maleo (Baker & Butchart 2000), are likely to be at increased risk of unsustainable harvesting.

1.3.2 Socio-economic factors affecting the sustainability of a harvest

The property rights regime under which a harvest operates is extremely important in determining its sustainability. Open access resources are inherently more likely to suffer unsustainable use than resources under private ownership or managed by a group with exclusive and long-term rights (Hardin 1968; Johannes 1978; Feeny *et al.* 1990). This is because a harvester of an open-access resource who increases his catch above the sustainable level gains the benefits of the extra extraction, but the costs (through reduced future yields) are shared among all the users (Milner-Gulland & Mace 1998). In addition, the property rights regime will also affect a harvester's discount rate (the rate at which he discounts future profits relative to current earnings; Howarth 1996). Communities with insecure tenure will prefer definite harvests today to uncertain harvests in the future. Poverty affects a harvester's discount rate as well; it is unrealistic, as well as unethical, to expect a very poor person to defer harvesting essential resources today in consideration for long-term sustainability. Commercialisation of wildlife harvesting tends to reduce the sustainability of its exploitation by increasing the number of people engaged in the harvest and by providing access to capital that allows harvesters to invest in technology which increases their efficiency (Bennett & Robinson 2000). Social taboos often play a role in management of local wildlife resources (McDonald 1977; Colding & Folke 2001); these are disrupted by immigration of outsiders, often resulting in less sustainable exploitation (Stearman 1990; Twine *et al.* 2003). Political corruption will determine how effectively laws are enforced and so could have an important role in how effectively exploited species can be managed (Smith *et al.* 2003).

1.4 Sustainable harvest as a conservation tool

There is increasing recognition that, in many parts of the developing world, the traditional protectionist approach to conservation is both unfeasible and unethical (Inamdar *et al.* 1999; Ostrom *et al.* 1999). The world's poor cannot be expected to bear the costs of conservation unless they receive benefits from

doing so (Ferraro 2001; Ferraro & Simpson 2002; Balmford & Whitten 2003). Proponents of sustainable use suggest that revenue from wildlife harvesting can provide incentives for maintaining wildlife populations (Gakou *et al.* 1994; Hutton & Dickson 2001; Shackleton 2001; Hutton & Leader-Williams 2003).

Those who promote sustainable use as a conservation strategy point to examples of successful resource management by communities with secure tenure (references in Feeny *et al.* 1990). They suggest that the breakdown of many such systems followed centralisation of power away from the local level by colonial administrations (Johannes 1978; Child 1996; Martin 1999). Sustainable use initiatives generally devolve responsibility for management of natural resources to communities (Kull 2002) and have become a mainstream conservation approach (Inamdar *et al.* 1999). Conservation decision-makers in Madagascar have embraced this sustainable use paradigm, recognising that communities need to receive significant revenue flows from forests in order for forest conservation to compete with prevailing patterns of forest use such as shifting agriculture (Erdmann 2004b).

1.5 Crayfish exploitation

1.5.1 The global context

Crayfish are a large and diverse group of decapod crustaceans containing more than 500 species (Holdich 2002a). They range in size from the Tasmanian giant freshwater lobster *Astacopsis gouldi*, which weighs over 4.5 kg (Horwitz 1994), to tiny burrowing species weighing only a few grams.

Crayfish have been harvested for food for thousands of years. Crayfish fragments and gastroliths have been found in aboriginal cooking hearths some 28,000 years old (Kefous 1981 quoted in Holdich 2002b), noble crayfish *Astacus astacus* have been harvested in Europe since at least the 13th century (Skurdal & Taugbol 2002), and crayfish were a traditional food of the Maori (Hiroa 1923). Today there are important fisheries for wild crayfish in many countries and

crayfish aquaculture is becoming increasingly important (Lawrence & Jones 2002; Lewis 2002; Skurdal & Taugbol 2002).

Between one third and one half of the world's crayfish are in decline or even threatened with extinction (Taylor 2002). The most serious threat to many species is the introduction of non-native species and the diseases they carry (Lodge *et al.* 2000; Gil-Sanchez & Alba-Tercedor 2002; Perry *et al.* 2002). Habitat loss and degradation and overharvesting are also important threats to some populations (Taylor 2002).

The vulnerability of a crayfish species to overexploitation depends on its life-history. The decline of the threatened Tasmanian giant freshwater lobster *A. gouldi*, is blamed partly on overharvesting, although habitat loss and pollution are also responsible (Horwitz 1994). The poor reproductive rate and low productivity of the large, slow-growing New Zealand species *Paranephrops zealandicus* means any commercial harvest is unlikely to be sustainable (Whitmore & Huryn 1999). Many other crayfish species, however, show resilience to harvesting. The economically important European noble crayfish *Astacus astacus* is able to withstand a high level of exploitation (Skurdal & Taugbol 1994). Momot (1977b; 1991) suggests that strong density-dependent regulation of survival and egg production means that many cool water crayfish can withstand removal of up to 50% of the adult population.

1.5.2 Crayfish harvesting in Madagascar

Madagascar's crayfish fauna consists of six described species in the genus *Astacoides* (Hobbs 1987). The only uniquely tropical crayfish genus, *Astacoides* crayfish are endemic to the streams and rivers of the forested eastern highlands of Madagascar (Crandall 2004). Records of villagers harvesting crayfish date back to early colonial times (Sibree 1915; Monod & Petit 1929) and today many villagers depend on crayfish harvesting for both subsistence needs and for small-scale trade (Dehgan 1990; Raberisoa *et al.* 1996; Guilhaume 1999). In a recent review of this poorly known group, Crandall (Crandall 2004)

suggests that all six described species of *Astacoidea* should be considered as vulnerable or endangered under the IUCN's red list criteria (IUCN 2003); citing harvesting as the most important threat. Malagasy regulations state that only crayfish larger than 100 mm total length (approximately 45 mm carapace length) may be harvested (regulation number 2.233-MAP/FOR, 22 December 1960 Article 6). However this law is not widely known and is not enforced.

Most of the very limited work on Malagasy crayfish has been carried out in the forests of Ranomafana National Park. Crayfish harvesting is very important to the local economy but there has been concern that the harvest may be unsustainable (Dehgan 1990; Dixon 1992; Ferraro 1994). In 1991 the Ranomafana forests were declared a National Park and all extractive uses, including crayfish harvesting, were banned (Ferraro 2002).

Conservation decision makers in Madagascar are looking beyond conservation within the limits of protected areas into sustainable use of forest resources outside of protected areas (Erdmann 2004b). Potential revenues from non-timber forest products, including crayfish, are seen as important in persuading villagers that sustainable forest use is preferable to slash-and-burn agriculture (Erdmann 2004b). However the lack of basic knowledge about Malagasy crayfish (Dixon 1992; Raberisoa *et al.* 1996; Crandall 2004) is an obstacle to promoting sustainable use of crayfish. In this thesis I investigate whether crayfish harvesting in Ranomafana National Park is sustainable under current conditions. I hope that the information provided on the ecology, population dynamics and socio-economic importance of the harvest will be helpful to those seeking to manage crayfish resources both in the Ranomafana area and in other forests in Madagascar.

1.5.3 Advantages of this study system

The Ranomafana National Park area offers an ideal opportunity to investigate the sustainability of crayfish exploitation in Madagascar. In the Ranomafana area some communities depend economically on selling crayfish while others, particularly those to the east of the park, have traditional taboos (*fady*) preventing commercial crayfish harvesting (Deghan 1990; Ferraro 1994). This results in areas with very different levels of harvesting occur close together making it possible to investigate the effect of harvesting on the crayfish population. I take a multi-disciplinary approach to the question of the sustainability of crayfish harvesting. By carrying out both ecological research to estimate vital rates of the crayfish and using interviews to estimate the spatial pattern and size distribution of the offtake I am able to compare the potential yield and the true harvest and use this to assess sustainability.

1.6 Structure of this thesis

The aim of this thesis is to assess the sustainability of the crayfish harvest in Ranomafana National Park, Madagascar. In chapter two I introduce the biological and socio-economic context of the study area and present the general methods. In chapter three I bring together prior knowledge concerning the biology, status and distribution of *Astacoides* crayfish and present new information concerning the species found in the Ranomafana area, their habitat requirements and reproductive biology. In chapter four I discuss the importance of the crayfish harvest in the Ranomafana area where it focuses on one species *A. granulimanus*. I estimate the value, and total number, of crayfish harvested annually by one village, and use interview data from five villages to describe the spatial pattern of harvesting. In chapter five I use mark-and-recapture data to estimate growth and survival in *A. granulimanus* and discuss the likely importance of density-dependent regulation of these parameters. In chapter six I use mark-and-recapture data to estimate the carrying capacity and investigate density-dependent regulation of fecundity in *A. granulimanus*. I then use the parameters estimated in chapters five and six to parameterise a series of size-structured matrix population models which I develop in chapter seven. In chapter eight I investigate the sustainability of the current level of crayfish harvesting in the Ranomafana area using two lines of evidence. Firstly I compare the population density and structure at sites exposed to very different levels of harvesting. Secondly I compare the annual offtake by one village with what would theoretically be sustainable given the area available to harvesters from that village, as predicted by the population models presented in chapter seven. In chapter nine I discuss the findings of the study.

Chapter 2

Study area and general methods

“The variety and luxuriance of the foliage, the great height of many of the trees, the countless creeping and climbing plants....all these make a journey through the Madagascar forests a new pleasure.” (Sibree 1915)



Much of Ranomafana National Park is drained by the Namorona River.

2 *Study area and general methods*

2.1 Study area

2.1.1 Madagascar: biodiversity and threats

Situated some 400 km off the east coast of Africa, the world's fourth largest island, Madagascar, is widely regarded as among the biologically richest places areas on earth. It has been defined as one of the 'hottest of the hotspots' of global biodiversity (Myers *et al.* 2000); one of the five regions of the world that represent the most urgent conservation priorities due to high concentrations of endemic species which are under high threat. Madagascar has more than 12,000 species of vascular plants of which > 90% are endemic (Schatz 2000), and more than 700 species of vertebrates, of which 58% of birds and more than 98% of amphibians, reptiles and mammals are endemic (Mittermeier *et al.* 1999).

Despite this fantastic wealth of biological diversity, the people of Madagascar are extremely poor economically. Annualised per capita income, adjusted for purchasing power parity, is only \$840 and average life expectancy at birth is just 52.6 years (UNDP 2002). The human population is expanding at 3% annually with 45% of the population currently under the age of 15 (UNDP 2002) putting growing pressure on the natural resources upon which the mostly rural population depends. Slash-and-burn agriculture (*tavy*) and burning to provide cattle pasture are both economic necessities for the nation's 11 million rural people and a major cause of Madagascar's biodiversity crisis (Erdmann 2004a; Kull 2004). In addition, rapidly rising demand for charcoal and timber in the growing urban centres adds to the deforestation (Engle & Lumpkin 1992). Though recent estimates are not available (Lowry *et al.* 1997), it is likely that less than 10% of Madagascar's natural vegetation cover remains (Ganzhorn *et al.* 2001).

2.1.2 Freshwater biodiversity

Madagascar's freshwater habitats are recognised as having great significance for global biodiversity (Olson & Dinerstein 1998; Benstead *et al.* 2003), yet conservation effort in Madagascar has so far focused overwhelmingly on terrestrial ecosystems (Reinthal & Stiassny 1991). The major threats facing freshwater biodiversity in Madagascar are deforestation (acting through increased sediment loads and water temperatures), overexploitation, and the introduction of exotic species (Benstead *et al.* 2003).

2.1.3 The eastern rainforests

Before humans colonised Madagascar (between 1500 and 2000 years ago), the tropical rainforests of Madagascar probably covered much of the eastern coastal plains and the escarpment that runs the 1600 km length of the island (Green & Sussman 1990). These eastern rainforests are rich in endemic species and have been identified as a major conservation priority within Madagascar (Olson & Dinerstein 1998; Stattersfield *et al.* 1998). The current rate of deforestation due to clearance for agriculture and cutting of fuel wood is very rapid (Nicoll 2004); approximately 50% was lost between 1950 and 1985 (Green & Sussman 1990).

2.1.4 Ranomafana National Park: geographic setting and history

Ranomafana National Park (RNP) was declared Madagascar's fourth National Park on 31 May 1991. Impetus for the establishment of the Park was the discovery of a new species of lemur: the golden bamboo lemur (*Hapalemur aureus*; Meier *et al.* 1987) in 1986. RNP is situated 60 km north east of the provincial capital of Fianarantsoa on the eastern escarpment of the high plateau (Figure 2.1) and contains 41,601 hectares of humid evergreen forest ranging in altitude from 500 to 1500 m (Randrianandianana *et al.* 2004). A partially paved major road, passable for most of the year, bisects the Park (Figure 2.1) but the majority of villages in the area are accessible only by foot.

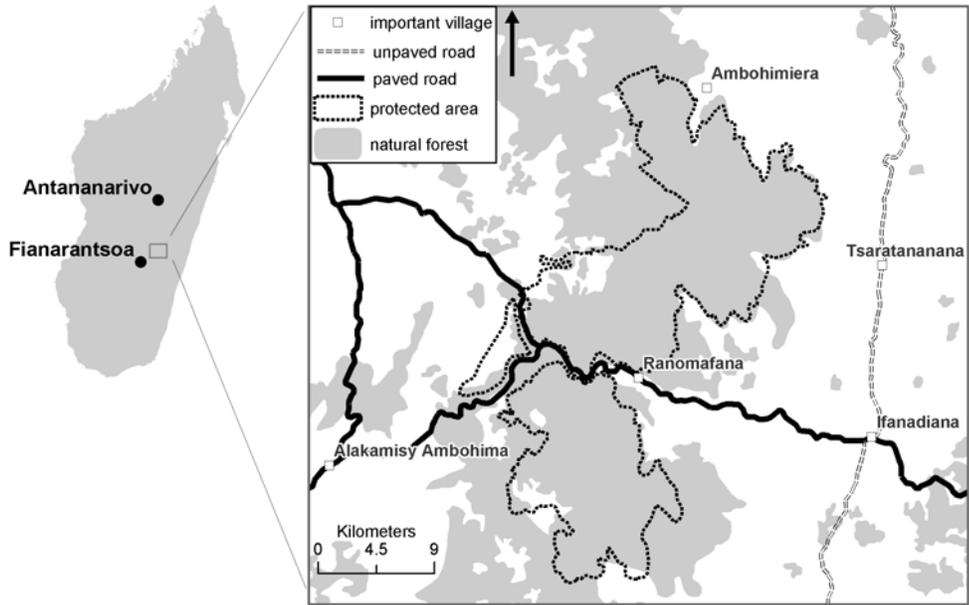


Figure 2.1 The location of RNP within Madagascar and the limits of the Park.

Rainfall in the Park averages 2300-4000 mm a year with most falling November to March; torrential rain and cyclones can occur in January, February and March. Mean monthly temperatures vary between 14 and 21 °C (Figure 2.2).

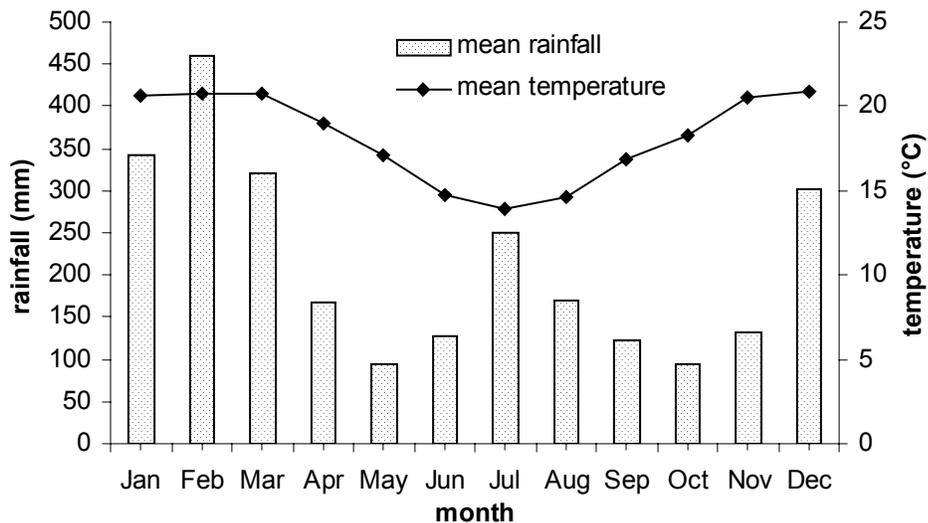


Figure 2.2 Mean monthly temperature and rainfall at Telatakely research camp, RNP, 1997-2001 inclusive (data provided by ICTE and ANGAP).

Until 1998, RNP was managed by the RNP Project, a US Agency for International Development (USAID) funded Integrated Conservation and Development Project (ICDP). As an ICDP, the RNP Project had both human development and conservation as central aims and worked to improve access to health and education and to introduce sustainable alternative income sources for the local communities (Kremen *et al.* 1994; RNPP 1994). Under the ordinances of the Park all extractive uses of the forest were banned (Decree 91-250 27 May 1991). How well the development interventions compensated villagers for their lost access to forest resources has been questioned by a number of authors (Peters 1998b; Marcus 2001; Ferraro 2002; Harper 2002). The management of the Park was transferred to the National Park service of Madagascar, the Association pour la Gestion des Aires Protégées (ANGAP) in 1998 (Randrianandianana *et al.* 2004).

2.1.5 The human context of the Ranomafana area

2.1.5.1 Population and poverty

Korhonen *et al.* (in press), extrapolating from the most recent census of 1995, estimates the human population of the peripheral zone of RNP at approximately 32,000 people in roughly 100 communities. Most of these people are extremely poor. Korhonen *et al.* (in press) found that 7.4% of children born alive in a health centre in 1999-2001 died before their first birthday. Given that less than 15% of births take place in a hospital and those that do are of wealthier mothers (Korhonen *et al.* in press), true infant mortality is likely to be much higher. Harrison (1992) suggests that as many as 20% of children in the area may not survive their first year. A public health study carried out in the villages surrounding the Park in the early 1990s found that 69% of children under the age of ten were underweight and 97% were infected with intestinal parasites (Kightlinger *et al.* 1992). During the 'hungry season', when rice stocks run out and the new harvest is not yet in, more families are pushed below the poverty line (Dostie *et al.* 2002). The unfortunate coincidence of seasonal food scarcity

with the onset of the rains, and the attendant increase in malaria and diarrhoea, may result in a tripling of child mortality during this period (Dostie *et al.* 2002).

2.1.5.2 *Economic activities and land use*

Ranomafana has had a tourist industry for more than 60 years (Peters 1998a) beginning with colonial French visiting the town to enjoy the hot water springs. Since the establishment of the National Park in 1991, and with political change opening up Madagascar, tourism has increased greatly with 16,000 tourists visiting RNP in 2001 (ANGAP 2000; Carret & Loyer 2003). Despite this growth, tourism benefits reach a relatively small proportion of the population (Hardenbergh 1993; Peters 1998a). Most people in the area rely on a mixture of irrigated rice production in the valleys and *tavy* rice and other crops on hill slopes. Many households also rely heavily on harvesting forest products such as crayfish, honey, tree ferns and fibres for weaving (Ferraro 2002), either for subsistence use or sale. Dependence on forest products is particularly high during the 'hungry season' (Ferraro 1994).

2.1.5.3 *Ethnic groups*

Traditionally Madagascar's people have been classified into approximately 20 ethnic divisions (Kottak 1971a). However, many ethnographers have sought to dispel the concept of 'natural' tribal divisions in Madagascar, suggesting instead that these ethnic groups are relatively recent constructions originating out of the expansion of a pre-colonial autocracy in the mid to late 19th century (Kottak 1971a; Kottak 1971b; Larson 1996). Most people in the region of RNP belong to the ethnic divisions of *Betsileo* and *Tanala*, with *Betsileos* being found to the west of the Park and the *Tanala* inhabiting the forested escapement and cleared valleys to the east. In interviews, most people self-identify with one of these groups (Ferraro 1994; Harper 2002), but Harper (2002) stresses that these classifications refer more to flexible cultural and economically adapted groups than ethnic tribes.

A system of traditional taboo or taboos known as *fady* (the word is both singular and plural) is extremely important throughout Malagasy culture (Gennep 1904; Rudd 1960; Lambek 1992; Jarosz 1994). There are a number of examples of traditional *fady* providing some protection to wildlife species in Madagascar: e.g. Verreaux Sifaka *Propithecus verreauxi deckeni* (Durbin 1994), golden-crowned Sifaka *Propithecus tattersalli* (Vargas *et al.* 2002) and radiated tortoise *Geochelone radiata* (O'Brien *et al.* 2003), or sacred forest areas (Horning 2004). Many *Tanala* villages have a traditional *fady* against selling crayfish (Dehgan 1990; Ferraro 1994). The existence of this *fady* was one of the main reasons I chose the Ranomafana area for this study as it afforded the possibility of areas with very different harvesting regimes occurring close together.

2.2 General methods

Throughout the thesis I use *we* when describing methods to explicitly acknowledge the help I had during fieldwork (see the acknowledgements at the start of this thesis).

2.2.1 Study period

The fieldwork for this thesis was carried out between February 2001 and January 2004. I was in Madagascar for 22 months during this period. During a four-month pilot study I carried out village interviews (2.2.7.1) to get a general overview of which villages depended how much on crayfish harvesting. This was important for selecting areas for more in-depth study. During this time I also developed the methods for the mark-and-recapture study and selected study sites (2.2.4.1). I returned to Madagascar initially for nine months during which I focused on the mark-and-recapture study (2.2.4.2). During a second nine-month stint in the field I continued the mark-and-recapture but also focused on the socio-economic study (my Malagasy language skills had progressed sufficiently) carrying out the daily harvester (2.2.7.3) and household interviews (2.2.7.2). After I left Madagascar in June 2003 the daily harvester interviews continued for a

further seven months monitored by colleagues working in the area: Jean Randriamboahary and Neal Hockley.

2.2.2 Catching crayfish

In total during this study we caught more than 30,000 crayfish. The crayfish were caught by hand by villagers, all experienced crayfish harvesters, using the two methods used locally: turning rocks and feeling underneath for sheltering crayfish, or 'fishing' with a stick with worms tied on with plant fibres. We carried out a large mark-and-recapture study for *Astacoides granulimanus* (see below). During the peak egg-bearing season (September to December) we also searched suitable habitat for other species of crayfish, establishing which habitats were suitable at first relied on local knowledge.

2.2.3 Species identification and measurements

Identification of crayfish follows the key provided in (Hobbs 1987). I also sent voucher specimens, stored in 95% alcohol, to Neil Cumberlandidge (Northern Michigan University, USA) and Keith Crandall (Brigham Young University, USA) for confirmation of identification using both morphometric and molecular techniques.

For each crayfish caught we recorded the sex, reproductive state (see section 3.2.5) and the number of eggs (if present). We measured carapace length CL; from the tip of the rostrum to the posterior edge of the carapace) to the nearest 0.1 mm using vernier callipers. For each species, we weighed a sample, using pesola scales accurate to the nearest gram. For *A. granulimanus* this was a sample of 200 individuals from four sites. For other taxa we weighed all undamaged individuals caught in dry weather.

2.2.4 Mark-and-recapture

2.2.4.1 Mark-and-recapture study sites

We carried out a mark-and-recapture study of *A. granulimanus* across 79 sites. We selected sites to represent a range of harvesting intensities through being at varying distances from communities known from previous studies (Dehgan 1990; Ferraro 1994) to harvest heavily (Vohiparara and Sahavondronana), or where little commercial crayfish harvesting occurs due to the existence of a local *fady* (Ambatovory, Andemaka, Antortosy and Bevoahazo; see Figure 2.3).

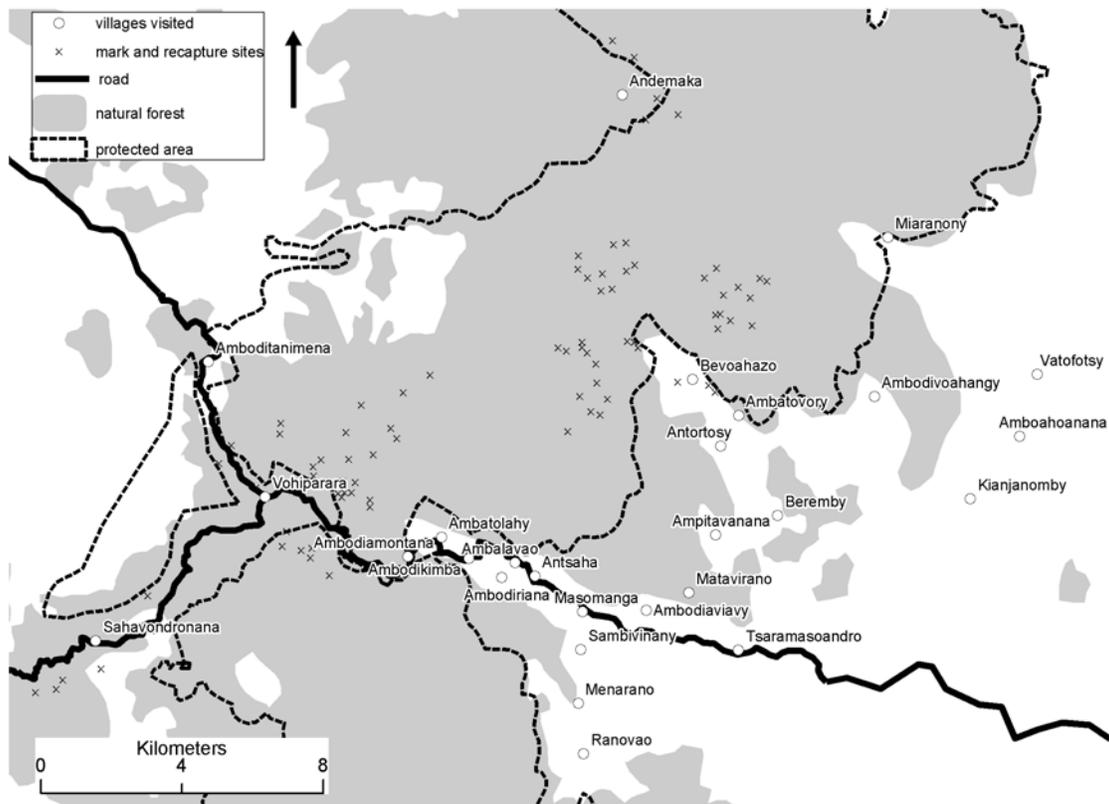


Figure 2.3 The study area showing the mark-and-recapture sites, and the villages visited during the interviews.

A site consisted of 100 m of stream in intact forest. Each mark-and-recapture session consisted of five consecutive days of mark-and-recapture as described below. We visited 33 of the sites for up to six sessions to allow survival

and growth to be estimated; we visited the remaining 46 sites for only a single five-day session.

2.2.4.2 Data collection

Each site consisted of a 100 m transect marked every 10 m. Two harvesters and a recorder (Fortunat Andriahajaina, Rosa Raslonjatovo, Roger Rakotomalala or myself) walked up the stream at a steady speed of 0.05 kmh^{-1} (two hours per transect). Each crayfish caught was placed in an individual cloth bag and handed to the recorder who noted gender, reproductive state, egg number and carapace length. We gave each new crayfish an individual identification mark using Visible Implant Elastomer (VIE) tags (NMT 2002). We marked each crayfish in each of four body positions out of a possible ten with one of five colours (Figure 2.4). In total we marked 26,096 *A. granulimanus* individually (marks were reused for male and females and at sites distant from one another). The 26,096 crayfish were, between them, caught a total of 44,286 times.

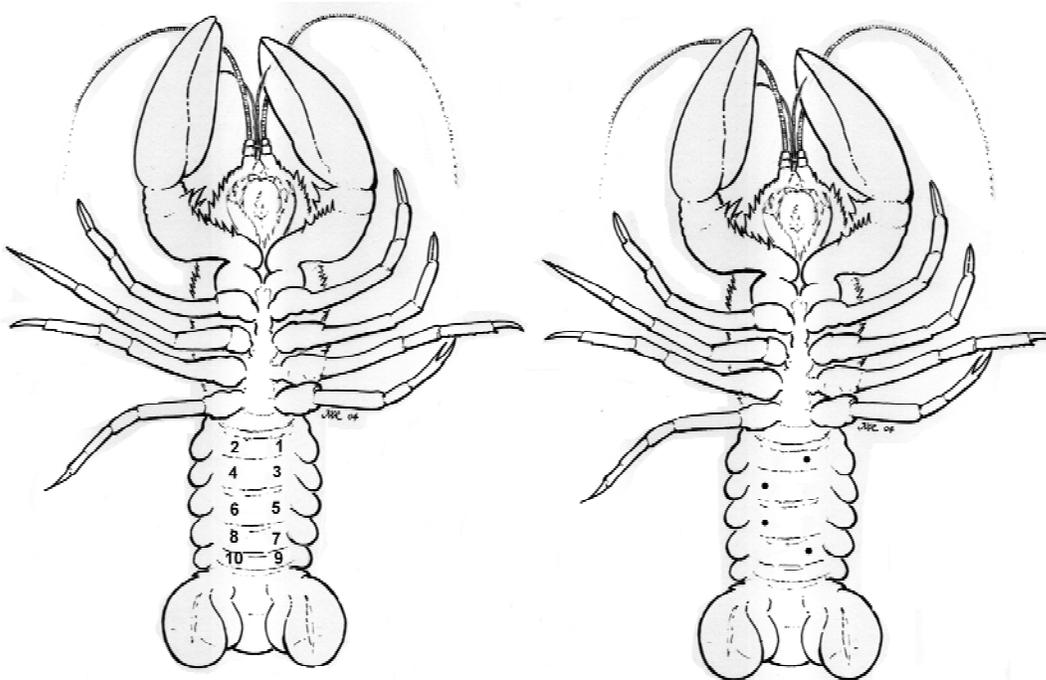


Figure 2.4 The ten body positions used to individually mark crayfish. The second picture shows a marked crayfish: number 1467. Drawing by J. Rodford.

2.2.4.3 Selection of size categories

For analysing the mark-and-recapture data (chapters five and six) and building size-structured matrix population models (chapter seven) it was necessary to group individuals into size-classes. Ideally, size-classes should be chosen which group individuals with similar demographic rates (Vandermeer 1978; Moloney 1986). No clear size-classes could be identified from the size-frequency distribution (Figure 2.5), so the choice of size-classes was arbitrary, the only criteria being sufficient individuals in each size-class for parameter estimation. I discarded crayfish less than 22 mm CL from the analysis as they were severely under-sampled and had very low recapture probabilities (Figure 2.5). I used three sizes classes for all analyses: small (22-34.9 mm CL) medium (35-49.9 mm CL) and large (> 50 mm CL).

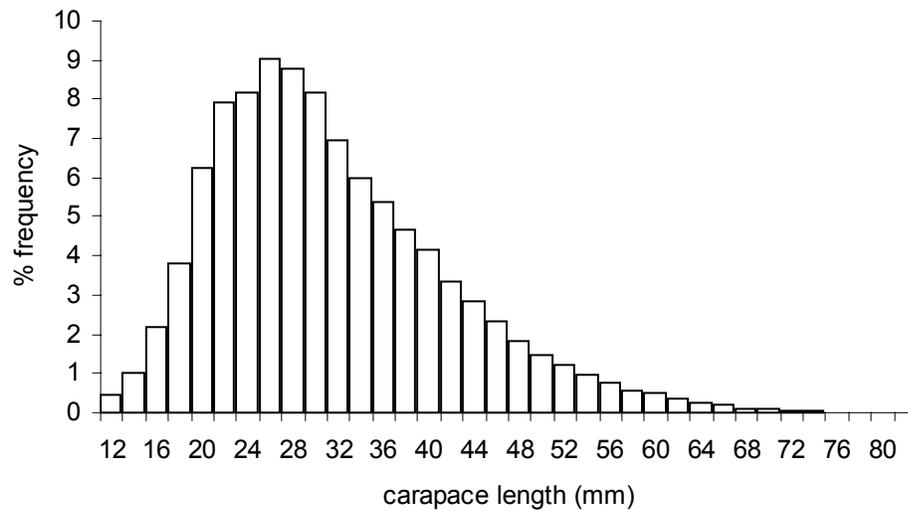


Figure 2.5 The size-frequency distribution of crayfish captured during the mark-and-recapture study (n = 26,094 individuals); crayfish less than 22 mm CL were discarded from the analysis.

2.2.4.4 Mark-and-recapture modelling and model selection

I carried out mark-and-recapture modelling using the programme MARK (White & Burnham 1999). For each analysis I identified a set of candidate models *a priori* (Chatfield 1995). Candidate model sets did not include time-dependence

in survival as these models are very parameter-rich and data sparseness was a problem.

I compared the statistical fit of the competing models from the candidate set using an information theoretic approach based on the Akaike Information Criterion (AIC; Akaike 1973; Burnham & Anderson 1998). AIC is defined in Equation 2.1:

$$\text{Equation 2.1} \quad \text{AIC} = -2\ln(L) + 2K$$

where L is the model likelihood and K is the number of parameters in the model. The accepted convention is that models with AIC which differ by <2 are indistinguishable statistically (Burnham & Anderson 1998). The best model explains most variation using a minimum number of parameters (i.e. it is the one which strikes a compromise between increased fit and decreased precision in parameter estimates). Programme MARK estimates a modified version of AIC known as QAIC_c (Equation 2.2) to account for differences in effective sample size (M) and goodness-of-fit of the most general model (c ; Burnham & Anderson 1998):

$$\text{Equation 2.2} \quad \text{QAIC}_c = \frac{-2\ln(L)}{c} + 2K + \frac{2K(K+1)}{M-K-1}$$

Where possible I follow the notation of Lebreton (1992). Models are presented with parameters (e.g. survival, Φ) varying by a group variable such as size e.g. $\{\Phi(\text{size})\}$, varying by two interacting variables such as size and sex $\{\Phi(\text{size.sex})\}$, or not varying $\{\Phi(\cdot)\}$.

2.2.4.5 *Estimating density*

I estimated the number of crayfish at a site using data from five consecutive days' mark-and-recapture using a closed population model, assuming that no birth, death, immigration or emigration occurred during the sampling period (Otis *et al.* 1978). Closed population models involve estimation of three parameters: P (initial capture probability), C (recapture probability) and N

(population size). When I refer in this thesis to the density of crayfish at a site I in fact mean the number of crayfish per unit length of river rather than the strict definition of number per unit area.

I did not include time variation in capture and recapture probabilities or individual heterogeneity in the models due to lack of data for parameter estimation in these more complex models. Four models were included in the candidate set: $\{P(\text{size})C(\text{size})N(\text{size})\}$, $\{P(\text{size})=C(\text{size})N(\text{size})\}$, $\{P(\cdot)C(\cdot)N(\text{size})\}$, $\{P(\cdot)=C(\cdot)N(\text{size})\}$. Using the model averaging function available in programme MARK, I calculated a mean from all the candidate models weighted by normalised QAIC_c weights to provide an estimate of number of crayfish of each size-class at each site. To ensure that five days was sufficient to achieve a good estimate of population size, at a sub-set of seven sites, we carried out eight days of mark-and-recapture. Figure 2.6 shows the correlation coefficients between the population estimate after two days and eight days, three and eight, etc. for each size-class. The results suggest that five days mark-and-recapture provided an adequate predictor of density at a site as a correlation coefficient of between 0.91 and 0.98 was achieved after five days for all size-classes.

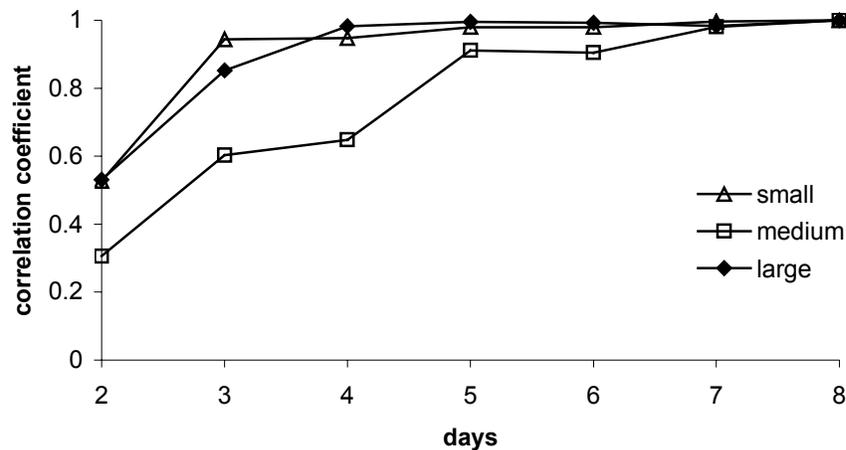


Figure 2.6 The correlation coefficient between the estimate after a given number of days against the estimate after eight days. Data comes from seven sites and are plotted separately for small, medium and large crayfish.

2.2.5 Habitat variables

At each site we recorded a number of habitat variables such as river width and depth, and measures of rock-cover and the suitability of the bank for burrowing crayfish (see section 8.2.1.2).

2.2.6 Statistical analysis

Generalised Linear Models (GLMs) are a multivariate statistical test, which extends the capabilities of ANOVA and multiple regression allowing both covariates and factors to be considered in the same model. Generalised Linear Mixed Models (IREMLS) allow fixed factors (such as observers) to be taken into account. I ran all GLMs and IREMLs using the Genstat 4.2 statistical software package. I carried out other statistical analysis in Minitab 13.31.

2.2.7 Socio-economic research

We used three methods with increasing level of detail to investigate the importance and spatial extent of crayfish harvesting in the region:

2.2.7.1 *Village interviews*

We initially carried out focus group interviews in the 27 villages in the periphery of Ranomafana National Park named in Figure 2.3 with the aim of getting a broad understanding of the importance of crayfish harvesting across the Park, and of perceived temporal changes in stock abundance. The villages visited ranged in size from ten to 60 households, and included communities with varying access to markets and forested land. We conducted interviews with self-selected groups usually including village elders (*ray aman-dreny*) and traditional leaders (*mpanjaka*). Semi-structured interviews were based on questions asked by Deghan (1990) and we emphasized informal discussion rather than a strict question-answer format (Mitchell & Slim 1991). Interviews were carried out by one of two teams: Nicole Rasoamana (a graduate from the University of

Fianarantsoa) and Brigitte Raharisoa (a senior member of the community of Bevoahazo) or Rosa Raslonjatovo (a man from Bevoahazo) and myself.

2.2.7.2 *Household interviews (Rapid Rural Appraisal)*

In five villages: Ambatovory, Antortosy, Bevoahazo, Sahavondronana and Vohiparara, we also carried more detailed household-level interviews using tools developed for Rapid Rural Appraisal (Chambers 1981; Chambers 1994; Freudenberg 1998). In each of these villages we carried out preliminary interviews with village elders, school teachers and elected leaders to learn about the history of the village, to enumerate the number of households and classifying each household into a general livelihood grouping. We then selected households to be interviewed according to a stratified sampling technique, focusing on households who depended more on the forest. Interviews were carried out by Filemona Razanamiadry (a man from Bevoahazo village) and myself, or Jean Randriamboahary and Fortunat Andriahajaina (graduates from the University of Fianarantsoa) and myself or Neal Hockley.

Each household took part in two interviews:

I) Participatory mapping: the informant drew a map of the area and annotated it with place names and told us what activities they do in each area. This was combined with ‘bean quantification’ where a pile of beans was used to represent all the crayfish caught in a year and the informant split the pile between the sites.

II) Annual calendar of activities: whereby we drew a matrix showing the seasons of the year (*lohatoana*, *fahavaratra*, *asotry* and *ririnina*) and the informant’s main activities. A pile of beans was used to represent the days in each season and the informant placed the beans on the matrix according to the days devoted to each activity.

2.2.7.3 *Daily harvester interviews*

A sub-sample (22/47) of households in Vohiparara took part in a more intensive interview schedule. The households selected were those identified in the RRA as crayfish harvesters. We carried out daily interviews (for five or eight consecutive days every three weeks) between January 2003 and January 2004. The households were split into groups and each group was asked to come each evening for an interview. From January to September 2003 there were three groups coming for five consecutive days. From September 2003 to January 2004 this was increased to eight consecutive days in two larger groups. Emma Ranambitsoa, a fully literate native of Vohiparara, carried out the majority of the interviews, assisted by Neal Hockley, Jean Randriamboahary or myself at least once a fortnight. Informants were asked about the main activities of the day for each member of their household over the age of ten, where these activities took place, and who was involved. Any forest products collected were brought to the interview, and the species, carapace length, sex and reproductive condition of all crayfish caught were recorded. The following day, the interviewer asked what they had sold, to whom and for how much.

2.2.8 Mapping the Ranomafana area

2.2.8.1 *Digital geographic data*

Vegetation cover and the National Park boundary in the year 2000 were available from GIS layers provided by PACT Madagascar. This uses the Inventaire Ecologique et Forestier National (IEFN) classification of forest types carried out between 1994 and 1996 (Dufils 2004). I needed stream and river information at a higher resolution than available, and therefore digitised them by hand using ArcGIS 8.3 from 1:50,000 maps of the Ranomafana area (FTM 1973a; FTM 1973b; FTM 1973c; FTM 1973d). These maps use the Laborde projection (a version of the Oblique Mercator), which is not supported by ArcGIS. I approximated the Laborde projection using the Hotine Oblique Mercator Azimuth Centre projection with parameters given in Table 2.1.

2.3 Summary

I studied the ecology and exploitation of *Astacoides* crayfish in Ranomafana National Park, south-east Madagascar over three years. The people in the area are very poor and many of them rely on harvesting forest products, particularly crayfish, to supplement their diet and/or income, especially during times of food scarcity.

The aim of this thesis is to assess the sustainability of crayfish harvesting in the Ranomafana area. An essential first step is to identify which species of crayfish are present and to understand a little of their biology. Chapter three introduces *Astacoides* crayfish in more detail, presents our current knowledge about the genus, and adds new information on their distribution, habitat requirements and reproductive biology in the Ranomafana area.

Chapter 3

Astacoides species in Ranomafana National Park

“[This review] should by no means be considered a definitive account of the crayfish of Madagascar. It may be hoped, however, that the assumptions and hypotheses offered will incite an intensive study by others of these unique crayfishes, the natural history of which is so little known.” (Hobbs 1987)



The ‘excessively spiny’ *A. betsileoensis*, probably the most ornate of any extinct or extant crayfish (Hobbs 1987).

3 *Astacoides* species in Ranomafana National Park

3.1 Previous knowledge

3.1.1 The genus *Astacoides* (Malagasy crayfish)

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). 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 2004) for a recent review).

The genus *Astacoides*, endemic to Madagascar, belongs to the southern hemisphere crayfish family: Parastacidae (Hobbs 1987). Before the advent of molecular techniques they were thought to be most closely aligned with the Tasmanian genus *Astacopsis* (Reik 1972). However, these similarities have been shown to be convergent and recent molecular evidence (Crandall 2004) places *Astacoides* with the South American genera (*Parastacus*, *Parastacoides*, *Samastacus* and *Virilastacus*).

Astacoides, the only uniquely tropical genus (Hobbs 1942), has a number of interesting features. As noted by Huxley (1896) *Astacoides* species have the lowest branchial count of any known crayfish; no adaptive explanation has been provided for this and it may be due simply to genetic drift during their long isolation on Madagascar. There is a huge diversity of forms within the genus and the “excessively spiny” *A. betsileoensis* probably exhibits the most ornate appearance of any extant or extinct crayfish species (Hobbs 1987).

3.1.2 Number of species in the genus *Astacoides*

Considering the striking diversity of crayfish within the genus *Astacoides*, such that most species are accorded different vernacular names (Hobbs 1987 and this study), it is surprising that until Hobbs' 1987 revision the recognised forms were listed as 'varieties' of a single species (Petit 1923; Monod & Petit 1929; Holthuis 1964). Hobbs (1987) raised the four existing varieties to species level and described two new species, resulting in the six species which are currently described: *Astacoides betsileoensis* (Petit 1923), *Astacoides caldwelli* (Bate 1865), *Astacoides crosnieri* (Hobbs 1987), *Astacoides granulimanus* (Monod & Petit 1929), *Astacoides madagascarensis* (Milne-Edwards & Audouin 1839) and *Astacoides petiti* (Hobbs 1987). More species await description (K. Crandall pers. comm.).

3.1.3 Distribution within Madagascar

The range of the six described species of *Astacoides* is poorly known (Hobbs 1987; Raberisoa *et al.* 1996). They are believed to be restricted to between 18° and 25° S and 46° and 48° E (Hobbs 1987; Figure 3.1). Reports suggesting a broader range (Dixon 1992) including the Masoala peninsula (approximately 17° S, 50° E) and the mountains of Andapa (approximately 14° S, 49° E) are uncorroborated and not supported by specimens (Crandall 2004).

The range of *Astacoides* in Madagascar is strongly related to altitude. They tend to live at high elevations, with most known localities between 800 m and 2000 m altitude Hobbs (1987). This restriction to high altitude is seen wherever crayfish, a predominantly temperate group, have successfully invaded the tropics (Hobbs 1987).

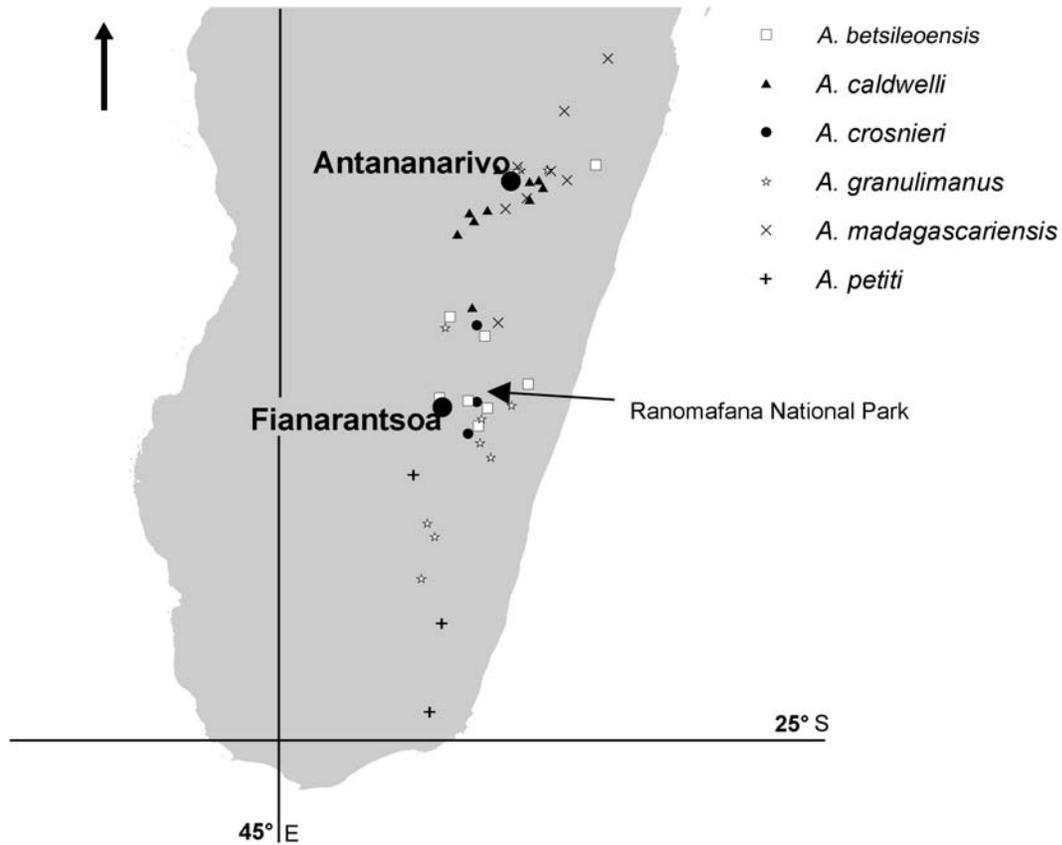


Figure 3.1 The distribution of described *Astacoides* species in Madagascar (data redrawn from Hobbs 1987). There are no records of *Astacoides* from the northern third of the country.

3.1.4 Habitat requirements of *Astacoides* species

There has been very little work on the habitat requirements of *Astacoides* (Hobbs 1987; Raberisoa *et al.* 1996). 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. These extrapolations from morphology were broadly confirmed by Dixon (1992) in a brief study in the Ranomafana area.

3.1.5 Status of *Astacoides* species

Freshwater ecosystems in general (Groombridge & Jenkins 2000), and crayfishes in particular (Taylor 2002), tend to be particularly vulnerable to human-

induced change. There has been concern about the adverse affects of harvesting, deforestation and introduced trout on crayfish populations in Madagascar for more than 70 years (Monod & Petit 1929). Available information on the distribution and status of *Astacoides* species is very limited, making it difficult to assess threat formally. However in 1996 *Astacoides* were assigned to IUCN threat categories based on their known range (IUCN 2003). Crandall (2004) has recently suggested alterations. Table 3.1 shows the current IUCN listing and suggested changes.

Table 3.1 The current and suggested IUCN conservation status of Malagasy freshwater crayfish (*Astacoides* spp.) from Crandall (2004) DD: Data Deficient; EN: B1+2c Endangered with a projected reduction of 50% over the next ten years due to small area of occupancy either severely fragmented or at less than five locations; VU A1cd: Vulnerable with a projected reduction of at least 20% over ten years due to a decline in area of occupancy, extent of occurrence and/or quality of habitat and actual or potential levels of exploitation; VU A1cde: as above but with the additional threat of introduced taxa, hybridisation, pathogens, pollutants, competitors or parasites.

species name	current status	suggested status
<i>Astacoides betsileoensis</i> Petit 1923	DD	VU A1cd
<i>Astacoides caldwelli</i> Bate, 1865	DD	VU A1cd
<i>Astacoides crosnieri</i> Hobbs 1987	EN B1+2c	EN B1+2c
<i>Astacoides granulimanus</i> Monod and Petit 1929	DD	VU A1cde
<i>Astacoides madagascarensis</i> Milne Edwards and Audouin 1839	DD	VU A1cd
<i>Astacoides petiti</i> Hobbs 1987	EN B1+2c	EN B1+2c

3.1.6 Crayfish in Ranomafana National Park (RNP)

A study in RNP (Dixon 1992) identified all six described species from the area. Dixon (1992) provides information on the habitat where she collected specimens, and notes (based on 6 weeks' field work in October and November)

that females are likely to bear eggs from August to October with young becoming independent in December or January. Ferraro (1994) observed that four species were exploited in the Park; he identified these as *A. betsileoensis*, *A. caldwelli*, *A. crosnieri*, *A. madagascarensis*.

3.2 New information on *Astacoides* ecology and distribution

3.2.1 Introduction

The main aim of this study was to investigate the sustainability of crayfish harvesting in the Ranomafana area. We therefore focussed our field effort on the most heavily harvested species, *A. granulimanus*, and its habitat. However, we also did some more limited work on the other taxa in the area to identify which species were present, their habitat requirements and basic reproductive biology. We searched potentially suitable crayfish habitat (based on local knowledge and the suggestions in Hobbs 1987) for all species during the breeding season. To investigate which, if any, species could tolerate disturbed habitat we also searched apparently less suitable habitat such as rice fields, irrigation canals and heavily silted streams and rivers strongly influenced by human activities. We caught and identified (see section 2.2.2) crayfish from throughout the study area and recorded the locations with a Global Positioning System (GPS).

3.2.2 Crayfish species present in Ranomafana National Park

During this study we caught more than 30,000 individual crayfish. The vast majority of these were *A. granulimanus* but we also caught nearly 3000 crayfish of other taxa. I identified the crayfish as belonging to six taxa, preliminarily identified (pending molecular work) as four species (see Figure 3.2). In cases where my identification differs from that of Dixon (1992) or Ferraro (1994), justification is given Table 3.2 below. Distributional data are summarised in Figure 3.4.

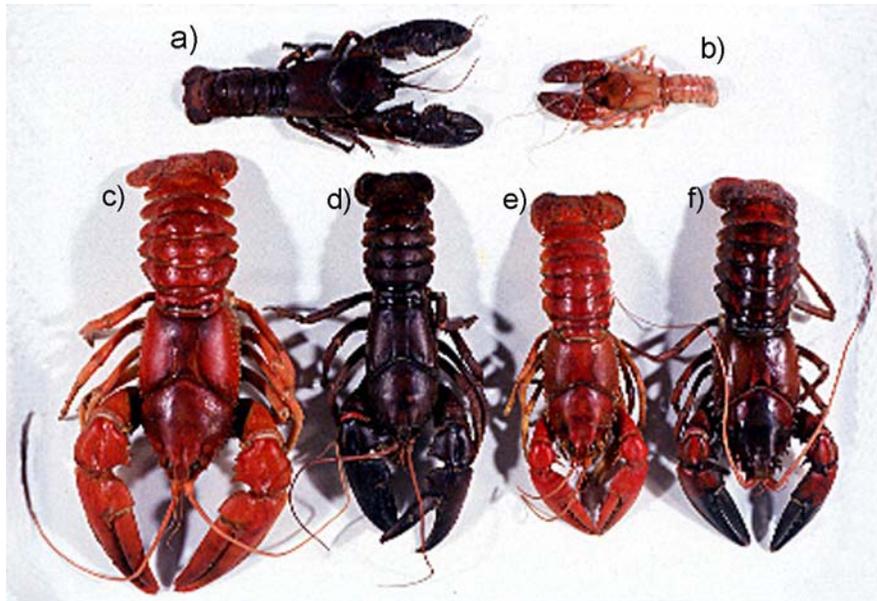


Figure 3.2 The six taxa found in the Ranomafana area during this study: a) *A. crosnieri* V, b) *A. crosnieri* B, c) *A. caldwelli*, d) *A. granulimanus*, e) *A. betsileoensis* red type, f) *A. betsileoensis* red/green type.

Table 3.2 The taxa recorded during this study with notes on identification.

scientific name	vernacular names (recorded during this study)	sub taxa	notes on identification by Dixon (1992) and Ferraro (1994)
<i>Astacoides betsileoensis</i> Petit 1923	<i>Orantsatria</i> (no translation) <i>Oramena</i> (red crayfish)	<i>A. betsileoensis</i> red/green type <i>A. betsileoensis</i> red type	
<i>Astacoides caldwelli</i> Bate, 1865	<i>Oramena</i> (red crayfish)		
<i>Astacoides crosnieri</i> Hobbs 1987	<i>Oramptoka</i> (mud crayfish), <i>Orambory</i> (round crayfish), <i>Oramalemy</i> (soft crayfish), <i>Oranjena</i> (lonely crayfish)	<i>A. crosnieri</i> B <i>A. crosnieri</i> V; see below	<i>A. petiti</i> identified by Dixon were probably slightly abnormal specimens of this species
<i>Astacoides granulimanus</i> Monod and Petit 1929	<i>Orambato</i> (rock crayfish) <i>Oramaintso</i> (green crayfish) <i>Oran'ala</i> (forest crayfish) <i>Peopeoka</i> (refers to method of locomotion)		Dixon recorded both this species and <i>A. madagascarensis</i> . Ferraro recorded just one of these two similar species which he identified as <i>A. madagascarensis</i> . Based on my larger sample, I conclude that just one species is present.

A. crosnieri found in the vicinity of Bevoahazo village to the east of the Park (*A. crosnieri* B) were much smaller than those found around Vohiparara village to the west (*A. crosnieri* V; see Figure 3.3) and slightly different in form with a particularly narrow areola. For the purpose of this study I treat the two populations separately, pending genetic analysis.

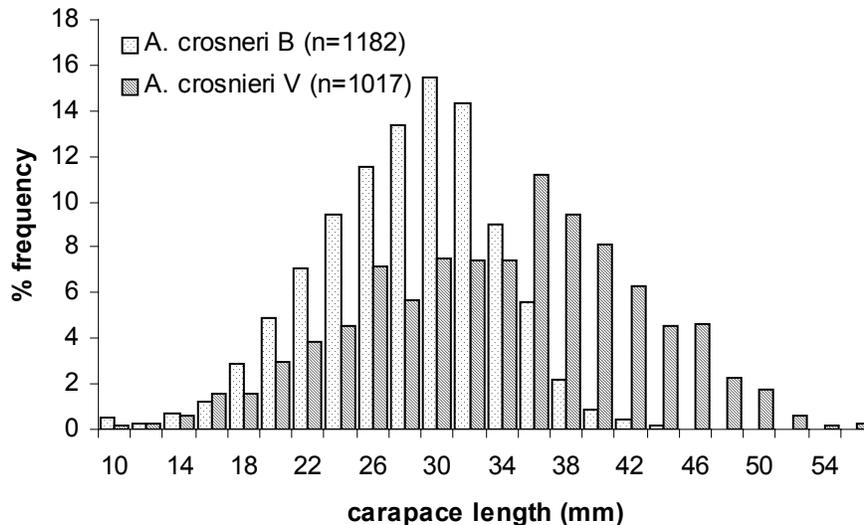


Figure 3.3 The size-frequency distribution of two populations of *A. crosnieri*: B from Bevoahazo and V from Vohiparara.

Hobbs (1987) described two forms of *A. betsileoensis*; the red type and the red and green type. We found both types in the Ranomafana area during this study. The red and green type was found in the large Namorona and Nanaroa rivers and, some of their tributaries, in the vicinity of Vohiparara and northwards (Figure 3.4). The red type was also found in the Nanaroa but further west towards the village of Sahavondronana. Locals suggested that the two forms were separated by a waterfall in the Nanaroa river but we were not able to confirm this as there was a gap where we did not sample. During this study *A. betsileoensis* was never recorded below 1000 m.

A. caldwelli were only found in the large Tsaratango river and in some of its tributaries in the lower lying area (600-700 m) to the east of the Park. Local people suggested that it was also present in the large rivers close to the villages

of Menarano, south of Ranomafana and Amboahoana in the east (see Figure 2.3) but we were unable to confirm these records. *A. crosnieri* (B) was recorded from a number of swampy sites in the Tsaratango valley close to Bevoahazo and Antortosy and from two sites up the Vatodirina river towards Andemaka. All sites where *A. crosnieri* (B) was recorded were between 600 and 800 m. *A. crosnieri* (V) was commonly found in swampy sites in the vicinity of Vohiparara at an altitude of approximately 1000 m.

A. granulimanus was found throughout the area in all rivers and streams in or close to natural forest so its distribution is not shown in Figure 3.4. The lowest altitude at which it was recorded was 600m and we observed it regularly up to 1200 m, above which we did not survey.

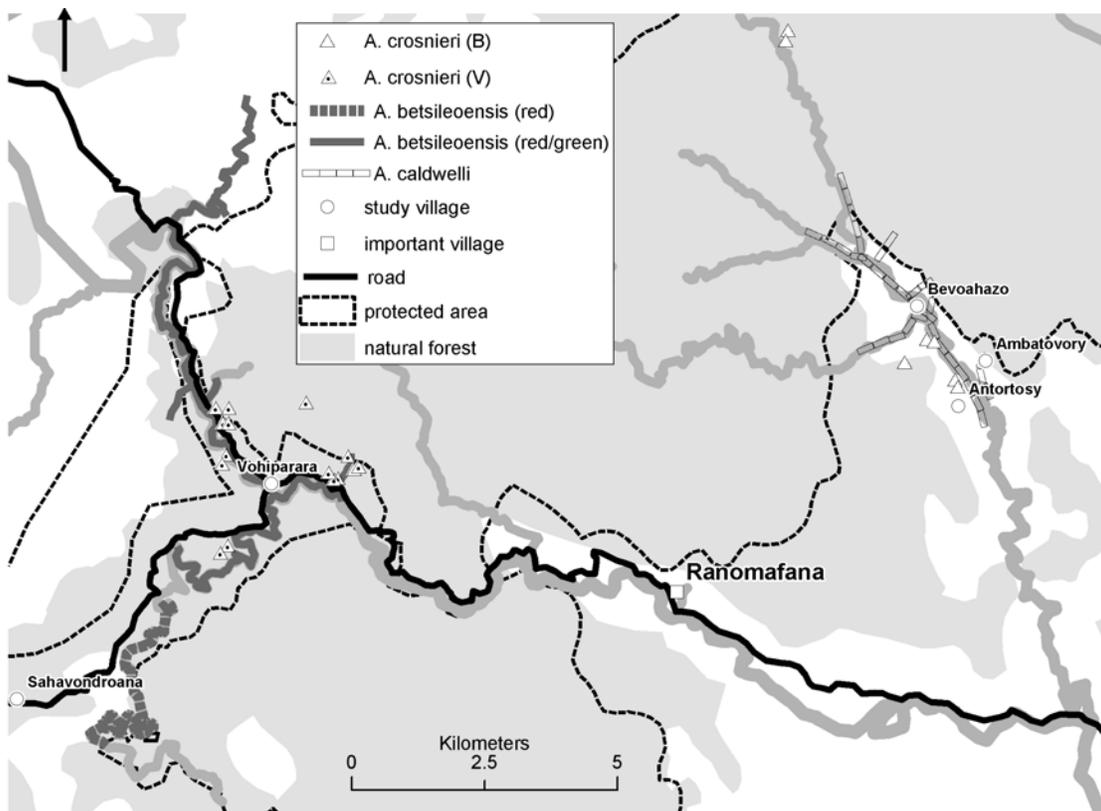


Figure 3.4 The distribution of *Astacoides* taxa in the study area. *A. granulimanus* is not shown as was widely distributed throughout the area. For taxa found in major rivers their distribution is interpolated between the numerous sampling locations. For taxa found in swampy areas (*A. crosnieri*), point locations where the species was recorded are shown.

3.2.3 Habitat requirements of the species present in RNP

We recorded the habitat where each crayfish taxon was found. To investigate what level of alteration of natural streams taxa could tolerate we also searched rice fields and irrigation canals for crayfish as well as more obviously suitable crayfish habitat.

It was impossible from this opportunistic study to draw quantitative conclusions about habitat preferences but it was possible to make some broad generalisations. The taxa of *Astacoides* found in RNP appeared to have different, but overlapping, habitat preferences (Table 3.3).

Table 3.3 The main habitats where each taxon of *Astacoides* was recorded in RNP.

✓: major habitat type where this species was recorded; †: occasionally found in this habitat. The number of crayfish of each taxon recorded during this study is given below the taxon name. The terms '*tapaka*', and '*hofa*' are explained in the text. Meters above sea level is indicated by 'asl'.

taxon	forest streams	large rivers (>900 m asl) mostly in forest	large rivers (<900 m asl) mostly not in forest	<i>tapaka</i>	<i>hofa</i> forest	rice fields/ canals
<i>A. betsileoensis</i> red/green (n = 457)	†	✓				†
<i>A. betsileoensis</i> red (n = 20)		✓				
<i>A. caldwelli</i> (n = 132)			✓			
<i>A. crosnieri</i> B (n = 1182)	✓				✓	
<i>A. crosnieri</i> V (n = 1017)				✓	✓	†
<i>A. granulimanus</i> (n > 27,200)	✓	✓	✓	†		†

A. betsileoensis was found mostly in deep, major rivers but occasionally in smaller tributaries, particular where deep pools mimicked the habitat offered by a larger river. A single specimen was recorded from an irrigation channel in the centre of a very large area of rice fields to the west of the Park, north of Sahavondronana.

A. caldwelli was recorded from very few rivers in this study. These were all low altitude major rivers to the east of the Park. The area where this species was recorded is mostly deforested.

A. crosnieri was always found in swampy habitat with a soft substrate. *A. crosnieri* B was found in the Tsaratango valley to the east of the Park. It was only recorded from *hofa* forest (natural swampy forest with standing water and a high-density of *Pandanus* spp). We looked for this taxa in an area of *hofa* forest close to Bevoahazo and an adjacent area which had been cleared the year before and had one crop of rice grown on it. We found no crayfish in the cleared area in a time during which we found 60 crayfish in the uncleared area suggesting it is very vulnerable to habitat conversion. *A. crosnieri* V appeared to be more tolerant of a range of habitat types. It was frequently recorded from *tapaka* (abandoned rice fields, of varying age but many dating from the gazetting of the Park in 1991) and in the forest. It was even occasionally recorded in the canals of active rice fields.

A. granulimanus was very common in clear, fast-flowing forest streams where it was the only crayfish present, appearing to prefer sandy or rocky substrate to mud or silt. It was also abundant in larger, deep rivers (sympatric with *A. betsileoensis* in the west or *A. caldwelli* in the east). *A. granulimanus* appeared to be susceptible to deforestation. It was found down to much lower altitudes in small forested streams than in deforested streams and was almost never found in streams with a high level of sedimentation such as streams whose banks had been recently cleared for agriculture.

3.2.4 Burrowing habit

Crayfish species have been classified by their burrowing habit into primary, secondary or tertiary burrowers (Hobbs 1942; Hobbs 1981; Gherardi 2002), depending on the proportion of the life cycle spent in burrows, and the burrow design. *Astacoides* shows a range of burrowing habits (see Figure 3.5):

A. crosnieri is probably a primary burrower (*sensu* Hobbs 1942) building a complex burrow system that seldom communicates with open water. The burrow systems found consisted of vertical tunnels extending down below the water table connecting with a series of horizontal ones. The burrows were between 0.5 and 1.5 m deep, depending on the depth of the water table.

A. betsileoensis is probably a secondary or tertiary burrower (*sensu* Hobbs 1942). It was found in burrows up to a metre long in stream banks, with extensive galleries running parallel to the bank. Juveniles were found in simple burrows beneath rocks on the riverbed.

A. granulimanus and *A. caldwelli* are probably also tertiary burrowers (*sensu* Hobbs 1942) but tend to make simpler burrows than *A. betsileoensis*. They were usually found in shallow tunnels or scrapes under rocks or tree roots. However, where no rocks were present they were found in tunnels dug in the bank, similar to those of *A. betsileoensis*. Young individuals were found sheltering under small rocks or amongst vegetation.

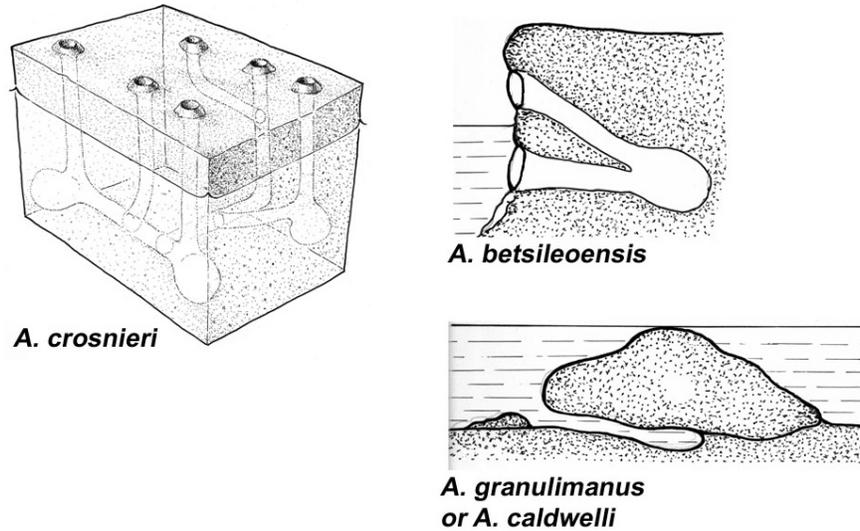


Figure 3.5 Diagrammatic representation of the burrowing habits observed in the four species of *Astacoides* during this study. Drawing by J. Rodford.

3.2.5 Reproductive biology

Crayfish, unlike most decapods which release numerous planktonic larvae, show parental care. After the eggs hatch the young go through three moults while still attached to the mother's pleopods (Reynolds 2002; Figure 3.6).



Figure 3.6 *A. caldwelli* female carrying stage I juveniles.

To investigate the reproductive biology of species present in RNP, we recorded the species, sex and carapace length of all crayfish caught during the study and noted the developmental stage of eggs or young. Reproductive stage was defined as in Table 3.4, and pictures of the stages of *A. granulimanus* are shown in Figure 3.7. Each egg-bearing pleopod was gently separated with a blunt pencil and the eggs counted; juveniles were not counted.

Table 3.4 The reproductive stages used in this study.

stage	description
egg	
stage I juvenile	domed head, eyes and chelae not yet properly developed
stage II juvenile	better developed with clear eyes though the head is still domed
stage III juvenile	eyes and chelae fully developed, able to move independently of the mother

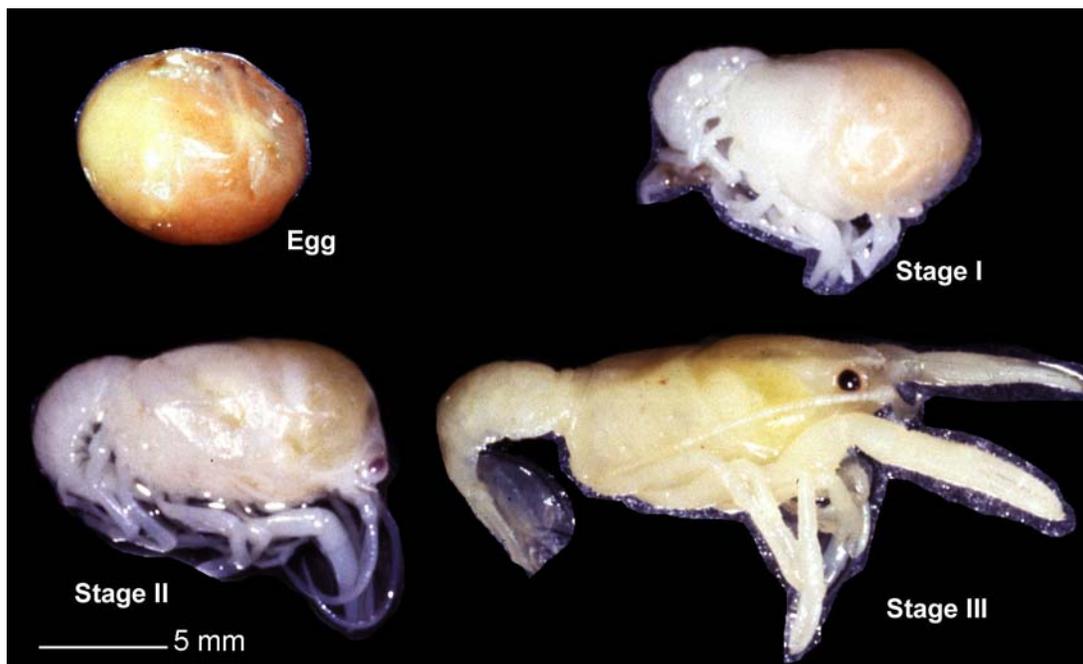


Figure 3.7 Photographs of the developmental stages of *A. granulimanus*: egg, stage I, stage II, stage III.

3.2.5.1 *The relationship between size and fecundity*

To investigate the relationship between size and fecundity and whether this relationship varied between taxa, I built a Generalised Linear Model (GLM) using egg number as the response variable, carapace length (CL) and CL^2 as covariates and taxon as a factor.

The minimal model described 71% of the variance. There was a strong relationship between size and fecundity for all species. There was a weakly significant interaction between CL^2 and taxon suggesting that this relationship differs between the taxa ($F_{6,486} = 2.44$, $p = 0.046$; Figure 3.8).

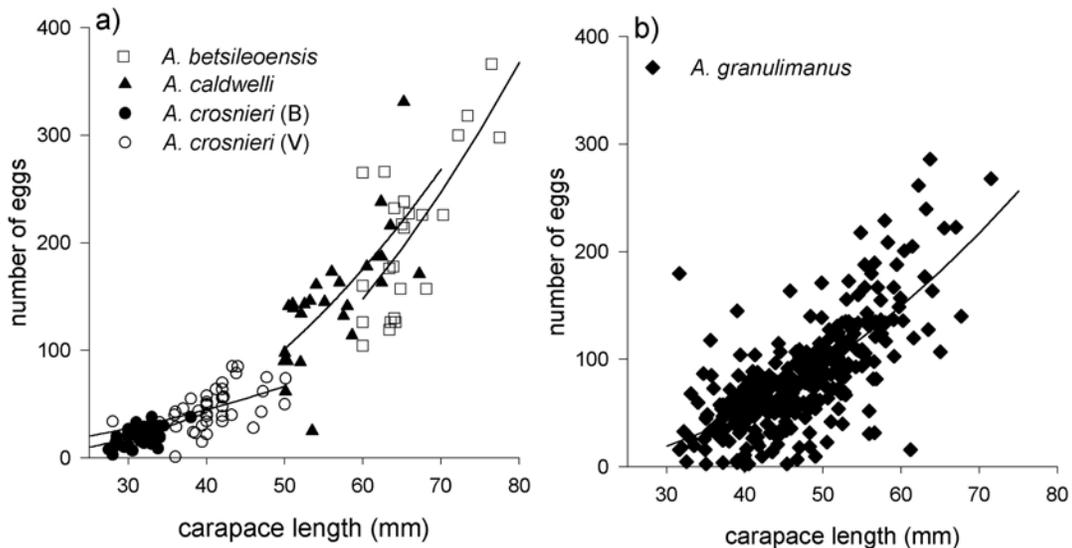


Figure 3.8 The relationship between size and fecundity of *Astacoides* in RNP; (a) shows all the taxa except *A. granulimanus* which is shown separately in (b) for clarity. The regression lines shown are predicted from the GLM.

3.2.5.2 *The relationship between size and the proportion breeding*

I investigated the proportion of females of each taxa bearing young each year using a GLM with binomial error structure with breeding or not breeding as the response variable. Only females caught between July and November inclusive were included (see 3.2.5.3).

There was a positive relationship between female size and the proportion breeding for all species (Figure 3.9). This relationship varied between taxon (there was a significant interaction between size and taxa; $F_{5,7846} = 6.07$, $p < 0.001$). The proportion of females of a given size bearing eggs in any one year therefore differed markedly; 50% of *A. crosnieri* from Bevoahazo were reproductive by 30 mm CL whereas 50% of *A. betsileoensis* were reproductive only at more than 60 mm CL.

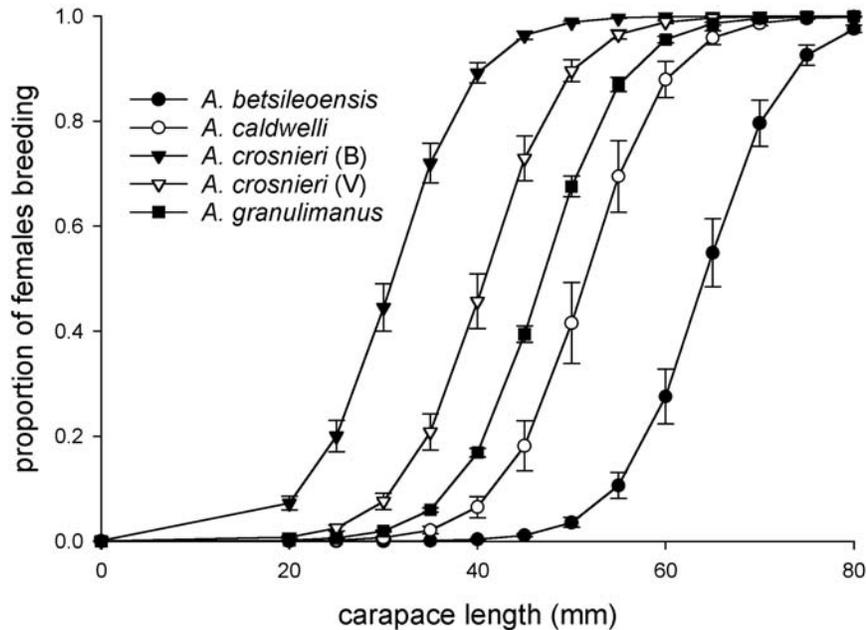


Figure 3.9 The predictions of a GLM with binomial error structure used to investigate the relationship between size and proportion breeding for each *Astacoides* species studied. Error bars show SEMs.

3.2.5.3 The timing of reproduction in *A. granulimanus*

I could only investigate the timing of reproduction in detail for *A. granulimanus* due to insufficient data for other species. The proportion of females greater than 40 mm CL carrying each reproductive stage was plotted by month. The timing of reproduction varied with altitude with crayfish at lower altitudes becoming reproductive earlier than those at higher altitude (pers. obs.) so only

individuals caught above 1000 m altitude were included in this analysis to reduce noise.

Astacoides granulimanus living above 1000 m altitude 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 (Figure 3.10). The apparent dip in August was probably an artefact due to the low sample size available for this month. Eggs were laid in June or July and carried for approximately four months, hatching in October or November. All juveniles were independent by the end of January.

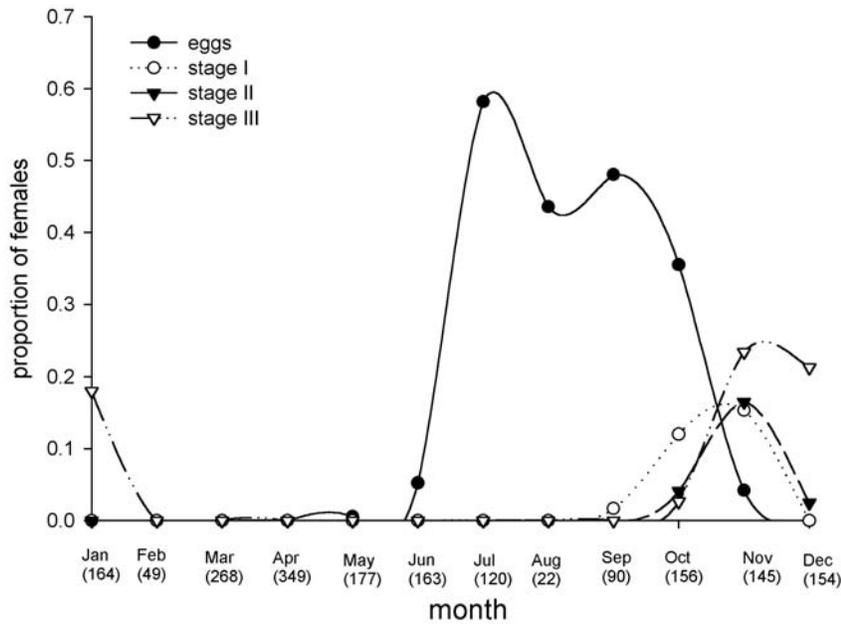


Figure 3.10 The proportion of female *A. granulimanus* (>40 mm CL) found bearing eggs or juveniles between January and December; the sample sizes are shown in parentheses below each month.

Opportunistic observations suggested that the other taxa found in the Ranomafana area had a broadly similar reproductive pattern with a single synchronous breeding period. Figure 3.11 shows the proportion of females of the various taxa found bearing eggs by month. The reason for the low proportion of *A. crosnieri* B bearing eggs in September was probably that this taxon was found

only at low altitude and by September many eggs had hatched (many had stage II juveniles still attached).

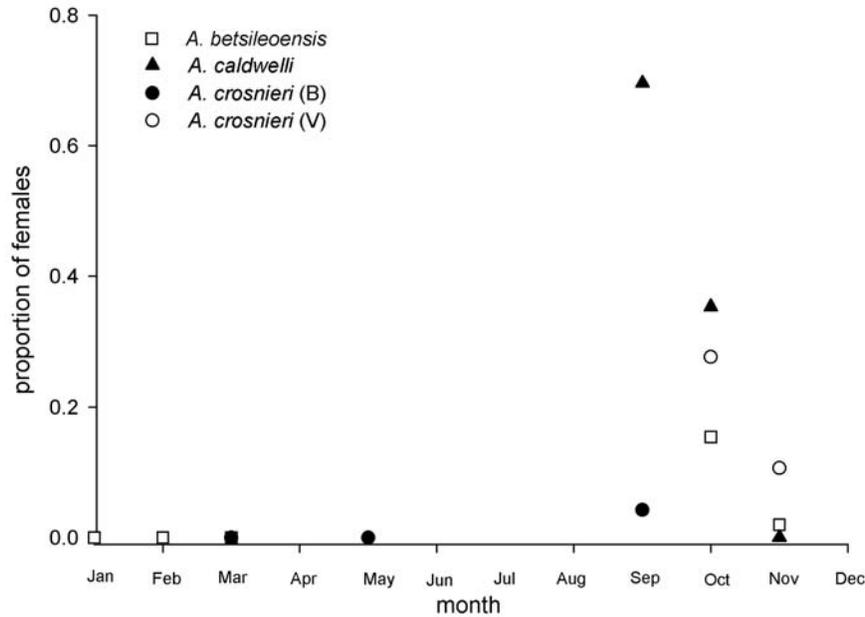


Figure 3.11 The percentage of females (all sizes) of *A. betsileoensis* (n = 198), *A. caldwelli* (n = 28), *A. crosnieri* B (n = 667) and *A. crosnieri* V (n = 571), which were found bearing eggs by month. Note that sampling did not occur every month.

3.3 Discussion

3.3.1 Crayfish species present in Ranomafana National Park

During this study we caught more than 30,000 individual crayfish in the Ranomafana forests. We identified these as belonging to six taxa from four described species: *A. betsileoensis*, *A. caldwelli*, *A. crosnieri* and *A. granulimanus*. Dixon (1992) in her study in the Ranomafana area identified all six described species of *Astacoides* from her total sample of 225 individuals. This included three specimens of *A. petiti*. Due to the lack of specimens from which to confirm her identification and the small total number of these species she found I believe it more likely that these specimens were unusual forms of *A. crosnieri*.

Ferraro (1994) recorded the most common species in the area, found in fast flowing mountain streams, as *A. madagascarensis*, whereas I identify it as *A. granulimanus*. These two species are very similar and probably closely related (Hobbs 1987). Dixon (1992) recorded both *A. madagascarensis* and *A. granulimanus* from the area. After looking at large samples of crayfish in the field over a two years period I believe just one of these species is present and it is most likely to be *A. granulimanus*. My specimens are available for examination at the University of Antananarivo, Madagascar and at Brigham Young University, USA.

3.3.2 Habitat requirements and associated threats

It is interesting to note how well Hobbs' (1987) predictions of habitat preferences for the various *Astacoides* species, based on functional morphology, match with my observations. For example Hobbs (1987) suggested that the spines of *A. betsileoensis* are adapted to relatively still waters, the weak abdomen, small eyes and strong chelae of *A. crosnieri* are adapted to a life centred on burrows in swamps, while the form of *A. granulimanus* is most suited to fast flowing head-water streams. These predictions match closely with my direct observations of habitat preferences.

A. betsileoensis appeared mainly restricted to large, deep and relatively slow flowing rivers, although we also found an individual of this species in an irrigation canal. Such large rivers tend to be quite polluted as people wash clothes and defecate in them. In addition, the Namorona and Nanaroa rivers have been invaded by the Asian snake-head, *Channa striata*, a predatory fish introduced in the 1960s which is devastating native fish fauna throughout Madagascar (Sparks & Stiassny 2004). *C. striata* do feed on *A. betsileoensis* (we found *A. betsileoensis* carapaces in the stomach of *C. striata*). The degree to which predation by *C. striata* and changes in water quality threaten *A. betsileoensis* is unknown.

We found *A. caldwelli* in only three rivers, all at lower altitude in the east of the Park. The banks of the rivers where *A. caldwelli* was recorded were quite deforested, but this does not necessarily signal tolerance of habitat loss. The rivers where we recorded the species were out of forest but they were fed by numerous tributaries, the catchments of which remain mostly forested. It is impossible to infer much about the habitat preference of *A. caldwelli* from this preliminary work.

The form of *A. crosnieri* found in the Bevoahazo area (*A. crosnieri* B) appeared to have very restricted habitat requirements. It was only recorded from natural swampy forest with standing water and a high-density of *Pandanus* species. This habitat type is very rare in the area and highly threatened due to its suitability for conversion to irrigated rice fields and heavy exploitation of *Pandanus* species for roofing, and weaving (Ferraro 1994; Callamander & Laivao 2004). *A. crosnieri* V appeared to be more tolerant of a range of habitat types, being frequently recorded from abandoned rice fields and even in the canals of working rice fields.

A. granulimanus is by far the most widespread crayfish taxon in the forests of RNP, being found wherever there are clean streams running through forest. However, it appears to be very dependent on forest; it was seldom recorded outside of forest and never where the stream banks were seriously eroded resulting in heavy sedimentation. This finding is in contrast to Dixon (1992) who suggested that *A. granulimanus* (which she identified as *A. madagascarensis*) may be found in relatively polluted waters close to population centres and concluded that it is hardy and tolerant. In this study we occasionally found *A. granulimanus* in such streams but the low frequency and absence of ovigerous females observed away from clean, forested streams leads me to conclude that the species is less tolerant than suggested by Dixon. The dependence of *A. granulimanus* on forest habitat is reflected in one of its local names in the area: the 'forest' crayfish (*oran'ala*). The Asian snake-head *C. striata* may affect populations of *A. granulimanus* in large rivers. However, the predatory fish tends

to be restricted to large rivers so the majority of *A. granulimanus* habitat may be safe from invasion.

3.3.3 Sympatry and *Astacoides* species

When Hobbs wrote his seminal account of *Astacoides* crayfish (Hobbs 1987) there was very little information available on which to base an assessment of reproductive isolation. Three of the forms previously considered as varieties had, however, been found at the same localities: evidence he used to support his universally accepted upgrading of the varieties to species level. In this study *A. granulimanus* and *A. betsileoensis* (in the west) and *A. granulimanus* and *A. caldwelli* (in the east) were commonly found sympatrically within the same river, often under adjacent rocks. This confirms, if any doubt remained, the reproductive isolation of *A. granulimanus* with *A. betsileoensis* and *A. caldwelli*. However, as noted by Hobbs, *A. betsileoensis* and *A. caldwelli* are very similar and their genetic isolation uncertain. Since the two species are not sympatric it is difficult to confirm the specific classification pending genetic analysis.

With the red and the red/green form of *A. betsileoensis*, Hobbs conservatively retained subspecies classifications. This is superficially supported by this study; the two forms were not found sympatrically but in different stretches of the same river, possibly separated by a waterfall. We found forms which appeared to be intermediates between the two types in the population. As has long been noted for *Astacoides* (Poisson 1947), colour is not a good feature on which to base taxonomic determination in crayfish.

3.3.4 Reproduction

Crayfish species show a great range in the number of times they reproduce in a year. Within the parastacid genus *Cherax*, species are found which breed just once a year (e.g. *Cherax tenuimanus* in south-western Australia) to up to 5 times a year (e.g. *Cherax quadricariantus* in the warm waters of northern tropical Australia (Barki *et al.* 1997). One New Zealand parastacid,

Parastacoides tasmanicus, only breeds in alternate years (Hamr & Richardson 1994). *Astacoides* in RNP breed just once a year, spawning towards the end of the cold season in June or July. The timing of reproduction varies with altitude, with crayfish in higher altitude, and presumably colder, streams and rivers breeding later than crayfish at lower altitude.

The relationship between size and fecundity varies between taxa in the Ranomafana area but the difference is only just significant at the 5% level. However, the taxa show very different reproductive strategies with respect to the size at which they become reproductive, with the larger species such as *A. betsileoensis* withholding reproduction until they have reached a large size (more than 60 mm CL). Other species, including even *A. granulimanus*, which reaches a similar eventual size to *A. betsileoensis*, start to reproduce when much smaller. These differences in reproductive strategy are likely to influence each taxon's relative vulnerability to exploitation (Milner-Gulland & Mace 1998; Kokko *et al.* 2001).

3.4 Summary

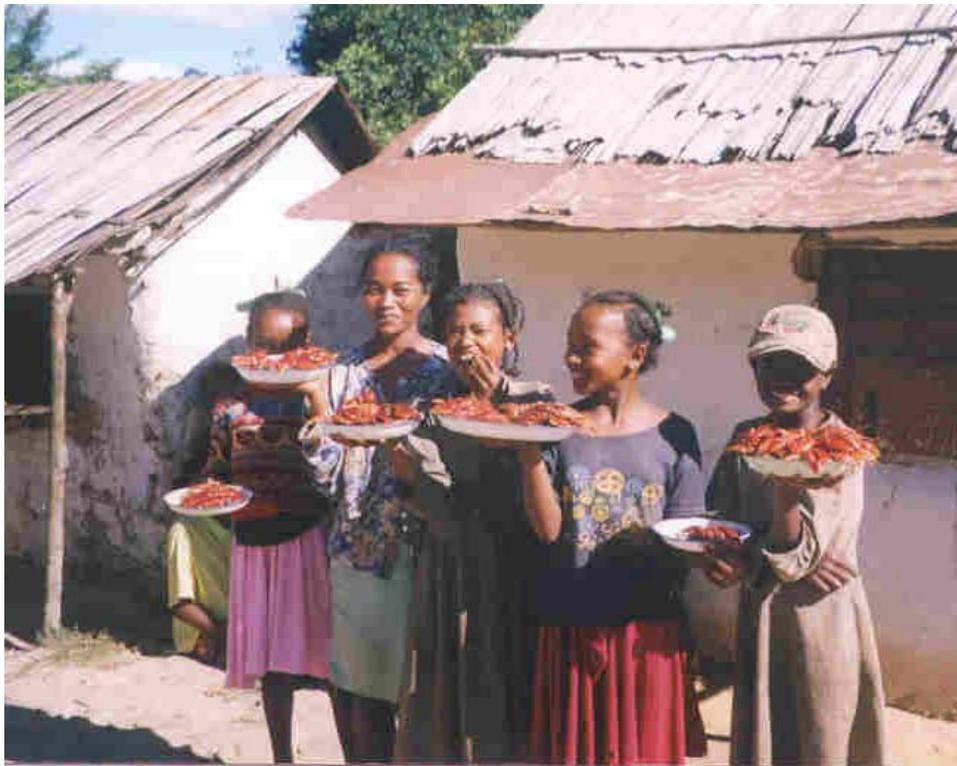
Astacoides, the crayfish genus endemic to Madagascar, contains six described species showing a great deal of morphological diversity. We found six taxa comprising four species in the Ranomafana area. This is in contrast to earlier studies which suggested that all six described species are found in the area. Some taxa may have very restricted habitat requirements (e.g. a form of *A. crosnieri* was found only in swampy forest rich in *Pandanus* species). The most common species in the area (*A. granulimanus*), which occurs widely in streams and rivers of any size, appears to be sensitive to loss of forest. An introduced predatory fish, *C. striata*, may pose a threat to *A. betsileoensis*, which appears to be restricted to large rivers in the Ranomafana area, prime habitat for the fish. The various crayfish taxa in the Ranomafana area become reproductive at very different sizes, which may influence their vulnerability to exploitation.

In this chapter I have introduced the crayfish of Ranomafana National Park. These crayfish are harvested for food and sale. In chapter four I will present information on the spatial distribution and economic importance of crayfish harvesting in the area.

Chapter 4

The socio-economic importance and spatial distribution of crayfish harvesting in RNP

“While staying near the upper forests, we had frequently brought to us for sale a basketful of crayfish, which seemed fairly plentiful in the streams. The flavour is excellent and they make a very good curry.” [Sibree, 1915]



Girls in Vohiparara selling crayfish by the roadside.

4 The socio-economic importance and spatial distribution of crayfish harvesting in RNP

4.1 Introduction

The importance of Non-Timber Forest Products (NTFPs), such as wild meat and fish, fruits and medicinal plants, has been overlooked in the past because much of their value is in small-scale trade or subsistence use, so not easily captured by conventional markets (Byron & Arnold 1999; Cavendish 2000; Gram 2001). However, in the last ten to 20 years interest in NTFPs has grown and the importance of forest products in sustaining rural livelihoods in many developing countries is now recognised (Grimes *et al.* 1994; Edwards 1996; Pimentel *et al.* 1997; Gram *et al.* 2001). It is difficult to estimate the number of forest-dependent people (Byron & Arnold 1999) but it is likely that more than 300 million people worldwide obtain part or all of their income and food from forest, harvesting a total of \$90 billion in NTFPs annually (Pimentel *et al.* 1997). Forest resources are often not the primary source of livelihood for the entire community but may be particularly important to poorer households (Appasamy 1993; Gunatilleke *et al.* 1993; Hegde *et al.* 1996; Cavendish 2000). The importance of forest products as natural insurance to smooth incomes during difficult times has been stressed (Hegde *et al.* 1996; Godoy *et al.* 2000; Pattanayak & Sills 2001). A number of factors will affect the reliance of people on forest product harvesting including market access (Anderson & Loris 1992; Grimes *et al.* 1994; Shanley *et al.* 2002; Seixas & Troutt 2003), available alternatives (Wilkie & Godoy 2000), the existence of laws and their enforcement (Clayton *et al.* 1997), personal skill (Bene & Tewfik 2001) and local taboos or cultural constraints (Koranteng *et al.* 2000; Colding & Folke 2001).

Many rural people in Madagascar rely, to some extent, on NTFP harvesting (Shyamsundar & Kramer 1997; Kremen *et al.* 1998; Brand *et al.* 2002). A study carried out in villages surrounding Mantadia National Park, in the eastern rainforests, estimated that villagers get more than 30% of their income from forest products (Shyamsundar & Kramer 1997). Brand *et al.* (2002) showed that farmers in north-east Madagascar would stop *tavy* for \$95 annual compensation and both forest product harvesting and *tavy* for \$195, suggesting the annual value of forest products to these households is approximately \$100 per year. Such values, while not high in absolute terms, are substantial in the context of local incomes (Ferraro 2002). For example, more than 88% of the population of Fianarantsoa province live on less than \$170 a year (INSTAT 2002).

Many methods have been used to assess forest product use, with the inevitable trade-off between quality of information and the cost of the study (Belshaw 1981; Godoy *et al.* 1993). There are essentially two type of studies: I) observed activity studies where the researcher observes forest product harvesting or collection, and II) reported activity studies, where the researcher relies on reporting of activities by the harvesters. Observation studies involve direct recording of forest products, by following harvesters (Zelevnik & Bennett 1991; Muchaal & Ngandjui 1999), recording products as they enter the village (Stearman 1990; Wilkie & Curran 1991), or monitoring forest entry points and recording the flow of harvesters and goods (Appasamy 1993; Wickramasinge *et al.* 1996). Reported activity studies include administered questionnaires (Shyamsundar & Kramer 1997; Ferraro 2002), focus group discussions or semi-structured interviews with key informants (Hegde *et al.* 1996; Paoli *et al.* 2001; Larsen 2002), and harvester diaries (Gram 2001). Such methods can get information much more quickly than through observation studies but at a cost to detail and possibly accuracy (Godoy *et al.* 1993). Rapid Rural Appraisal (RRA), and the closely related Participatory Rural Appraisal (Chambers 1981) techniques are reported activity methods which combine semi-structured interviews with participatory tools, such as transect walks and mapping, and

emphasise informal information sharing over formal questionnaire-based interviews. RRA has become widely used to investigate forest product use (Hellier *et al.* 1999; Sambou *et al.* 2002; Marshall & Newton 2003). Recent work (Smith 2003) has suggested that participatory mapping using lists of locally used toponyms, geo-referenced using a global positioning system in the field, can be a very useful tool for collecting data on the spatial extent of harvesting activities. There has been much debate about the use of such 'quick and dirty' methods relative to more detailed methods (Stocking 1980) and few studies are available which validate the techniques (Adams *et al.* 1997). Adams *et al.* (1997) demonstrate that RRA wealth-ranking approaches are successful when compared with the results of a formal household survey but I have been unable to find any study which validates RRA tools in assessing forest product use (but see Smith 2003).

Crayfish are one of the most important NTFPs in the Ranomafana area, both as a source of protein (Hardenbergh 1993) and in local trade (Dehgan 1990). In this chapter I investigate the use of crayfish, commercially and for subsistence, across a number of villages. I also examine factors that influence this such as the existence of traditional taboos (*fady*). Using a detailed study of the crayfish harvest in one harvesting village I look at the value of the trade and who benefits from it. I compare the results of an observed activity study (daily interviews with harvesters as they return to the village with their crayfish) with results from an RRA, to investigate the validity of simple methods of assessing resource use by communities. Finally, I investigate the spatial pattern of harvesting by five communities and group the mark-and-recapture sites by the level of harvesting to which they are exposed. This will be important in the next two chapters where I estimate population parameters (growth, survival and fecundity) for *A. granulimanus* populations at unharvested sites.

4.2 Methods

4.2.1 General methods

We used three methods with increasing level of detail to investigate the patterns of crayfish harvesting in the Ranomafana area: village interviews, RRA interviews with households, and daily harvester interviews. We carried out village interviews with self-selecting groups of elders and forest product harvesters in 27 villages (see Figure 2.3).

In two harvesting villages (Sahavondronana and Vohiparara) and three non-harvesting villages (Ambatovory, Antortosy and Bevoahazo) we carried out RRA interviews. In each village we started with preliminary interviews and village mapping exercises with village leaders to stratify households into broad economic groups; this was used as a sampling frame to select households for interviewing. In total we interviewed 85 households (Table 4.1) using semi-structured interviews, participatory mapping and calendar tools (see section 2.2.6).

Table 4.1 The number of households interviewed in each village where RRA interviews were carried out.

village	number of households interviewed	total number of households in the village
Ambatovory	8	12
Antortosy	10	45
Bevoahazo	25	50
Vohiparara	25	47
Sahavondronana	11	48

We carried out daily harvester interviews between January 2003 and January 2004 in one heavily harvesting village: Vohiparara. Twenty-two harvesting households took part in the daily interviews (see section 2.2.6.3). Some entered and left the project but on average 19 households were interviewed each month. During this time 599 interview days were spent crayfish harvesting and 13,256 crayfish were brought to the interviews, identified and measured.

The exchange rate between the Malagasy Franc (FMG) and the US dollar (\$) fluctuated over the study period. The mean of the exchange rate during the period was 5830 FMG = \$1.

4.2.2 The importance of crayfish harvesting in the Ranomafana area

4.2.2.1 The number of villages involved in commercial harvesting

In the village-level interviews we asked informants to list the top economic activities of the village in order of importance and to estimate the number of households who harvested crayfish commercially. Open-ended discussions were used to identify reasons why villages relied on crayfish harvesting to different extents.

4.2.2.2 The fady against crayfish selling: its origin and prevalence

We asked households interviewed in the RRA interviews about their personal *fady*. If they had *fady* that affected selling crayfish we asked about its origin. Reasons for exceptions to local trends (e.g. people not *fady* in generally *fady* villages) were investigated through open-ended discussions with all households.

4.2.2.3 The importance of subsistence crayfish harvesting

We investigated the frequency of crayfish harvesting by households in three villages where most people were *fady* for commercial crayfish harvesting

(Ambatovory, Antortosy, Bevoahazo). Factors affecting the frequency of crayfish harvesting were noted.

4.2.3 Details of the crayfish trade in one harvesting village

In the harvesting village of Vohiparara, 25 households were identified in the RRA and village interviews as harvesting crayfish; 22 of these took part in the daily interviews.

4.2.3.1 What do harvesters harvest?

The species composition and the size-frequency distribution of the crayfish caught by harvesters in Vohiparara was recorded. The size-frequency distribution was compared with that of *A. granulimanus* found in the rivers during the mark-and-recapture study (see section 2.2.3.1) to investigate whether harvesters are size-selective. A size-frequency distribution for *A. betsileoensis* was not available as only very limited mark-and-recapture was carried out on this species. I used the relationship between size and the probability of reproduction (see Figure 3.9) to estimate the proportion of the individuals caught of each species which would have reproduced prior to harvesting.

4.2.3.2 How far do harvesters travel?

For those harvesting days recorded during the daily interviews for which the information was available, I used ArcGIS to estimate the mean distance from Vohiparara to the centroid of the main site at which the day's crayfish were collected. I compared the mean distance travelled by male and female harvesters using a t-test.

4.2.3.3 What factors affect the value of crayfish caught?

The destination of each batch of crayfish (sold direct to a passer-by, sold to a stallholder in the village, sold to another villager for consumption, or eaten within the harvester's household) was recorded in the daily interviews. To investigate factors influencing the price of a batch of crayfish, I used batch price

as the response variable in a General Linear Model (GLM) with normal error structure. Explanatory factors tested were the state in which the batch was sold (cooked or raw), the season in which it was sold (hot or cold), the buyer (villager or passer-by), the number of individuals in the batch, the total mass of the batch and the species. Mean monthly temperature for Ranomafana Park 1997-2001 (see Figure 2.2) was used to define the hot season (November to April: 19.0 to 20.9°C) and the cold season (May to October: 13.8 to 18.2°C). The mass was estimated from the carapace lengths (CL) using an equation derived from a subset ($n = 186$) of crayfish for which both CL and mass (M) was recorded (Equation 4.1; $r^2 = 0.94$).

$$\text{Equation 4.1} \quad M = 27.2 - 2.1 \times CL + 0.05 \times CL^2$$

Where a proportion of the batch remained unsold, the batch mass and number were multiplied by the proportion sold, assuming that the size of individuals sold and unsold was the same.

4.2.3.4. *What revenue does Vohiparara earn from crayfish?*

For each of the 22 harvesting households which took part in the daily interviews, I estimated annual earnings from crayfish harvesting using Equation 4.2. Unsold crayfish were eaten in the harvester's household and I gave these a subsistence value equivalent to the raw village price (Godoy *et al.* 1993).

$$\text{Equation 4.2} \quad E = \sum_{i=1}^n \left[\left(\frac{H_i}{I_i} \right) \times (\mu_{Ei} + \mu_{Si}) \right] \times 365$$

where H_i is the number of days harvester i spent crayfish harvesting during the I_i interview days, μ_{Ei} is the mean price obtained for a batch of crayfish sold by harvester i and μ_{Si} the subsistence value obtained from a day's harvesting. The mean earning per harvester was summed across the n household members to give E ; the total annual value of crayfish to a harvesting household.

The three harvesting households that did not take part in the daily interviews were known, from interviews with other harvesters, not to be very

heavy harvesters. They were assumed to earn the mean annual earnings of the lower earning 50% of harvesters. The total revenue earned from harvesting crayfish by harvesters from Vohiparara for the year 2003/2004 was calculated by summing across all 25 harvesting households.

To estimate the value of crayfish in Vohiparara to stall holders, I estimated the mean mark-up for a batch of crayfish of mean size and mass (the difference in value if sold raw to another villager and if sold cooked and direct to a passer-by) from the GLM above. I assumed that stallholders obtain a similar mark-up and that they always buy the crayfish raw from the harvesters, sell them cooked to consumers and manage to sell all the crayfish they buy. I used this mark-up, the proportion of batches sold to middlemen and the estimated total number of crayfish batches harvested annually in Vohiparara to estimate the gross value of crayfish harvesting to stallholders in Vohiparara.

4.2.3.5 *How many crayfish were harvested in Vohiparara in 2003/2004*

The total number of crayfish caught by harvesters in Vohiparara was estimated for the 22 harvesting households which took part in the daily interviews using the total number of days spent harvesting a year by harvesters (see above) multiplied by their mean number of crayfish caught per trip and summed within households. As above, the three harvesting households that did not take part in the daily interviews were assumed to collect the same number of crayfish as the lower collecting 50% of harvesting households. The percentage of crayfish caught by harvesters which fell into each size-class (small: 22-34.9 mm CL, medium: 35-49.9 mm CL and large: > 50 mm CL) was recorded and used to estimate the total number of crayfish in each size-class collected by harvesters in Vohiparara between January 2003 and January 2004.

4.2.3.6 *Who depends on crayfish harvesting?*

We identified the economic activities of households in Vohiparara during the preliminary interviews. In most cases we were able to confirm these during

subsequent household interviews. Economic activities were split into six major groupings: forest product harvesting (including crayfish), forest product harvesting (not including crayfish), farming, running a stall, working for the government (teacher or park guard), and waged labour. Many people had more than one major economic activity. Whether the head of the household was male or female was recorded for each household. Informal interviews with harvesting and non-harvesting households addressed the reasons people depended on crayfish harvesting.

4.2.4 Validating the RRA interviews

For 15 harvesters in Vohiparara both RRA data and daily interview data were available. I used this to investigate how useful RRA data were in assessing harvesters' activities. Two aspects were investigated: the spatial pattern of harvesting and the number of crayfish caught in a day. I calculated the mean distance travelled to harvesting sites by each harvester by averaging the distance to the centroid of the rivers at which they harvested, weighted by the relative frequency with which they harvested at that site using the two data sets separately. I compared the two estimates using a linear regression weighted by the annual number of days spent harvesting by each harvester, and plotted a map showing the distribution of harvesting effort in the Ranomafana area as determined by the two methods. Likewise, during the RRA interviews, harvesters estimated the number of crayfish they caught at the sites they visited. I compared these reported mean daily catches with each individual's actual mean number collected during harvesting trips, recorded during the daily interviews.

4.2.5 The spatial pattern of harvesting

A central aim of the household interviews was to investigate the spatial pattern of harvesting in the area covered by the mark-and-recapture sites. Interviewees in the RRA interviews took part in two exercises (see section 2.2.6.2) which resulted in a list of sites they visit for crayfish harvesting with information on the relative frequency they visited each site and an approximate

number of days spent crayfish harvesting each year. The visits to a site were summed across all households.

In villages with few commercial harvesters (Ambatovory, Antortosy and Bevoahazo) we carried out interviews with all households likely to be most involved in crayfish harvesting (those not *fady* for selling crayfish, those with cows in the forest, or those identified by other villagers as ‘forest people’ [*olona mahay ala*]). None of the people not identified in advance as people going to the forest a lot were found to harvest in the forest, so I assumed that nearly all forest harvesting in these villages was covered by the interviews, though harvesting close to the villages may have been underestimated.

In harvesting villages (Sahavondronana and Vohiparara) many people were involved in crayfish harvesting. In Vohiparara 22 out of the 25 harvester households were interviewed. In Sahavondronana only 11 out of approximately 48 harvesting households were interviewed. To extrapolate to the people for whom we do not have data, I assumed the households that were interviewed collected on the same number of days as the less frequently harvesting 50% and with the same spatial distribution as the mean of the all harvesters in that village.

I estimated the total number of harvesters visiting each river each year by summing across all harvesters in all villages. The estimated number of harvesting days at each river was divided by its length to give a value for each river of annual harvesting days per metre. Using ArcGIS, I overlaid a grid of 600 m by 600 m cells on the river layer (see Figure 4.1 for an example). I multiplied the length of each river segment within a cell by the harvesting days per metre for that river and calculated the total number of harvesting days within each cell by summing for all the rivers occurring within the cell (see Table 4.2).

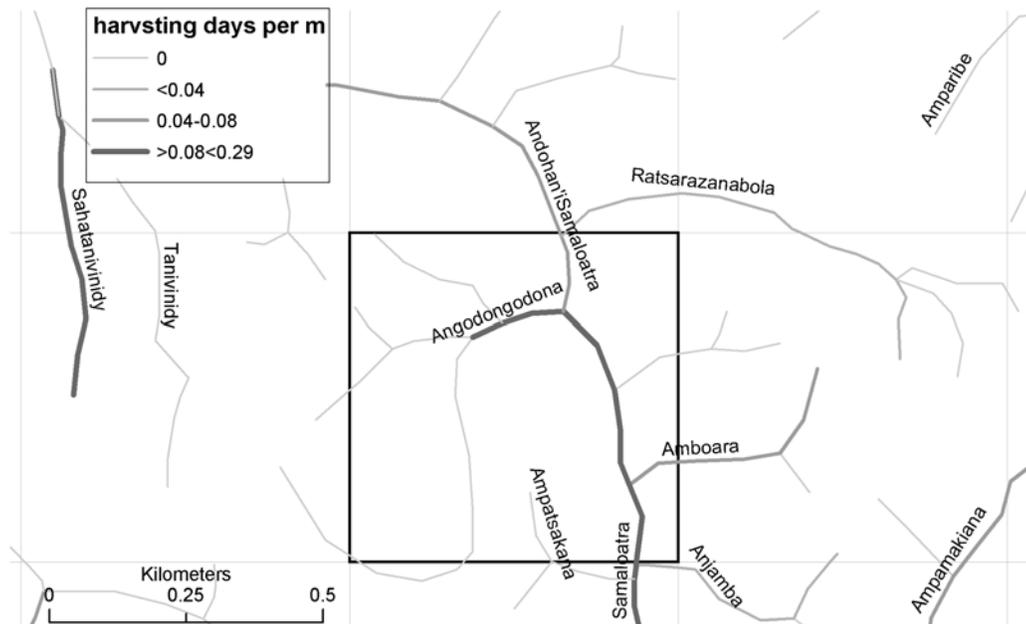


Figure 4.1 A grid of cells 600 m by 600 m overlaid on the layer containing information on rivers.

Table 4.2 The calculation of total number of days spent harvesting in a cell for the example cell highlighted in Figure 4.1.

river name	length in the cell (m)	annual harvest days/total length
Andohani'iSamaloatra	146	0.05
Angodongodona	173	0.17
Amboara	103	0.08
Samaloatra	497	0.11
TOTAL	99.62	

We visited three other villages (Amboditanimena, Ambatolahy and Ambodivoahangy) whose harvesting activities may have impacted on the mark-and-recapture sites, but preliminary interviews suggested they did not use the forest in the area so they were not included in the more detailed study. Unfortunately we did not carry out interviews in Andemaka so the harvesting level is not known for sites close to this village.

4.3 Results

4.3.1 The importance of crayfish harvesting in the Ranomafana area

4.3.1.1. The number of villages involved in commercial harvesting

Of 27 villages visited, three villages (Ambalavao, Sahavondronana and Vohiparara) reported that commercial crayfish harvesting was very important to their village economy and a further village (Ambodiriana) said it was quite important. Unsurprisingly, the three villages which reported crayfish harvesting to be important had the highest numbers of households involved in commercial crayfish harvesting (17, 30 and 25 respectively; Figure 4.2).

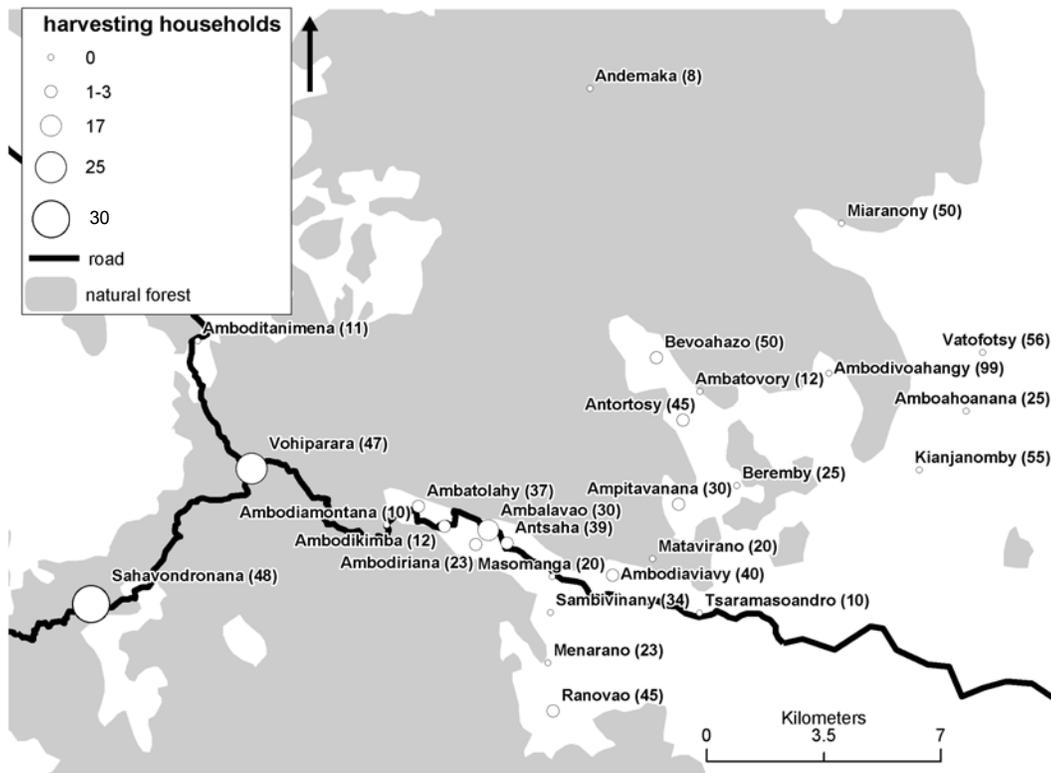


Figure 4.2 A map showing the 27 villages interviewed. The size of the spot indicates the number of households harvesting crayfish commercially. The approximate number of households present in each village is given in parentheses after the name.

These commercially harvesting households did not harvest to the same extent. For some it was their only income but for many others, particularly those

in Sahavondronana, harvesting crayfish was only seasonally important. In eight villages where harvesting was not considered economically important at the village level, certain families did carry out commercial crayfish harvesting.

In villages where crayfish harvesting was not commercially important, a number of reasons were reported. In many villages, particularly the *Tanala* villages to the east, but also in the *Betsileo* village of Amboditanimena, there are strong traditional *fady* against harvesting crayfish for sale. Other villages (Amboahoanana, Kianjomby, Masomanga, Tsaramasoandro and Vatofotsy) reported that they are too far from the forest to harvest crayfish. Some of these communities (Amboahoanana, Vatofotsy) reported that more crayfish harvesting occurred in the past, before the loss of forest through *tavy* (slash-and-burn agriculture) resulted in the local extirpation of crayfish. All villages with access to forest reported some harvesting of crayfish for subsistence.

4.3.1.2. *The fady against crayfish selling: its origin and prevalence*

In three, predominantly *Tanala* villages, studied using the RRA approach (Ambatovory, Antortosy, Bevoahazo), between 90 and 100% of households reported *fady* which prevented them selling crayfish. This pattern was reversed in the predominantly *Betsileo* villages, Sahavondronana and Vohiparara, where 0 and 6% respectively had *fady* preventing them selling crayfish (Figure 4.3).

Of the 35 households interviewed who had *fady* preventing them selling crayfish, 43% were *fady* for selling any forest products (*fadivarotra remby*), 46% were *fady* for selling products of freshwater only (*fadivarotra laokandrano*) and 11% were *fady* for selling crustaceans only (*fadivarotra orana sy foza ihany*).

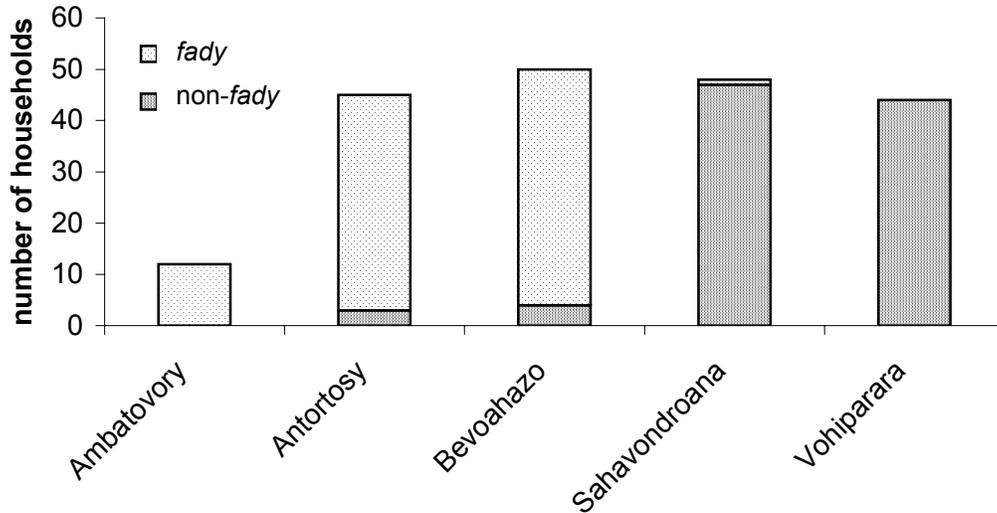


Figure 4.3 The number of households in each of the five RRA study villages which are *fady* or not *fady* for selling crayfish.

Most people interviewed did not know the origin of the *fady* preventing crayfish selling; all agreed that the origin was in the distant past. However two elders, one in Bevoahazo and one in Ambatovory told the same story explaining its origin. They said the ancestors were wise (*hendry ny razana*) and knew that money was slippery and that men can be stupid (*malama ny vola ary misy lehilahy sasany adala mandanindany vola*). Men should therefore tend to their fields first so their family has food to eat, and only collect forest products to provide extra food for their families. If men spend their time collecting forest products and taking them to the road to sell, they may come back empty-handed, because of not selling them or wasting the money. This fits with a sentiment repeated by a number of people when questioned on the origin of *fady* preventing selling of crayfish: ‘you can’t eat money’.

Eight households interviewed in the predominantly *fady* villages lacked *fady* preventing them selling crayfish. Four independent origins of lacking the *fady* in a *fady* area were identified (some of the eight families being close relatives). Two of these were due to the head of the household or a recent ancestor being an incomer from a non-*fady* area. In the other two cases, their ancestors had been *fady* but had broken the *fady* through dire need, had made

money from selling crayfish, and had declared that henceforth crayfish selling was no longer *fady* for their descendants.

In the predominantly non-*fady* village of Vohiparara, three families were *fady* for selling crayfish. All three were relatively recent immigrants from the *fady* village of Amboditanimena. One such family abandoned the *fady* but suffered serious illness and now only harvest crayfish for home consumption.

4.3.1.3 *The importance of subsistence crayfish harvesting*

In the three predominantly *fady* villages (Ambatovory, Antortosy and Bevoahazo) where we carried out RRA interviews, the majority (93%) of households reported crayfish harvesting, but most did so less than five times a year (Figure 4.4). Households which were not *fady* for selling crayfish and or had cows in the forest reported crayfish harvesting more frequently.

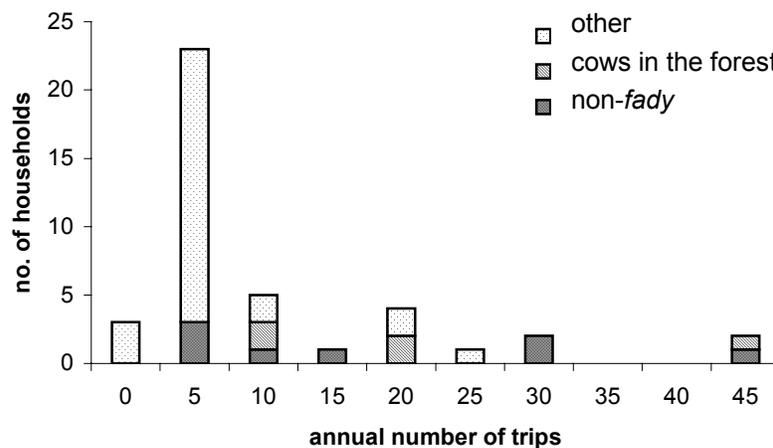


Figure 4.4 The estimated annual number of crayfish harvesting trips by households in *fady* villages for non-*fady* households (n = 8), households with cows in the forest (n = 5) and others (n = 28).

4.3.2 Details of the crayfish trade in one harvesting village

4.3.2.1 What do harvesters harvest?

The daily interviews with harvesters in Vohiparara showed that more than 95% of the crayfish harvest was *A. granulimanus* (n = 13,256). *A. betsileoensis* and *A. crosnieri* were much less commonly caught and made up only 3.3 and 1.4 % of the catch respectively.

Harvesters were selective for larger crayfish. Figure 4.5 below shows the size-frequency distribution of *A. granulimanus* found in the rivers during the mark-and-recapture study, and those caught by harvesters. *A. betsileoensis* caught by harvesters tended to be larger than *A. granulimanus*. Seventy five percent of *A. granulimanus* caught were in the medium size-class (35-49.9 mm CL; see chapter two) while 20% were large (> 50 mm CL) and only 5% were small (22-34.9 mm CL).

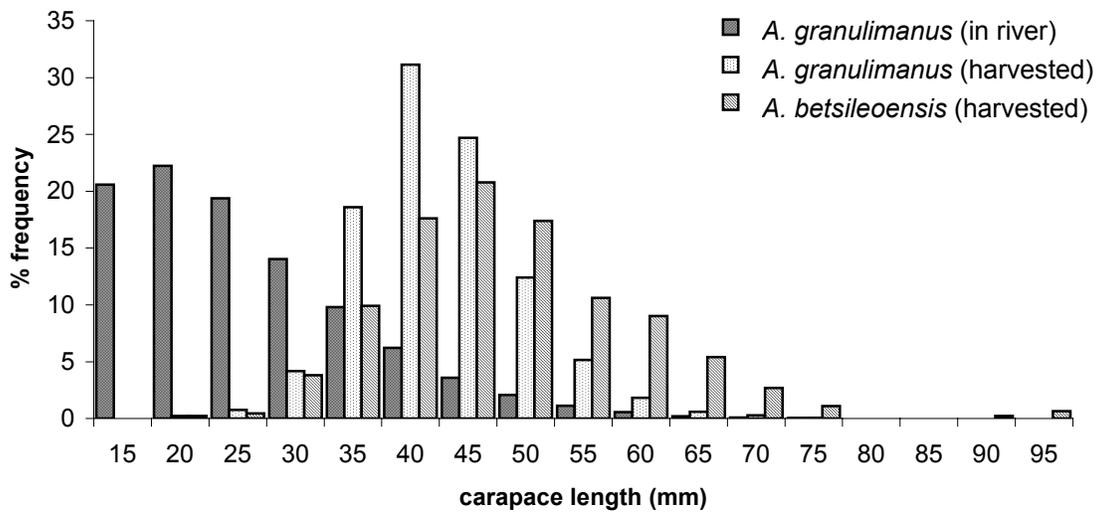


Figure 4.5 The size-frequency distribution of *A. granulimanus* (n = 12,628) and *A. betsileoensis* (n = 457) collected by harvesters from Vohiparara compared with that of *A. granulimanus* in the rivers (n = 26,096).

Using the relationship between size and the proportion of females which were reproductive I estimated that more of the *A. granulimanus* caught by harvesters would be expected to have bred already (42.3%) than of the *A. betsileoensis* (25%). *A. granulimanus* (in river) *A. granulimanus* (harvested) *A. betsileoensis* (harvested)

4.3.2.2. How far do harvesters travel?

The mean distance travelled by female harvesters was less than that travelled by male harvesters ($t_{327} = 6.52$, $p < 0.001$; see Figure 4.6). The maximum distance travelled from the village was the same for both sexes (6.5 km). Overall the mean distance travelled was 2.4 km and 75% of trips were within 3.1 km of the village.

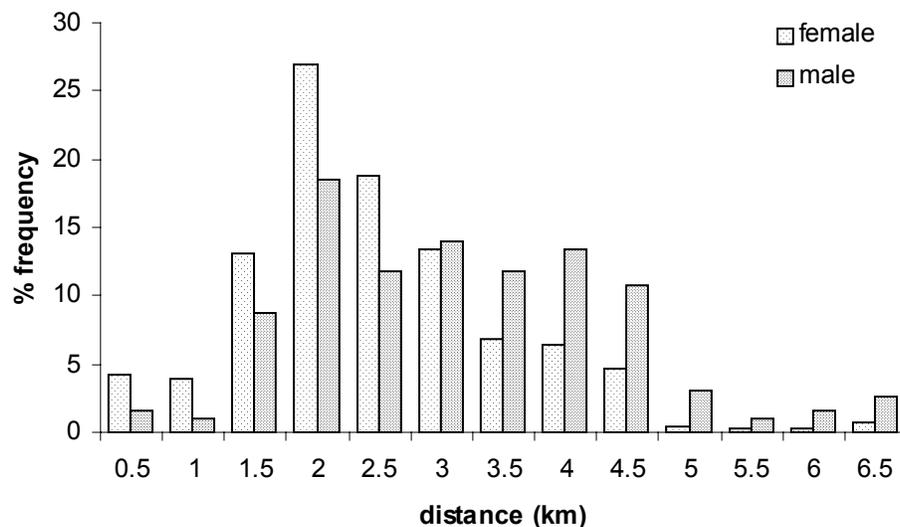


Figure 4.6 The distance travelled by male (n = 194) and female (n = 405) harvesters on trips from Vohiparara.

4.3.2.3. What factors affect the value of crayfish caught?

The destination of 422 batches of crayfish was known; 50% were sold to passers-by on the road direct from harvesters, 45% were sold to village stallholders who then sold to passers-by, 5% were sold to others in the village for home consumption, and less than 1% were kept by the harvesters with no attempt made to sell them (Figure 4.7). However, in 11% of cases when the crayfish were sold, some of the batch remained unsold and were eaten by the harvester's family.

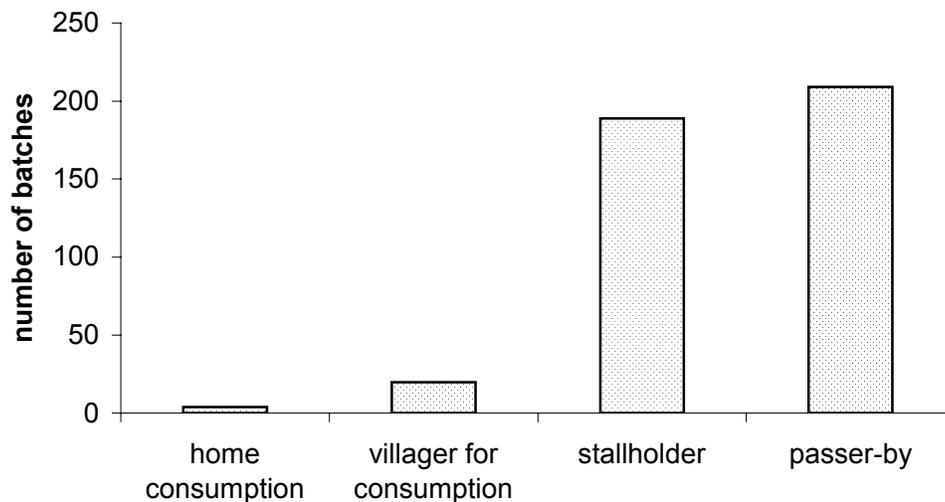


Figure 4.7 The destination of batches of crayfish caught by harvesters (n = 422).

For 358 batches of crayfish sold by harvesters in Vohiparara, all the information was available to carry out a GLM investigating the factors affecting the price obtained by harvesters. The price of a batch of crayfish depended on both the number of crayfish and, independently, its total mass (Table 4.3) suggesting that the size of crayfish was important, with larger crayfish being of higher value. Cooked crayfish had a higher sale value than raw and the price for a batch of crayfish was higher in the cold season than in the hot season. If the crayfish were sold to passers-by rather than to other villagers the price was also higher. The species of crayfish had no significant affect on its price, however data for species other than *A. granulimanus* were sparse.

Table 4.3 GLM of the factors predicting the price (\$) of a batch of crayfish (n = 358). The minimal model comprised only significant terms and explained 59.1% of the total variance. Significant terms are shown in bold.

model term	F statistic	d.f.	p
<i>full model</i>			
number of crayfish	57.71	1	< 0.001
total mass of the batch	356.28	1	< 0.001
state (cooked or raw)	36.38	1	< 0.001
season (hot or cold)	10.66	1	0.001
buyer (villager or passer-by)	8.47	1	0.004
species	0.15	2	0.86
	<i>average effect</i>	<i>SEM</i>	
<i>minimal model</i>			
constant	0.247	0.0412	
number of crayfish	0.0184	0.00242	
total mass of the catch (g)	0.000204	0.0000512	
state			
cooked	0	0	
raw	-0.210	0.0347	
season			
hot	0	0	
cold	0.0746	0.0229	
buyer			
villager	0	0	
passer-by	0.0751	0.0258	

4.3.2.4 *What revenue does Vohiparara earn from crayfish?*

The mean annual earnings from crayfish harvesting to harvesters in Vohiparara in the year 2003/2004 was \$82 (±\$12.7). There was a lot of variation with the most heavily harvesting household earning \$246.5 and the least earning \$21 annually (Figure 4.8). The majority of the revenue (98%) was from cash earnings, as most of the catch was sold. Extrapolating for all 25 harvesters, the estimated gross annual revenue from crayfish to harvesters from Vohiparara was \$2074.

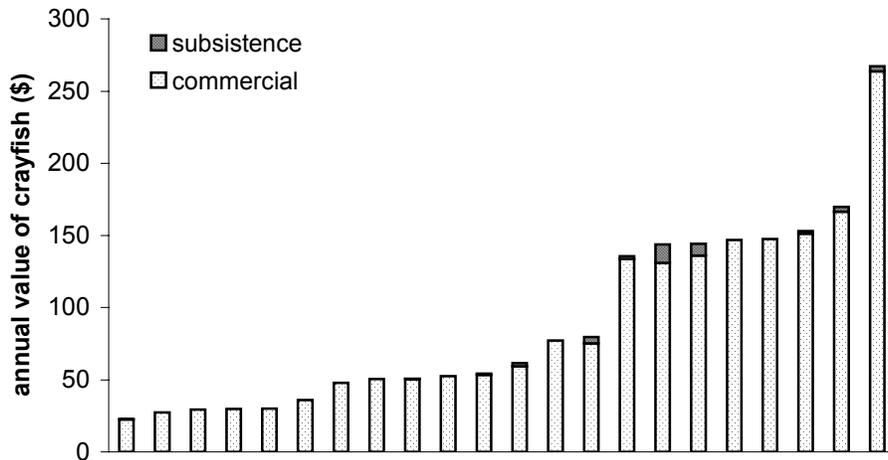


Figure 4.8 The estimated annual value of crayfish to the 22 harvesting households in Vohiparara which took part in the daily interviews showing the spread between the subsistence value and commercial value.

Harvesters in Vohiparara spent approximately 2443 days crayfish harvesting in the year 2003/2004 and therefore produced 2443 batches of crayfish, 45% of which were sold to village stallholders (see above). The mark-up for a batch of crayfish of average size, bought raw from a villager and sold cooked to a passer-by, was \$0.28 (see GLM above) giving an approximate earning to the stallholders of Vohiparara of \$308. The total gross revenue from crayfish to the community of Vohiparara in 2003/2004 was approximately \$2382.

4.3.2.5 *How many crayfish were harvested in Vohiparara in 2003/2004?*

The 25 harvesting households in Vohiparara collected approximately 51,017 crayfish in the year 2003 to 2004.

4.3.2.6 *Who depends on crayfish harvesting?*

Of the 47 households in Vohiparara, 25 relied, at least partly, on crayfish harvesting for their livelihood. A higher proportion of female-headed (10/13) than male-headed (16/34) households relied on harvesting, but this trend was only weak ($\chi^2_1 = 3.39$, $p = 0.071$). Many crayfish-harvesting households were also involved in agriculture (7/25) and in waged labour (10/25). Respondents said crayfish harvesting was an unpopular activity as the forest is often cold (*mangasiaka loatra*) and full of leeches (*be dimatika*). The lack of opportunities for waged labour and the high investment costs and deferred benefits of agriculture were the reasons given for why they harvest crayfish.

4.3.3 **Validating the RRA interviews**

The mean distance travelled on harvesting trips estimated from RRA interviews significantly predicted the mean distance as estimated from the daily interviews (weighted regression $r^2 = 0.5$, $F_{1,14} = 30.35$, $p = 0.003$). Figure 4.9 shows the estimated number of days spent harvesting at sites by Vohiparara harvesters estimated using the RRA and the daily interview data. The general spatial extent was well described by the RRA data.

RRA interviews were less good at estimating the number of crayfish caught in a day's harvesting. There was no significant relationship between the two data sets (weighted regression $r^2 = 0.11$, $F_{1,14} = 2.69$, $p = 0.13$). Harvesters consistently overestimated the number of crayfish they caught in a day (Figure 4.10).

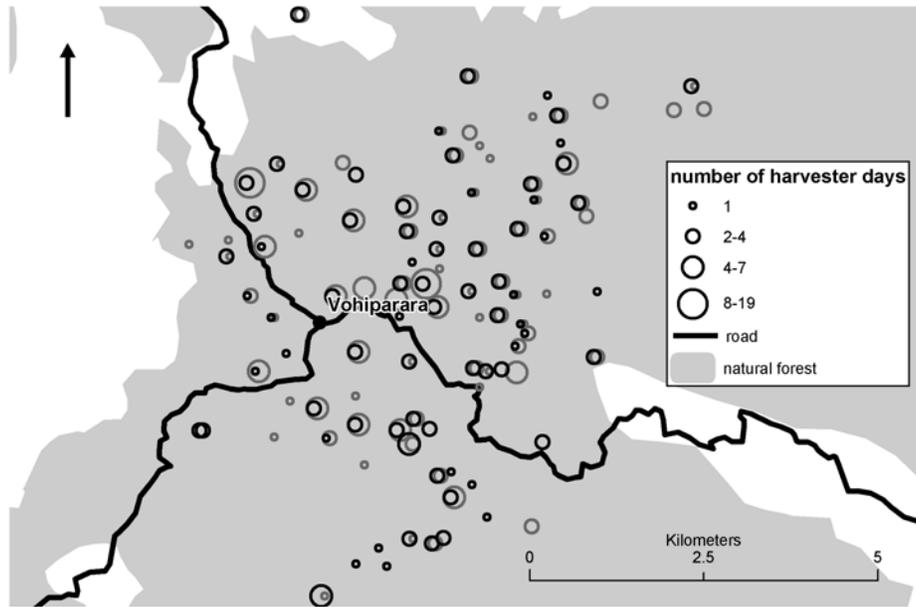


Figure 4.9 The estimated number of harvesting days by harvesters from Vohiparara by site as estimated from the RRA (dark grey) and from daily interviews (black). The size of the spot indicates the annual number of visits.

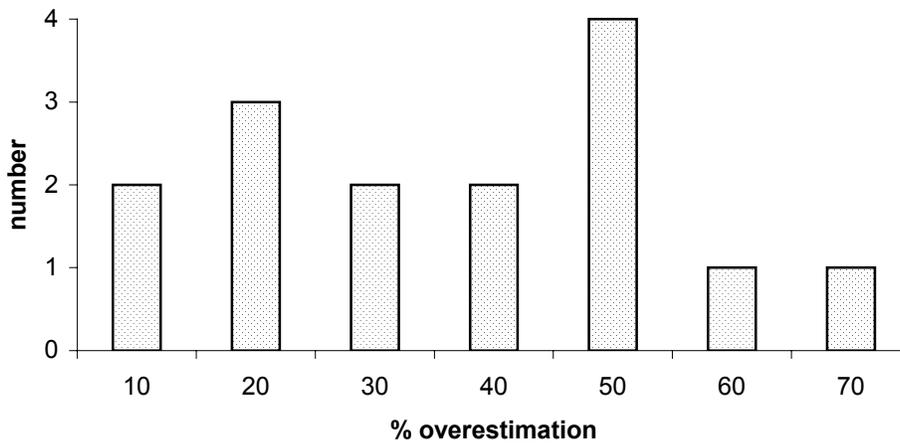


Figure 4.10 The percentage by which harvesters (n = 15) overestimated the number of crayfish caught in a day in RRA interviews when compared with the number recorded in the daily interviews.

4.3.4 The spatial pattern of harvesting

Figure 4.11 shows the harvesting effort around the five villages where we carried out RRA interviews. Harvesting was a lot more intense surrounding Sahavondronana and Vohiparara than it was in the areas surrounding Ambatovory, Antortosy and Bevoahazo. We did not carry out interviews in the village of Andemaka so the level of harvesting there remains unknown. Figure 4.12 below shows the position of the mark-and-recapture sites.

Most of sites surrounding Ambatovory, Antortosy and Bevoahazo were exposed to very little harvesting. However, interviews with villagers in Bevoahazo revealed that illegal gold miners and forest product collectors from Ambalakinresy (a major village on the road north of Amboditanimena; Figure 4.12) used the forest to the north west of Bevoahazo and harvest crayfish there. This impact was probably relatively low but since there was no way to quantify it, I excluded these sites from the sub-set of sites I considered unharvested. I also excluded one site in an area where the harvesting level was known to be generally low from the unharvested set as it is very close to a cave where villagers regularly stay overnight so there may be intense localised harvesting. In total I identified 17 sites as unharvested (see Figure 4.12).

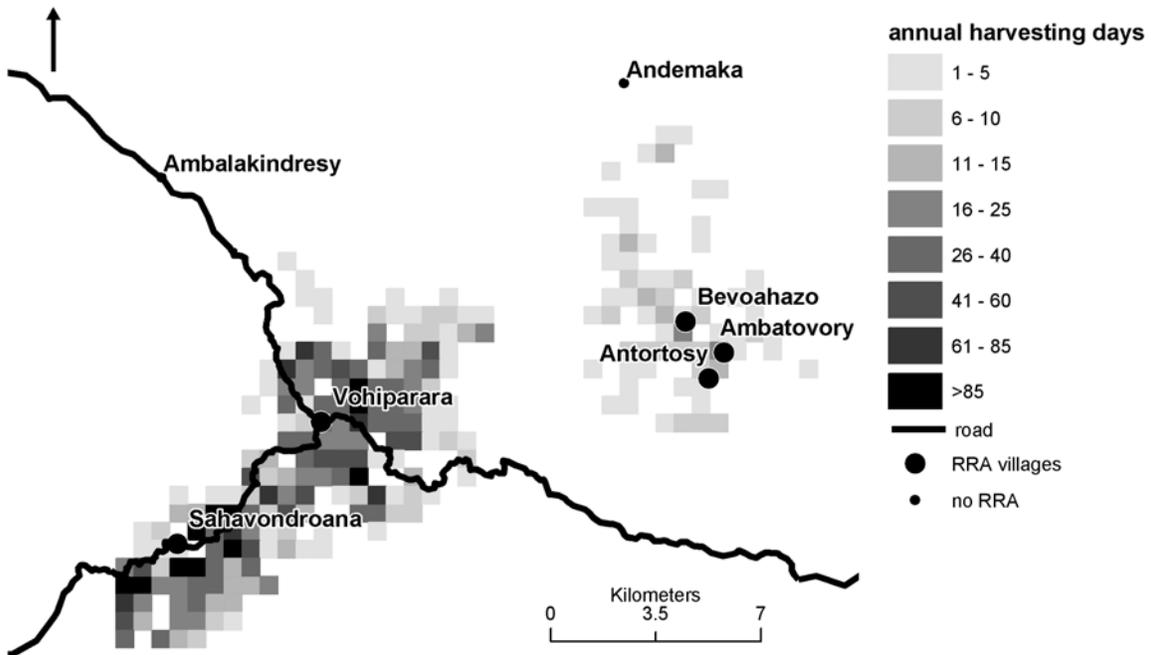


Figure 4.11 The spatial distribution of harvesting effort by the 5 villages where RRA interviews were carried out.

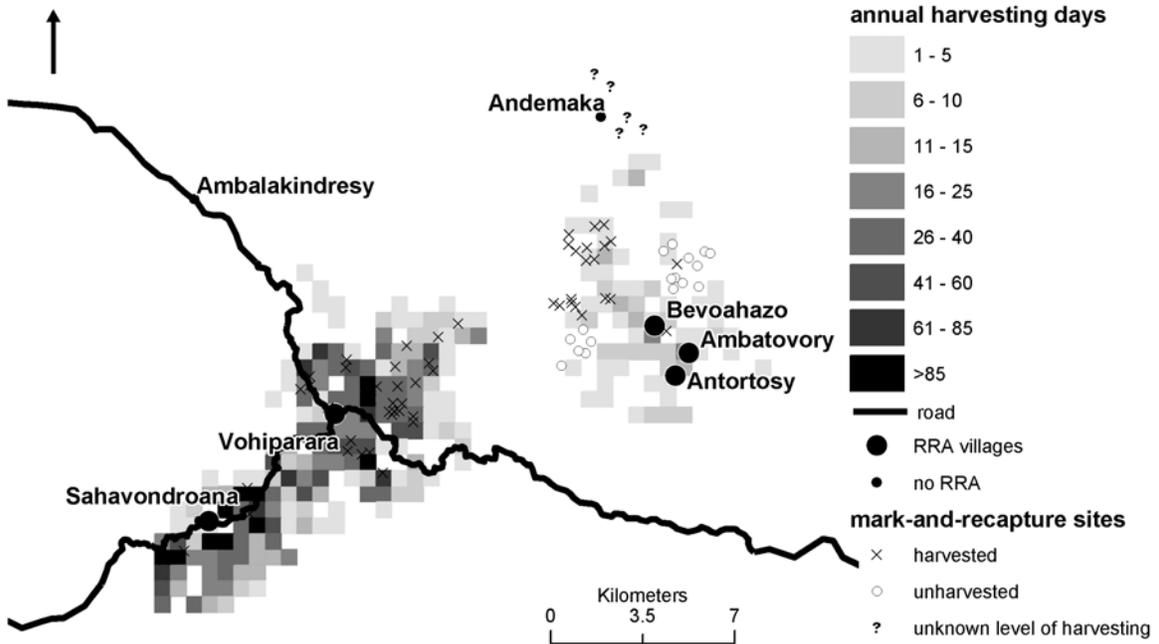


Figure 4.12 Locations of the mark-and-recapture sites in relation to the spatial distribution of harvesting effort by the 5 villages where RRA interviews were carried out.

4.4 Discussion

4.4.1 The importance of crayfish harvesting in the Ranomafana area

Three villages, out of the 27 we visited, rely heavily on commercial crayfish harvesting: Ambalavao, Sahavondronana and Vohiparara. Unsurprisingly these are all on the road with good market access and lack widespread *fady* against crayfish harvesting. In eight other villages one or two families lack the *fady* and will catch crayfish for sale within the village or take them the road to sell.

In most villages visited (21/27), respondents reported that people carry out subsistence harvesting of crayfish. In the three *fady* villages where we investigated the frequency with which people go on crayfish harvesting (Ambatovory, Antortosy and Bevoahazo), most households (93%) harvest crayfish but many reported harvesting to be only very occasional. People who are often in the forest to check on their cows or collect medicinal plants or *laro* (bark used to flavour local rum) reported collecting crayfish more frequently than other members of the community. It is likely that crayfish harvesting for subsistence use was underreported: I observed women returning from water collection with a few crayfish and children collecting and consuming crayfish but this was not reported in the interviews. Households often underreport kills of smaller animals or kills made by children as they consider them unimportant (Godoy & Bawa 1993; Smith 2003). Such small-scale opportunistic crayfish collecting may provide a significant source of protein as people in the area have a very protein-poor diet (Hardenbergh 1993). Harvesters in the harvesting village studied (Vohiparara) appear to get very little subsistence value from crayfish harvesting. The great majority of crayfish they catch are sold and although they will eat what is unsold this tends to be a small proportion of their catch. Again collecting by children, or opportunistic collecting by adults may well have been underreported.

4.4.2 The importance of crayfish harvesting within a harvesting village

More than 50% of households in Vohiparara are involved in commercial crayfish harvesting, and other households profit from selling crayfish bought from the harvesters. Despite this high involvement, the revenue earned from crayfish harvesting by the village may seem low; only \$2382 a year. However, put in the context of local incomes it is significant. More than 88% of rural households in Fianarantsoa province live on less than \$170 a year (INSTAT 2002). Harvesters in Vohiparara earn between 12.4 and 145% of this amount from crayfish harvesting.

The households which rely on crayfish harvesting appear to be disproportionately poorer. Female-headed households in Vohiparara depend more on crayfish harvesting than male-headed households. Female-headed households are often poorer (Quisumbing *et al.* 2001), due to a number of factors including a high dependency ratio (Quisumbing *et al.* 2001) and a lack of opportunities for wage labour (Canagarajah *et al.* 2001; Tschirley & Benfica 2001). Male-headed households involved in crayfish harvesting tended to be the less well off and claimed they harvested crayfish because of the lack of alternatives due to their poverty. Agriculture requires investment of seeds and labour and the benefits are deferred by between three and nine months, depending on the crop. This may be a severe barrier to entry for poorer members of the community. Although it is difficult to separate 'use' and 'dependency' (Bennett 2002), it is likely that, due to limited alternatives, many people in Vohiparara are effectively dependent on crayfish harvesting for their livelihood. This agrees with the general finding of Peters (1998b) who suggested that crayfish harvesting in the Ranomafana area is only done when there is no alternative income source.

4.4.3 The species harvested

The majority of crayfish harvested in Vohiparara are *A. granulimanus*. Our opportunistic observations and interviews suggest that this species, very

common in streams and rivers wherever there is forest (see section 3.2.3), also dominates the crayfish harvest in other villages. *A. betsileoensis*, found only in large rivers, are also harvested but less commonly. Catching *A. betsileoensis* using worms tied to the end of a long stick, the preferred technique in Vohiparara, is very skilled as the rivers are deep and dangerous because most people cannot swim. During interviews in Sahavondronana, villagers told us that *A. betsileoensis* make up a significant proportion of the catch there during the warm months of *lohatoana* (approximately September to December). This is because at that time the crayfish are very active and readily enter eel traps; eel trapping is an important activity in Sahavondronana. *A. betsileoensis* may be more vulnerable to overexploitation than *A. granulimanus* as they become reproductive at a larger size (see Figure 3.9), affecting their vulnerability to recruitment overfishing. The proportion of *A. granulimanus* likely to have reproduced before they were caught (43%) was higher than the proportion of *A. betsileoensis* likely to have reproduced before they were caught (25%; see Figure 4.5). *A. crosnieri* are very seldom targeted by harvesters because of their muddy taste (*fofom-potaka*), small size and the difficulty of harvesting this species in its swampy habitat.

4.4.4 *Fady* and natural resource management

Anthropologists have described many cases where traditional taboos benefit conservation (Colding & Folke 2001). There is debate between those who consider such taboos to have developed with the purpose of conserving important natural resources (McDonald 1977; Ross 1978; Colding & Folke 2001) and those who consider this attitude as a return to the much discredited 'noble savage' paradigm (Buege 1996; Alvard 1998). Alvard (1998) stresses the importance of empirical evidence before assuming that dietary prohibitions and taboos have their origin in resource management.

Malagasy culture is well known for its extensive system of *fady* (Lambek 1992) many of which have natural resource management implications (O'Brien *et*

al. 2003; Durbin *et al.* 2004; Horning 2004). *Fady* against selling wild-harvested species (ranging from all forest products to crayfish and crabs specifically) are widespread in the Ranomafana area. Do these *fady* demonstrate a concern about the status of the resource among the ancestors who made the *fady*? It is impossible to know, as those who made the *fady* are long dead. The *fady* certainly seems to have the effect of reducing pressure on the resource: *fady* villages harvest much less crayfish than do villages in non-*fady* areas. However, it seems unlikely that in this case the *fady* was developed for reasons of natural resource management. No one interviewed in a *fady* area thought of crayfish as a limited resource and human population densities were lower, and the forested area greater, in the past so there would have been less pressure then. Instead, two elders suggested to me that the *fady* is there to ensure people concentrate on farming, providing them with enough staple foods, rather than exposing themselves to the vagaries of a market economy.

A number of authors have lamented the loss of taboos and the negative impacts on natural habitats or populations of exploited species (Brooke & Tschapka 2002; Anoliefo *et al.* 2003). The *fady* affecting sales of crayfish are still very strong, at least in Bevoahazo, Ambatovory and Antortosy, where extensive interviews were carried out. Only four indigenous households (corresponding to two independent origins) in these villages have lost the *fady*. In both of these cases the *fady* was lost some time in the past (probably in the 1950s) during a period of great need, demonstrating that *fady* have some flexibility in face of economic necessity. However there was no evidence of a widespread breakdown of the *fady*.

4.4.5 Validating the RRA interviews

RRA data, or more traditional questionnaire surveys, are often relied on to provide an assessment of natural resource use where time and/or funds are not available for a more in-depth study (Belshaw 1981). Recall accuracy is much higher for more recent events (Young & Young 1961; Bernard 1984) so methods

such as RRA, which rely on people summing their activities across a time period, may be subject to considerable error. The findings presented here suggest that the RRA approach may yield useful information on some aspects of harvesters' behaviour but not on others. The RRA data described the spatial extent of harvesting well. However harvesters were not able to accurately estimate how many crayfish they caught during a day's harvest; the RRA interviews did not yield useful information either on the relative size of catches between individual harvesters or on the absolute size of catches. There was a strong tendency for harvesters to overestimate the number of crayfish they caught in a day. RRA is a useful tool but care should be taken in interpreting results, as people may be prone to exaggeration.

4.4.6 The spatial pattern of harvesting

4.4.6.1 How unharvested are the unharvested sites?

I used the interview data in the villages surrounding the mark-and-recapture sites to assess the level of harvesting to which each site was exposed. I identified seventeen sites as unharvested. I selected this subset conservatively, discarding any sites likely to be impacted by villages for which we did not have data. Although no sites are likely to have been entirely unharvested, these sites were largely unaffected by crayfish harvesters.

4.4.6.2 Harvesting distance

The spatial extent of non-timber extractive activities are hard to monitor as, unlike slash-and-burn agriculture or logging, they can not be recorded remotely (Godoy & Bawa 1993). To get information on where harvesters go it may be necessary to follow them and record their activities, but the presence of researchers is likely to have a large effect on the success of foraging trips (Gram 2001). Consequentially few researchers have identified the spatial extent of harvesters' activities. We developed toponym maps and found, like Smith (2003) in his study of hunting extent of the Buglé in Western Panama, that many of the

numerous small streams that dissect the landscape have individually identifiable names. The toponym map allowed the location of harvesting to be recorded with some accuracy without following harvesters every day.

During this study we found that harvesters from Vohiparara travel a mean of 2.4 km and a maximum of 6.5km from the village on their collecting trips. This is similar to the findings of other studies: hunters in settled villages in the Americas who travel by foot tend not to go further than 10 km (references in (Novaro *et al.* 2000) and Godoy *et al.* (2000) demonstrated using hunter-follows that forest-dwelling Amerindian households in Honduras forage up to approximately 3 km from their village.

4.4.7 Data quality

4.4.7.1 Sampling

Proper sampling in the selection of households for inclusion in a study is a serious problem in social research (Bernard 2002). Some households or sub-sets of the community will be particularly willing to be interviewed (Agar 1973) while more distant households, often the poorer members of a community, will be less likely to be included (Borgerhoff-Mulder & Caro 1985). A full village census is the ideal sampling frame (Bernard 2002). In each village we carried out preliminary interviews to identify the households and therefore our sampling frame. My research assistant, Fortunat Andriahajaina, and I lived in Vohiparara and Bevoahazo respectively for more than one year before starting the formal interview process so identifying the sampling frame was a relatively simple process in these villages. We spent much less time in Ambatovory, Antortosy and Sahavondronana (between one and two weeks full time in each village, although we had carried out sporadic work in these communities beforehand), so the identification and stratification of the samples there may have been imperfect.

4.4.7.2 *Interview responses*

Asking questions and getting answers about people's activities is a much harder task than it may seem at first (Fontana & Frey 2000). Informants may not always tell the truth, either to conceal specific activities or information, or in a misguided attempt to please the researcher (Borgerhoff-Mulder & Caro 1985; Catania *et al.* 1996). Deliberately hiding information is especially likely where research touches on illegal activities (Wickramasinge *et al.* 1996; Gram 2001). The attitudes of the interviewer, and the interviewee's perceptions of those attitudes, can also affect responses (Katz 1942). How questions are worded and the order of questions asked can also have large effects (Catania *et al.* 1996). Inaccuracies due simply to respondents' imperfect memories are probably the most important cause of inaccuracies in interview data. They may be non-directional but such inaccuracies may be so large as to render any conclusions based on interview data meaningless (Bernard 1984). The skill and experience of the interviewer can influence how well people recall events (Aunger 1994), with probing people for forgotten information or using a check list of possibilities often improving recall (Bernard 1984; Brewer & Yang 1994).

It is important when considering the results presented here to remember that people were not naïve as to the possible outcomes of their answers. In all villages we stressed that we were independent from the National Park authority, ANGAP, we did not have fixed ideas about whether crayfish were or were not being sustainably harvested, and we wanted to learn what the respondents had to say. This was certainly successful in the villages where we worked extensively and had ample opportunity to verify what we were learning in the interviews by observation of people's activities and informal conversations. In villages that were only visited for a few days in the broad village-level survey, we can have less confidence of the honesty with which our questions were answered. However, wherever possible we crosschecked our general findings with other villagers and I believe that the results presented here accurately reflect the patterns of crayfish harvesting in the Ranomafana area.

4.5 Summary

In this chapter I investigated the pattern of crayfish exploitation within Ranomafana National Park. One species, *A. granulimanus*, dominates the crayfish harvest in the area. Commercial crayfish harvesting is very important to only a relatively small proportion of villages but subsistence harvesting occurs in most communities. Within the villages where commercial harvesting occurs, crayfish are very important, particularly to the poorer households. In this chapter I also provide some cautious support for the use of RRA approaches in assessing natural resource use. Although detailed information such as numbers of crayfish caught in a trip cannot be relied on, the method may be useful for monitoring large changes in spatial extent of harvesting.

In the next chapter I use data from the mark-and-recapture study to estimate growth rates and survival probabilities for *A. granulimanus*. I use these to parameterise a series of size-structured population models with a view to testing the sustainability of the Ranomafana area crayfish harvest.

Chapter 5

Estimating growth and survival parameters for *A. granulimanus* and evidence for density-dependent regulation

“Crayfishes are guilty of cannibalism in its worst form [...] and, not content with mutilating or killing their spouses, after the fashion of animals of higher moral pretensions, they descend to the lowest depths of utilitarian turpitude, and finish by eating them.” (Huxley 1896)



The entrance to an *A. granulimanus* burrow: competition for shelter, to avoid cannibalism during the moult, is likely to be a major factor in density-dependent regulation of populations.

5 Estimating growth and survival parameters for A. granulimanus and evidence for density-dependent regulation

5.1 Introduction

Size-structured matrix population models (Lefkovitch 1965; Caswell 2001) have become important tools in the management of harvested species (Burgman & Possingham 2000). Estimates of vital rates, such as growth, survival and fecundity, and how they respond to changes in density, are essential parameters for such models. This chapter provides estimates of growth and survival in *A. granulimanus* as well as investigating the influence of density-dependence on these parameters. This information will be used to parameterise a series of size-structured matrix population models which I develop in chapter seven.

The relative importance of density-dependent to density-independent factors in population regulation is a much-debated topic in ecology (Krebs 2002). Information concerning such regulation is vitally important in the study of harvested populations as density-dependence has a fundamental effect on the resilience of populations to harvesting (Kokko & Lindstrom 1998). Density-dependence is thought to be an important regulator of crustacean populations (Caddy 1986) but very few studies are available which investigate such regulatory mechanisms in wild crayfish.

Many methods are available for obtaining demographic parameters where individuals can be identified and followed through time. These work well for studies of sessile animals and plants (Aberg 1992) or studies in which the fate of all individuals can be known such as radio-tracking (Esler *et al.* 2000). However

for mobile populations which can only be sampled periodically and for which capture probability is < 1 for each capture session, a probabilistic mark-release-recapture framework is needed (Caswell 2001).

Traditionally, methods for parameterising matrix models have involved estimating growth and survival functions separately and using these to estimate the survival of each size-class and the probability of movement between size-classes (transition probability). However, it has been suggested (Nichols *et al.* 1992; Fujiwara & Caswell 2002) that recently developed multistrata models are ideal for simultaneously fitting both survival and transition probabilities for size-structured matrix models. Nichols *et al.* (1992) suggests this approach is preferable to the two-step approach because both the transition probabilities and their variances are estimated directly so the variances are therefore lower than in the two-step process.

In this chapter I have two aims: I) to obtain the best possible estimates of survival and transition probabilities for *A. granulimanus* in unharvested populations, and II) to investigate whether these parameters are regulated by density. I applied both of the approaches mentioned above for estimating survival and transition parameters: I) the two-step approach involving fitting growth curves and separately estimating survival, and II) the multistrata model one-step approach (Table 5.1). I used a number of methods to estimate survival. Firstly I used a simple Cormack-Jolly-Seber (CJS) group effects recaptures model. However, there are a number of key assumptions inherent in the use of this model (Lebreton 1992) that may be violated in this study. The effect of possible violations of one such assumption (no movement in or out of the study site) was in part tested using Pollock's robust model (Pollock 1982; Pollock *et al.* 1990), which explicitly models temporary migration, to estimate survival. Another central assumption of mark-and-recapture is that handling and/or marking does not affect survival. I tested possible violations of this assumption by including the number of times each crayfish was caught as an individual covariate in an extension of the CJS group effects model.

It was impossible to use the data collected in this study to investigate density-dependence in survival as differences in density between sites were likely to be due, in a large part, to differences in harvest mortality. Hence I use evidence from the literature to discuss whether such regulation is likely to be important for *A. granulimanus*. To investigate whether growth was density-dependent, I separated sites into low, medium and high-density groups, and estimated transition probabilities from the fitted growth curve and the multistrata model approach for each group of sites in turn.

Table 5.1 The methods used in this chapter to estimate transition and survival probabilities for unharvested populations and to investigate the influence of density on transition probability. The numbers refer to the paragraph in the methods section where I introduce each method.

method	transition probabilities (γ)		survival probabilities (Φ)	
	unharvested population estimate	density-dependence	unharvested population estimate	density-dependence
growth function (VBGF)	5.2.2.3	5.2.2.4		not possible with the data using any method
CJS			5.3.2.1	
robust design			5.3.2.2	
handling-mortality model			5.3.2.3	
multistrata model	5.2.3.4	5.2.3.4	5.2.3.4	

5.2 Methods

5.2.1 Data selection

We carried out five-day mark-and-recapture at 79 sites across a range of harvesting intensities (see section 2.2.3.1). Thirty-three of these sites were visited repeatedly over a 22-month period. Data from all these 33 sites could be

used to investigate growth rates, but for investigating survival I used only those sites visited four or more times over the whole study period in order to have sufficient time over which to estimate survival. Data from four sites visited four or more times could not be used in survival estimates, as the timing of the visits was too different to allow the data to be combined; this left 19 sites which I used to estimate survival. Nine of these sites were exposed to very little harvesting and were essentially unharvested (see section 4.4.6.1). I used capture histories from these nine sites to estimate parameters for *A. granulimanus* in the absence of harvesting, assuming these populations were at carrying capacity (see section 6.4.1.2). To investigate the effect of density on growth, I grouped sites based on their number of large crayfish (> 50 mm carapace length [CL]) at the site, estimated using a closed population model approach with model averaging in programme MARK (see section 2.2.3.5). Low-density sites were defined as those that had less than five large crayfish in the 100 m transect as estimated from the mark-and-recapture data, medium-density sites had between five and 15 and high-density sites had more than 15 large crayfish in 100 m transect. I use density to refer to number per unit length rather than the strict definition of number per unit area (see section 2.2.3.5).

5.2.2 Estimating growth rates

Where repeated measures of the same individuals were available, I fitted the change in size and the time interval between measurements to the specialised Von Bertalanffy growth function (VBGF; Equation 5.1) using the programme FiSAT II (FAO 2004):

$$\text{Equation 5.1} \quad L = L_{\infty} - (L_{\infty} - L_0) \exp^{-kt}$$

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 (Mytilineou & Sarda 1995; Company & Sarda 2000; Cartaxana 2003), including that of crayfish (Anastacio *et al.* 1999; Fidalgo *et al.* 2001).

Due to measurement error, a number of individuals, which presumably had not grown or had grown very slightly, appeared to have shrunk slightly between measurements. As FiSAT does not accept negative growth, I set the increase for these individuals to 0.1 mm, equivalent to the accuracy with which carapace length was recorded. Crayfish smaller than 22 mm CL were not marked so no information on the growth of crayfish between leaving the egg and reaching 22 mm CL is available. I made the assumption that crayfish reach 22 mm CL in their first year. This assumption seems justified based on the observed growth of the few crayfish less than 22 mm CL which were marked with single marks (indicating only when they were marked). Length at time 0 was therefore set at 22 mm (size at one year) and one year added to all the age estimates produced from the fitted VBGF curve. FiSAT estimates asymptotic length (L_{∞}) and the growth parameter (k), with standard error and r^2 values for each model.

5.2.2.1 *The influence of sex on growth rates*

To test whether growth of *A. granulimanus* was sex-dependent, I fitted the VBGF separately to the data from each sex. The maximum size in the samples was different for the two sexes. To check whether this was likely to be due to a real size difference or to sampling error, I compared the size-frequency distribution for all male and female crayfish measured in the study (Figure 5.1). There was no clear difference between the two sexes in the tail of the distribution, so I set L_{∞} for both sexes to the maximum size observed (76.8 mm CL) and compared the estimate of k for males and females.

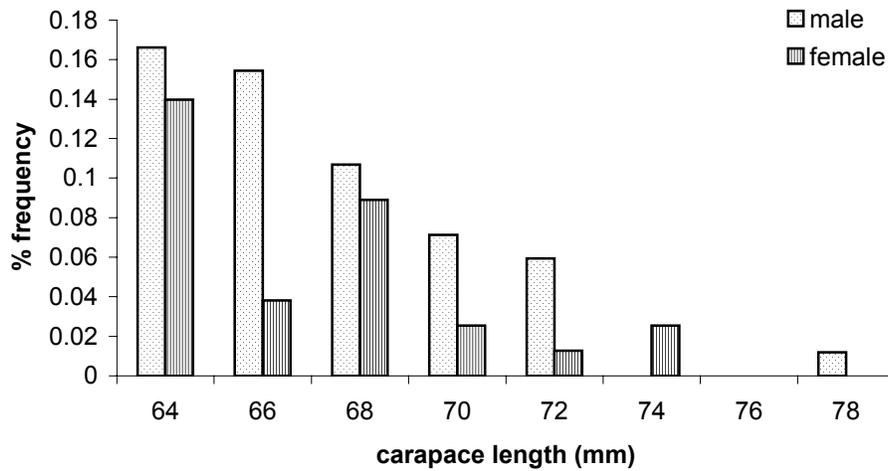


Figure 5.1 The tail of the size-frequency distribution for male and female crayfish from unharvested sites ($n = 8422 \text{ ♂}$, 7871 ♀).

5.2.2.2 *The effect of handling on growth rates*

To test whether handling and marking the crayfish affected growth, I separated individuals into two groups: those caught twice (the minimum for inclusion in the analysis of growth) and those caught more than three times, and compared the estimate of k for each group.

5.2.2.3 *Growth rates and transition probabilities in unharvested populations*

I fitted the VBGF to crayfish from unharvested sites. To estimate transition probabilities between the size-classes, the VBGF can be rearranged to calculate the age at which individuals reach a certain size (Equation 5.2):

$$\text{Equation 5.2} \quad t = \frac{\ln \left[\frac{(L_t - L_\infty)}{-(L_\infty - L_0)} \right]}{-k}$$

I used this to estimate the average age of individuals in each size-class and so estimate the transition probability γ (Equation 5.3):

Equation 5.3

$$\gamma_{ij} = \frac{1}{t_j - t_i}$$

where γ_{ij} is the probability that an individual in stratum i at time t will be in stratum j at time $t+1$ given that it survives the time interval, t_i is the age estimate for stratum i . Crayfish leave the largest size-class on death so there is no transition probability from large and only the transition probability from small to medium and from medium to large were estimated.

5.2.2.4 *The influence of density on growth rates*

To investigate whether growth in *A. granulimanus* is regulated by density, I separated capture histories into three groups: individuals from sites with low, medium or high-density of large crayfish. The size distribution of individuals at low-density (harvested) sites is truncated, with (by definition) few large crayfish. To allow comparison of the growth parameter k , I only used data from crayfish up to 50 mm CL for each group and set L_∞ at 76.8 mm CL, the longest crayfish recorded in the mark-and-recapture study. This assumes that there has not been selection resulting in quick maturation and small maximum size at heavily harvested sites. I consider this assumption is justified given the close proximity of sites (see Figure 2.3), as there is likely to be considerable gene flow between sites exposed to different level of harvesting intensities making it unlikely that there are evolved differences between them.

5.2.3 **Mark-and-recapture modelling**

I carried out mark-and-recapture modelling using programme MARK (White & Burnham 1999). Crayfish were assigned to one of three size-classes: small 22-34.9 mm CL, medium 35-49.9 mm CL and large > 50 mm CL. I discarded crayfish less than 22 mm CL from the analysis as they were severely under-sampled and had very low recapture probabilities (see Figure 2.5).

It is important to test for goodness-of-fit of the global (the most highly parameterised) model (Lebreton 1992). Goodness-of-fit tests were carried out

using programme RELEASE (Burnham *et al.* 1987) run within the programme MARK. The combined χ^2 statistic from tests two and three in programme RELEASE tests for violations of the central mark-and-recapture assumptions (equal trapability and no heterogeneity in survival). I accepted a p-value greater than 0.05 as showing the observed data were not significantly different from that predicted by the model. Tractable goodness-of-fit tests are not available for multistrata models (Lebreton & Pradel 2002; Reed *et al.* 2003), so instead for these models I used goodness-of-fit tests using the equivalent single stratum model run in programme RELEASE. Data sets meeting the single stratum assumptions are probably robust for multistrata analysis (Brown *et al.* 2003).

I compared the statistical fit of the competing models from the candidate set using an information theoretic approach based on Akaike Information Criterion (see section 2.2.3.4). The accepted convention is that models with AIC_c which differ by < 2 are indistinguishable statistically (Burnham & Anderson 1998). For each analysis only the five most parsimonious models are shown. I follow the notation of Lebreton (1992) where possible (see section 2.2.3.4).

5.2.3.1 *Survival estimates for unharvested sites using the CJS model*

I grouped individuals by their size-class at first encounter and used a CJS recaptures model with group effects (Cormack 1964; Jolly 1965; Seber 1965) to estimate survival. The basic CJS model estimates two parameters, survival (Φ) and capture probability (P). At least two capture sessions are needed separated by an interval over which mortality may occur. In this study there were four capture sessions spread over a period of 22 months. Each capture session was made up of five days of mark-and-recapture. Individuals were scored as caught (1) or not caught (0) during each capture session. Thus the capture history 1001 indicates a crayfish which was caught some time during the first five days of mark-and-recapture, was not caught during the second and third sessions, but was caught again during the final session. It is impossible to separate emigration

from the study site and death; animals that emigrate from the study area are not available for recapture, so appear to have died in this model.

Individuals may have increased in size during the study, thus moving size-class, but this model treats size-class as a fixed group effect. If survival increased with size and individuals grew during the study, the survival estimates would be underestimated. To deal with this problem, I estimated survival and capture probability separately for the first interval ($\Phi_1 P_1$) and for each subsequent interval ($\Phi_{2,3} P_{2,3}$) after initial capture and only used the parameters estimated over the first period.

5.2.3.2 *Taking temporary emigration into account*

The simple CJS group effects model described above assumes that any emigration is permanent. Pollock's robust design model (Pollock 1982; Pollock *et al.* 1990) provides unbiased estimates of demographic parameters in the presence of temporary emigration. I used a robust design model to investigate whether temporary emigration is important over the time scale of this study and, if so, to incorporate this effect to obtain the best possible estimate for survival in unharvested populations. The robust design model is a combination of the CJS live recapture model described above and a closed capture (Otis *et al.* 1978) model. Instead of just one capture occasion between survival intervals, multiple capture occasions are used with the assumption of no mortality or emigration during these short time intervals. The power of this model is that the probability of an animal being captured at least once in a trapping session can be estimated from just the data collected during the session using the closed capture model. The longer intervals between trapping sessions allow estimation of survival, temporary emigration from the trapping area, and immigration of marked animals back to the trapping area.

For example, the capture history 1 1 1 0 1 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 shows four trapping sessions, each consisting of five occasions (the set-up in this study). In this example, the individual was caught on the first three occasions

of the first trapping session, was not caught on the fourth occasion but was caught again on the fifth. It was not caught at all during the second and third trapping sessions but was caught again during the fourth trapping session.

Survival probability (Φ), probability of temporary emigration from the study area (G''), and the probability of staying away from the study area given that the animal has left the trapping area (G') can vary with attribute group (size-class in the case of this analysis). Parameters for capture probability (P), recapture probability (C) and population size (N) can vary between trapping sessions and by attribute groups.

I tested the importance of sex and size on survival, probability of emigration and returning, and capture probabilities. Emigration was modelled as markovian (G'', G'), random ($G''=G'$), or absent ($G''=G'=0$). For simplicity, sex was not included in these models.

5.2.3.3 *Taking handling-induced mortality into account*

A central assumption of all the models described above is that the marking process does not affect survival. To test whether this assumption is valid and, if not, to take account of any handling mortality in the survival estimates, I included the number of times an individual was captured as an individual covariate in the CJS recaptures model. The number of times individual crayfish were caught varied from one to 20. Four sites had been included in a pilot study. Crayfish at these sites had been handled an unknown number of times so were excluded from the analysis.

Survival (Φ) and capture probabilities (P) could vary by size-class; depicted s (small), m (medium) and l (large). Survival in each size-class could vary with the number of captures ($_{[captures]}$) or not. For example, a model that included $\Phi(s, m, l_{[captures]})$ allowed survival to vary with size, and survival of large individuals to have a linear relationship with the number of times caught. For simplicity, sex was not included in these models.

5.2.3.4 *Investigating survival and transition probabilities concurrently*

The multistrata Arnason-Schwartz model (Arnason 1973; Schwartz *et al.* 1993) is a generalisation of the CJS recaptures model to s strata ($s > 1$). It considers capture histories with k occasions and s strata. Strata were geographic sites in the original conception but can equally be applied to size-classes (Nichols *et al.* 1992), as in this analysis. The capture histories consist of 0 (individual not captured) or a letter (A,B.....s) designating the strata where any capture took place. For example, 0A0B would be the capture history covering four capture sessions where the individual was not captured during the first session, was captured in stratum A during the second, was not captured during the third, then captured in stratum B during the fourth session.

The model estimates combined survival/transition probabilities. However if survival from time t to $t + 1$ is assumed to be independent of stratum at time $t+1$ then these can be separated (Nichols *et al.* 1992). The model can therefore be used to estimate survival probabilities for each size-class (e.g. Φ_A the probability that an individual in stratum A at time t will survive to time $t + 1$) and survival-dependent transition probabilities (e.g. γ_{AB} , the probability that an individual in stratum A at time t will move to stratum B at time $t + 1$ given it is alive at time $t+1$).

Transitions are assumed to be markovian (i.e. to depend only on the current stratum to which an animal belongs and not any previous strata). Survival estimates based on the CJS model tend to be robust to heterogeneity in capture probabilities (Pollock *et al.* 1990) and some initial simulations (Nichols *et al.* 1992) indicate that the multistrata model survival-transition parameters are similarly robust to heterogeneous capture probabilities.

Three parameters are estimated in multistrata models: survival (Φ), capture probability (P) and transition probability (γ). Crayfish move to a new stratum (size-class) if they grow sufficiently in time period t . I set all but two transition probabilities to zero, since crayfish can only move to a larger size-class

but cannot jump from small to large or shrink from a larger to a smaller size-class.

I carried out two analyses using the multistrata models.

I) Survival and transition estimates for unharvested sites

I tested for an effect of sex and stratum (size-class) on survival, capture probability and transition probability using only capture histories from unharvested sites.

II) Density-dependence of transition probabilities

I tested for an effect of density (ρ) and stratum (size-class) on survival, capture probability and transition probability using data from sites grouped into low, medium and high-density sites. It is important to remember that differences in survival between crayfish at sites with different density do not imply density-dependent regulation of survival as any differences are likely to be due to differences in harvesting mortality between sites. The influence of sex was not tested, as data sparseness meant models including sex did not converge.

5.3 Results

5.3.1 Growth rates

5.3.1.1. *The influence of sex on growth rate*

There was no difference in the growth parameter k estimated from the VBGF fitted to data from the two sexes (Figure 5.2) so for subsequent analysis the two sexes were combined.

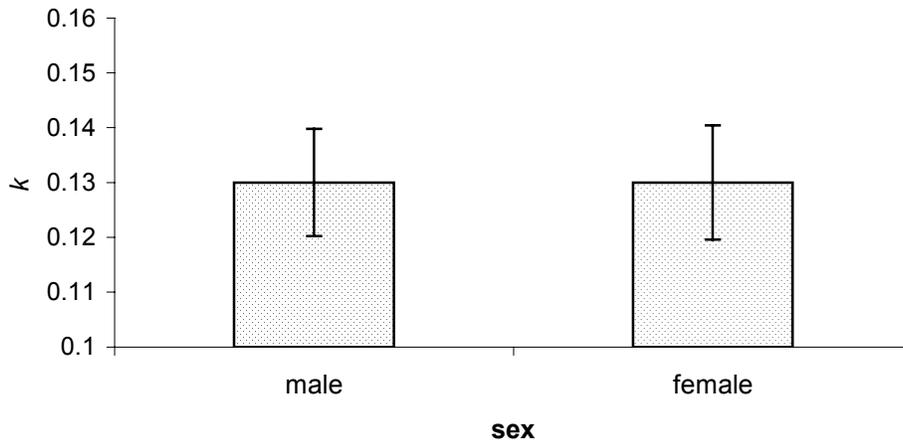


Figure 5.2 The growth parameter k from the VBGF estimated for male and female crayfish ($r^2 = 0.34$ and 0.39 respectively). Error bars show SEMs.

5.3.1.2 *The effect of handling on growth rate*

To test for an effect of handling on growth rate, I compared k estimated from individuals caught only twice, and those caught more than 3 times (Figure 5.3). There was no significant difference ($t_{\infty} = 0.01$, $p = 0.99$) between the values of k estimated from the two data sets, suggesting that handling during this study had little effect on growth.

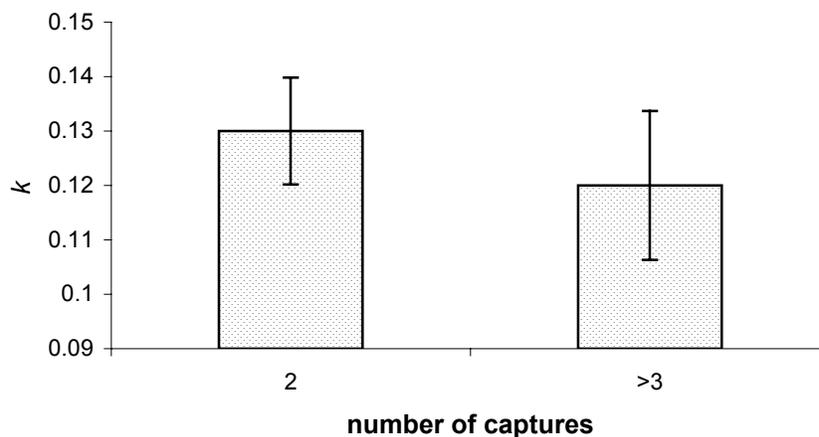


Figure 5.3 The growth parameter k from the VBGF estimated for individuals caught twice and individuals caught more than three times ($r^2 = 0.36$ and 0.42 respectively). Error bars show SEMs.

5.3.1.3 Growth rate and transition probabilities in unharvested populations

The VBGF fitted to data from unharvested sites is shown in Figure 5.4.

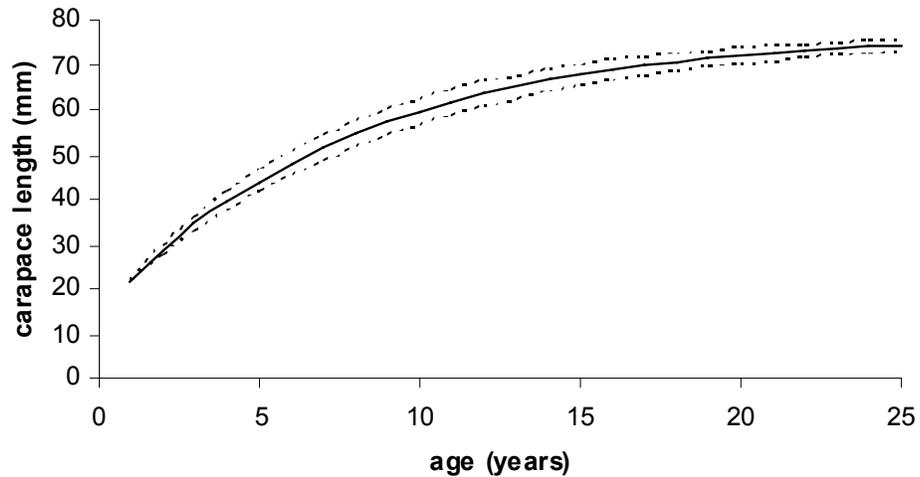


Figure 5.4 The VBGF fitted to growth increments from unharvested sites (both sexes combined, $r^2 = 0.39$). Error envelope shows 95% confidence intervals.

I used the above curve and equations 4.2 and 5.3 to estimate the transition probabilities from small to medium and from medium to large size-classes (Figure 5.5).

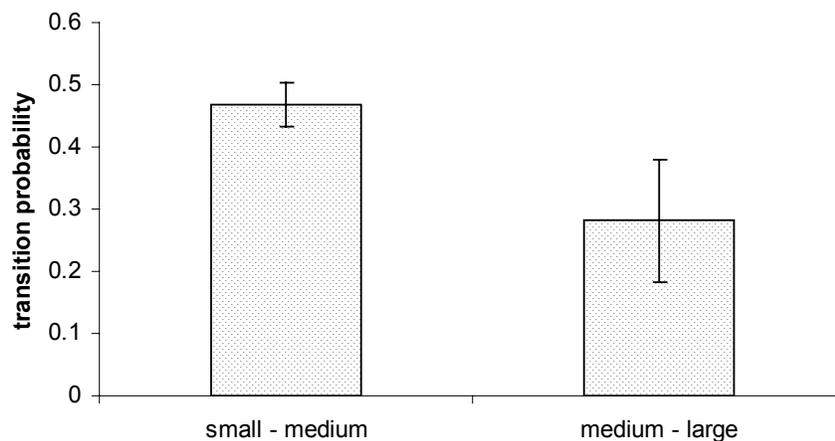


Figure 5.5 Transition probabilities for unharvested crayfish (both sexes combined). Error bars show SEMs.

5.3.1.4 *The influence of density on growth rates*

There was an apparent trend towards decreased growth rate at higher density sites (Figure 5.6), but this difference was not significant ($t_{\infty} = 0.02$, $p = 0.98$) between the value of k at high and low-density sites.

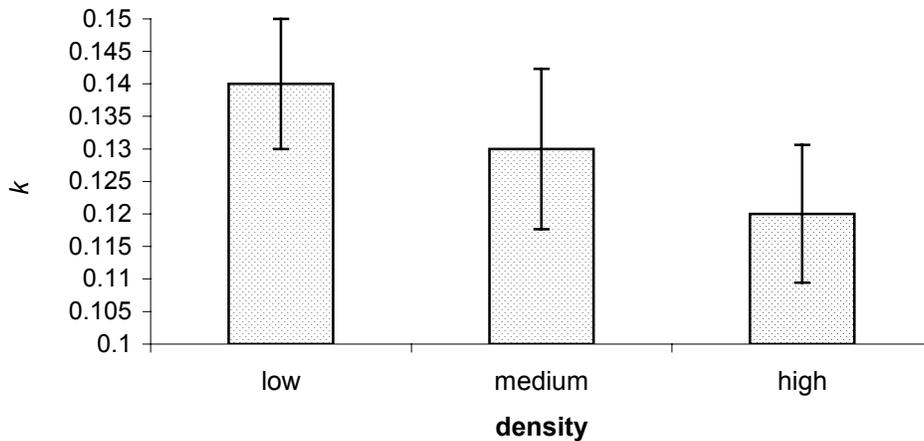


Figure 5.6 The growth parameter k from the VBGF estimated for crayfish from low, medium and high-density sites ($r^2 = 0.36, 0.37$ and 0.40 respectively). Error bars show SEMs.

5.3.2 **Mark-and-recapture analysis**

5.3.2.1 *Survival estimates for unharvested sites using the CJS model*

The goodness-of-fit of the most highly parameterised model showed acceptable fit to the data ($\chi^2_{24} = 28.8$, $p = 0.23$). The most parsimonious model selected by AIC_c was $\{\Phi_1(\text{size})\phi_{2,3}(\text{size})P_1(\text{size})P_{2,3}(\text{size})\}$ suggesting that survival and capture probability depended on size-class (see Table 5.2). However, this model was not significantly different ($AIC_c < 2$) from the model with capture probability dependent on sex rather than size. The parameter estimates from the most parsimonious model are given in Figure 5.7.

Table 5.2 Group effects model selection: using data from unharvested sites to estimate survival (Φ). Two group effects were investigated (size and sex). no. is the number of parameters.

model	AICc	Δ AICc	no.	deviance
$\{\Phi_1(\text{size})\Phi_{2,3}(\text{size})P_1(\text{size})P_{2,3}(\text{size})\}$	4516.97	0	12	86
$\{\Phi_1(\text{size})\Phi_{2,3}(\text{size})P_1(\text{sex})P_{2,3}(\text{sex})\}$	4518.61	1.64	10	91
$\{\Phi_1(\text{size})\Phi_{2,3}(\text{size})P_1(\text{size,sex})P_{2,3}(\text{size,sex})\}$	4519.13	2.16	18	76
$\{\Phi_1(\text{size})\Phi_{2,3}(\text{size})P_1(\cdot)P_{2,3}(\cdot)\}$	4520.26	3.29	8	97
$\{\Phi_1(\text{sex})\Phi_{2,3}(\text{sex})P_1(\text{sex})P_{2,3}(\text{sex})\}$	4521.31	12.23	8	98

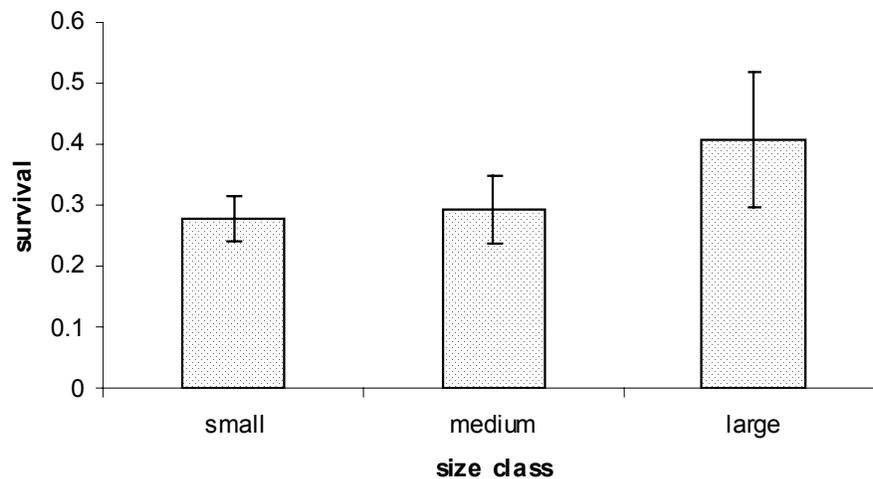


Figure 5.7 The estimates of survival for unharvested sites from the model $\{\Phi_1(\text{size})\Phi_{2,3}(\text{size})P_1(\text{size})P_{2,3}(\text{size})\}$. Error bars show SEMs.

5.3.2.2 Taking temporary emigration into account

The most parsimonious model was:

$$\{\Phi_1(\text{size})\Phi_{2,3}(\text{size})G'(\text{size})=G''(\text{size})P_1(\text{sess})P_{2,3}(\text{sess})C_1(\text{sess})C_{2,3}(\text{sess})N(\text{size})\}$$

suggesting that survival depended on size, emigration was random, and capture probability and recapture probability varied between sessions (Table 5.3). There was strong support for temporary emigration; the best model without temporary emigration had a Δ AIC_c of more than 100 (models where Δ AIC_c > 2 are usually considered significantly different). However there was equal support for markovian ($G''G'$) and random ($G''=G'$) emigration. The estimates of survival provided by the most parsimonious model are given in Figure 5.8 below.

Table 5.3 Robust design model selection: using data from unharvested sites to estimate survival taking temporary emigration into account. no. is the number of parameters in the model.

model	AIC _c	Δ AIC _c	no.	deviance
$\{\Phi_1(\text{size})\Phi_{2,3}(\text{size})G'(\text{size})=G''(\text{size})P_1(\text{sess})P_{2,3}(\text{sess})C_1(\text{sess})C_{2,3}(\text{sess})N(\text{size})\}$	-911.27	0.00	26	279
$\{\Phi_1(\text{size})\Phi_{2,3}(\text{size})G'(\text{size})G''(\text{size})P_1(\text{sess})P_{2,3}(\text{sess})C_1(\text{sess})C_{2,3}(\text{sess})N(\text{size})\}$	-909.85	1.42	27	279
$\{\Phi_1(\text{size})\Phi_{2,3}(\text{size})G'(\text{size})=G''(\text{size})P_1(\text{sess})P_{2,3}(\text{sess})C_1(\text{sess})C_{2,3}(\text{sess})N(\text{size.sess})\}$	-897.94	13.33	35	275
$\{\Phi_1(\text{size})\Phi_{2,3}(\text{size})G'(\text{size})G''(\text{size})P_1(\text{sess})P_{2,3}(\text{sess})C_1(\text{sess})C_{2,3}(\text{sess})N(\text{size.sess})\}$	-896.94	14.33	36	273
$\{\Phi_1(\text{size})\Phi_{2,3}(\text{size})G'(\text{size})=G''(\text{size})P_1(\text{sess})=C_1(\text{sess})P_{2,3}(\text{sess})=C_{2,3}(\text{sess})N(\text{size.sess})\}$	-896.89	14.38	28	290

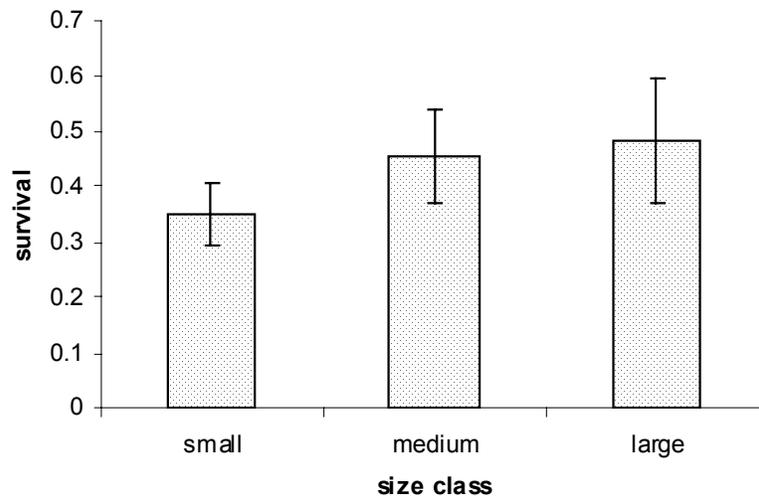


Figure 5.8 The estimates of survival for unharvested sites from the model $\{\Phi_1(\text{size})\Phi_{2,3}(\text{size})G'(\text{size})=G''(\text{size})P_1(\text{sess})P_{2,3}(\text{sess})C_1(\text{sess})C_{2,3}(\text{sess})N(\text{size})\}$. Error bars show SEMs.

5.3.2.3 Taking handling-induced mortality into account

The goodness-of-fit of the most highly parameterised model was good ($\chi^2_{24} = 18.54$, $p = 0.78$). There was strong support for models including the number of times caught as an individual covariate: ΔAIC_c between the most parsimonious model $\{\Phi(s,m,l_{[\text{captures}]})P(s,m,l_{[\text{captures}]})\}$ and the same model without

covariates $\{\Phi(\text{size})P(\text{size})\}$ was very large (> 700). The most parsimonious model included the individual covariate for large crayfish only; suggesting that survival of small and medium sized crayfish was less affected by handling than was survival of large crayfish.

Table 5.4 handling mortality model selection: using data from unharvested sites to estimate survival taking handling mortality into account. no. is the number of parameters in the model.

model	AIC _c	Δ AIC _c	no.	deviance
$\{\Phi(s, m, l_{[\text{captures}]})P(s, m, l_{[\text{captures}]})\}$	1977	0.00	10	1957
$\{\Phi(s_{[\text{captures}]}, m_{[\text{captures}]}, l_{[\text{captures}]})P(s_{[\text{captures}]}, m_{[\text{captures}]}, l_{[\text{captures}]})\}$	1980	2.99	12	1956
$\{\Phi(s, m, l_{[\text{captures}]})P(s_{[\text{captures}]}m_{[\text{captures}]}l_{[\text{captures}]})\}$	2612	635.05	8	2596
$\{\Phi(\text{size})P(\text{size})\}$	2685	708.07	6	2673
$\{\Phi(\text{size.sex})P(\text{size.sex})\}$	2692	714.78	12	2668

The relationship between survival and number of times caught is given in Figure 5.9. The 95% confidence intervals around the line were very large and included the horizontal, suggesting that the affect of handling on survival did not affect all individuals to the same extent.

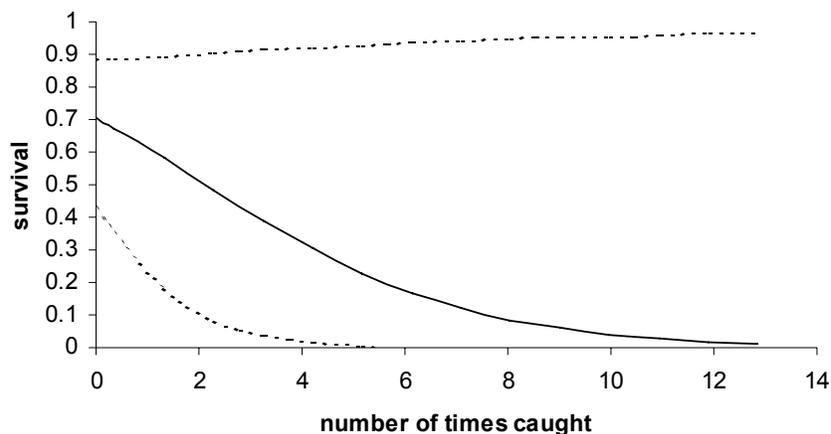


Figure 5.9 The relationship between the number of times caught and survival for large crayfish at unharvested sites estimated from the model $\{\Phi(s, m, l_{[\text{captures}]})P(s, m, l_{[\text{captures}]})\}$. The error envelop shows 95% confidence intervals.

The survival estimates for the most parsimonious model, extrapolated back to zero times caught, are given in Figure 5.10.

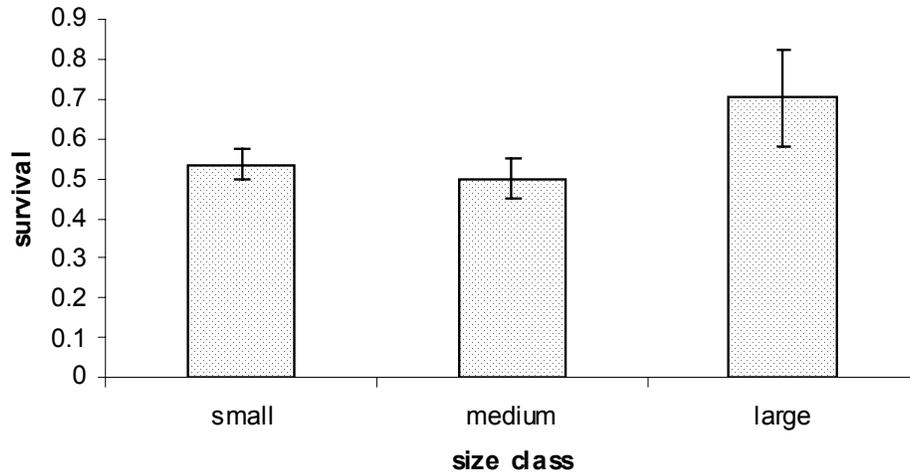


Figure 5.10 The parameter estimates of survival at unharvested sites from the model $\{\Phi(s,m,l_{[captures]})P(s,m,l_{[captures]})\}$ for when the number of captures is zero. Error bars show SEMs.

5.3.2.5 *Investigating survival and transition probabilities concurrently*

l) Survival and transition estimates for unharvested sites

The fit goodness-of-fit of the most general single-stratum model was acceptable ($\chi^2_{24} = 29.2$, $p = 0.21$). The most parsimonious model was $\{\Phi(\text{size})P(\text{sex})\gamma(\text{size})\}$ (see Table 5.5). This model did not include an effect of sex on survival or transition probability suggesting that survival and growth were the same in male and female crayfish. However, the top three models had very similar values of AIC_c ($\Delta AIC_c < 2$). The parameter estimates from the most parsimonious model are shown in Figure 5.11.

Table 5.5 Multistrata model selection: using data from unharvested sites to produce estimates of survival (Φ) and transition parameters (γ).

model	AIC _c	Δ AIC _c	parameters	deviance
{ $\Phi(\text{size})P(\text{sex})\gamma(\text{size})$ }	14322.81	0	7	9307
{ $\Phi(\text{size.sex})P(\text{sex})\gamma(\text{size})$ }	14323.56	0.75	10	9301
{ $\Phi(\text{size.sex})P(\cdot)\gamma(\text{size.sex})$ }	14324.28	1.47	11	9300
{ $\Phi(\text{size})P(\cdot)\gamma(\text{size})$ }	14324.95	2.13	6	9311
{ $\Phi(\text{size.sex})P(\text{sex})\gamma(\text{size.sex})$ }	14325.94	3.13	12	9300

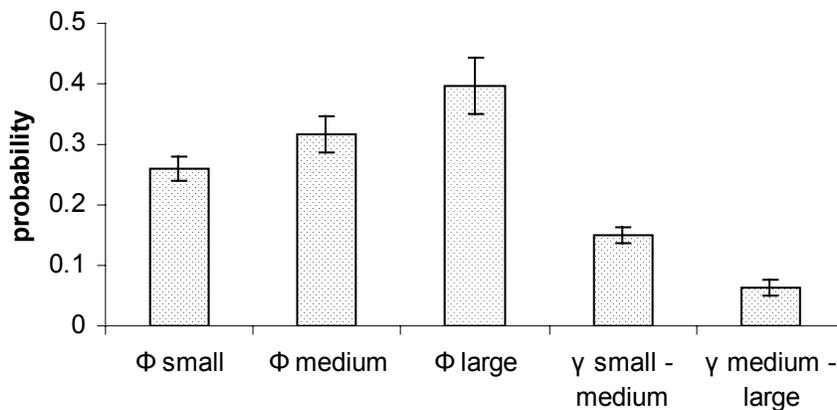


Figure 5.11 The estimates of survival (Φ) and transition (γ) probabilities from the model { $\Phi(\text{size})P(\text{sex})\gamma(\text{size})$ } for unharvested crayfish. Error bars show SEMs.

(II) Density-dependence of transition probabilities

The fit of the general single-stratum model with size and density as group variables was poor ($\chi^2_{32} = 51.98$, $p = 0.01$). However, the cause of this poor fit was the lack of fit of the data for very large crayfish at low-density sites only. There were extremely few data for this attribute group (large crayfish were, by definition, rare at low-density sites). All other attribute groups showed acceptable ($P > 0.05$) fit to the model.

The most parsimonious model was { $\Phi(\text{size.p})P(\text{size.p})\gamma(\text{size.p})$ } suggesting that survival, capture and transition probabilities varied with both size and with density of large crayfish (see Table 5.6).

Table 5.6 Multistrata model selection: testing for differences in survival (Φ) and transition probabilities (γ) with density of large crayfish.

model	AIC _c	Δ AIC _c	parameters	deviance
{ $\Phi(\text{size}, \rho)P(\text{size}, \rho)\gamma(\text{size}, \rho)$ }	19666.03	0.00	24	10331
{ $\Phi(\text{size}, \rho)P(\text{size}, \rho)\gamma(\text{size})$ }	19669.25	3.23	20	10342
{ $\Phi(\text{size}, \rho)P(\rho)\gamma(\text{size}, \rho)$ }	19671.70	5.68	18	10349
{ $\Phi(\rho)P(\text{size}, \rho)\gamma(\text{size}, \rho)$ }	19672.99	6.96	18	10350
{ $\Phi(\text{size}, \rho)P(\cdot)\gamma(\text{size}, \rho)$ }	19677.69	11.67	16	10359

The parameters estimated by the most parsimonious model are shown in Figure 5.12. The pattern of survival in high-density sites was similar as for unharvested sites with survival increasing with size. This pattern was not seen for low and medium-density sites where there was no such increase in survival with size and survival was generally lower. This difference in survival between sites at different density, particularly clear for large crayfish, is likely to be due to differences in fishing mortality.

The transition probability from small to medium crayfish was significantly higher for low-density sites than for high-density sites ($t = 2.55$, $p = 0.01$) indicating a possible density-dependent response in growth. However, the effect was in the opposite direction for the transition from medium to large crayfish with a higher transition probability at high-density sites than low-density sites ($t = 2.27$, $p = 0.02$).

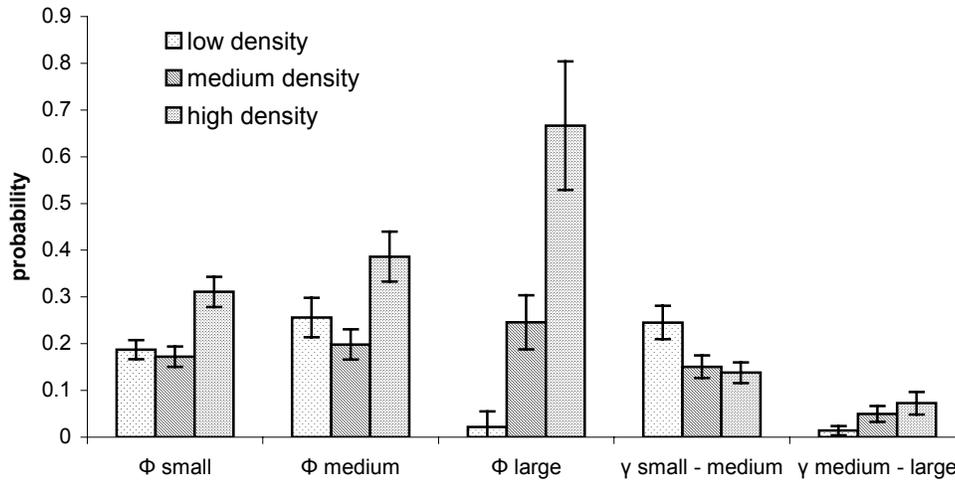


Figure 5.12 Survival (Φ) and transition parameters estimated from the multistrata model $\{\Phi(\text{size}, \rho)P(\text{size}, \rho)\gamma(\text{size}, \rho)\}$. Error bars show SEMs.

5.3.2.6 Transition probabilities from the growth curve and the multistrata model compared

The transition probability estimates from the growth curve and the multistrata model are compared in Figure 1.13. Both methods suggested that transition probability was lower for the transition from medium to large than for small to medium size-classes. The estimates from the growth curve were much higher than those from the multistrata model.

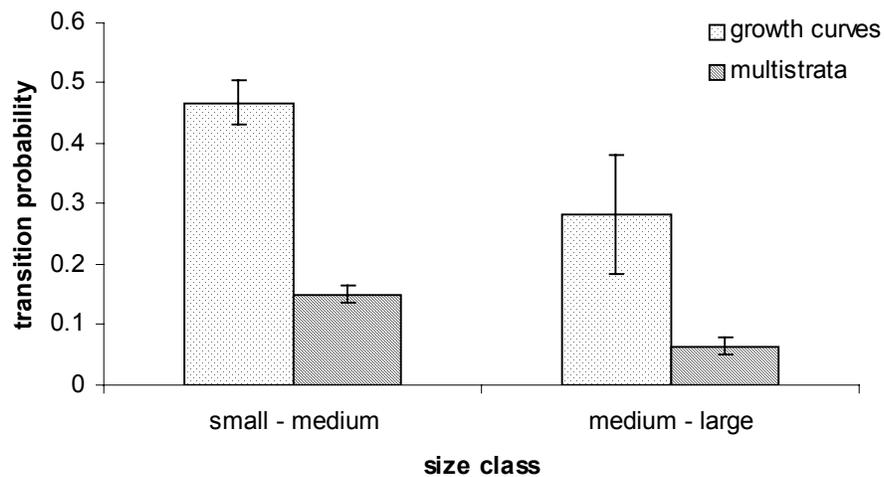


Figure 5.13 The estimates of transition probability for unharvested sites from the growth curve and the multistrata model.

5.3.2.7 Survival probabilities from all the methods compared

The survival estimates for unharvested crayfish produced by the four modelling approaches discussed above are compared in Figure 5.14 below. All four models showed a similar pattern of higher survival at larger size. The estimates of survival from the multistrata model and the simple CJS group effects model were low compared to those provided by the other modelling approaches. Taking temporary emigration into account (the robust design model) increased the estimates of survival. Taking handling mortality into account further increased the estimates of survival, particularly for large crayfish.

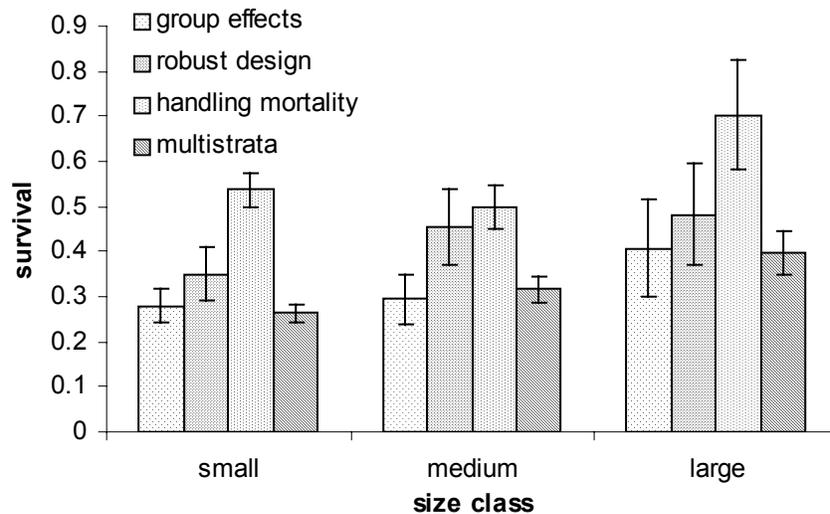


Figure 5.14 The estimates of survival for unharvested sites using the four modelling approaches described above. Error bars show SEMs.

5.4 Discussion

In this chapter I had two aims: I) to obtain the best possible estimates of survival and transition probabilities for *A. granulimanus* in unharvested populations, for use in the models developed in chapter seven, and II) to investigate whether these parameters are regulated by density. A number of factors influence the choice of modelling approaches to obtain the best estimates. I discuss these below before presenting the best estimates and discussing the influence of density-dependence on survival and growth.

5.4.1 The influence of sex on growth and survival

Both the methods of estimating growth rates suggested that sex was not an important predictor of growth in *A. granulimanus*. Fitting the VBGF to data from male and female crayfish resulted in identical estimates of the growth parameter k , while the multistrata model including sex as a predictor of transition probability was not supported by the data. Figler *et al.* (1999) similarly found no sex difference in growth in juvenile red swamp crayfish *Procambarus clarkii*. However, Kawai *et al.* (1997) did find sex differences in growth rates of wild Japanese crayfish *Cambaroides japonicus*, as did Sagi *et al.* (1997) in a captive population of Australian red-claw *Cherax quadricarinatus*. However, in this study there was little support for sex differences in survival. Similarly, Figler *et al.* (1999) found no sex difference in survival in juvenile red swamp crayfish *Procambarus clarkii*.

For the more complex models (the robust design model, the handling mortality model, and the multistrata model investigating the effect of density on transition probability), sex was not included as a possible explanatory variable due to problems of data sparseness. I consider this is justified as the above results suggest that sex is not an important factor affecting growth and survival in *A. granulimanus*.

5.4.2 Possible biases in the survival estimates

Mark-and-recapture analysis depends on a number of assumptions, violations of which will bias the results (Lebreton 1992). Three factors, discussed below, may have resulted in biases in the estimates of survival in this study. These are: tag loss, movement out of the study area, and increased mortality due to handling.

5.4.2.1 Tag loss

A central assumption of mark-and-recapture studies is that tags are not lost over time; significant tag loss results in under-estimates of survival (Lebreton

1992). The Visible Implant Elastomer (VIE) tags used in this study have shown very good tag retention in studies of other crustaceans. Nearly two thousand juvenile shrimp *Penaeus vannamei* marked with VIE tags showed > 99.9% tag retention after 14 weeks and 17-23 moults (Godin *et al.* 1995) and 260 adults tested showed 100% tag retention. Tag retention of > 92% was observed with juvenile yabby crayfish *Cherax destructor* over ten weeks and three to five moults (Jerry *et al.* 2001). Juvenile (12-16 mm CL) lobsters, *Homarus* sp., showed > 99% tag retention over three months in one study (Linnane & Mercer 1998), and 100% in another (Uglen *et al.* 1996). These studies were all shorter than the 22-month duration of this study, but they also involved juveniles, which moult more frequently. I consider tag loss was of minor significance in this study.

5.4.2.2 *Emigration*

A second possible source of bias in the survival estimates is the length of transect used relative to the movement patterns of crayfish. Mark-and-recapture techniques estimate apparent survival (i.e. probability of surviving and staying in the study site). If crayfish movements over the period of the study are greater than the length of the study transect, survival will be underestimated. A study of the movements of *Orconectes virilis* crayfish in the wild found little movement: the maximum distance moved over 1 year was 308 m (mean = 33 m, mode < 5 m; Hazlett *et al.* 1974). However, a study of white-clawed crayfish *Austropotamobius pallipes* (Robinson *et al.* 2000) found greater movement, with individuals moving up to 300 m over a 10-day period. No information on movement rates of *A. granulimanus* crayfish is available. The robust design model allows temporary migration to be modelled, and therefore improves the survival estimates if such movements are important. However, it cannot separate permanent emigration from death so if significant numbers of crayfish left the transect permanently during the study, the estimates of survival using the robust design model will still be biased downwards.

5.4.2.3 *Influence of marking or handling*

A third central assumption of mark-and-recapture studies is that marking or handling does not influence survival. A study on wild slipper lobsters (*Thenus* sp.; Courtney *et al.* 2001) suggested that introduction of pathogens when injecting VIE tags reduced survival: addition of antibiotic ointment to the injection site increased recapture probability. However, studies using VIE tags generally report very little effect on survival: juvenile lobsters in captivity marked with VIE showed 97% survival after 3 months, although no comparison was given with unmarked mortality (Linnane & Mercer 1998). Only two studies have looked directly at the effects of VIE tags on crayfish survival; both in captive populations. Isley and Stokett (2001) compared 80 marked and 20 unmarked juvenile red swamp crayfish *Procambarus clarkii*. There was no mortality in the marked group and final lengths and weights were not significantly different between the groups after the five-month study. Jerry *et al.* (2001) found no significant mortality differences between marked and unmarked juvenile yabby crayfish *Cherax destructor*. In this study I saw no evidence of infection around the injection site and it seems unlikely that excessive mortality was caused by the marks themselves.

However, handling may have increased mortality. Handling of lobsters is known to increase loss of chelae (Linnane *et al.* 1997), which reduces foraging efficiency and increases vulnerability to inter- and intra-specific attack (Figiel & Miller 1995; Juanes & Smith 1995). The possible effect of handling mortality was investigated in this study using the number of times crayfish were caught as an individual covariate. The results suggested that handling had a negative effect on survival of large crayfish, although no effect was detected for small or medium crayfish. There is no evidence that this survival effect was caused by excessive injury or chelae loss: at a sub-sample of eight sites where I recorded injuries there was no significant difference ($\chi^2_{521} = 0.21$, $p = 0.65$) in the proportion of crayfish with one or more chelae or walking legs missing between animals which had been previously caught and those not previously caught. This is supported

by the fact that I detected no effect of repeated captures on growth; an effect would be expected if handling increased the number of crayfish regenerating damaged limbs. Instead, I suggest that the reduction in survival of marked crayfish was due to increased aggressive interactions or risk of predation while looking for a new shelter site following release.

In summary, tag loss probably had a negligible effect on the survival estimates. However, emigration from the study site may have had an important, but unquantifiable, effect on the estimates of survival. There is strong evidence that handling-induced mortality had a significant effect on survival but fortunately it was possible to take this into account by including the number of times each individual was caught as a covariate.

5.4.3 The best possible parameter estimates for unharvested sites

5.4.3.1 The best estimates of transition probabilities

This chapter presents two methods for estimating transition probabilities: the fitted growth curve and the multistrata model. The estimates from the fitted growth curve were more than twice as high as those derived from the multistrata model. The estimates of transition probabilities from multistrata models were based on relatively sparse data compared with the estimates for fitting the growth curve. This is because only data from sites visited more than four times, with appropriate spacing of visits, could be included in the mark-and-recapture analysis, whereas data from any site visited more than once could provide information on growth. I therefore suggest that the estimates from the growth curve approach are better and I use them in future analysis.

5.4.3.2 The best estimates of survival

This chapter presents four methods of estimating survival. The multistrata model gave the lowest estimates of survival. This is unsurprising if there is any effect of handling on survival as the multistrata model used data from across the whole study period yet had no mechanism for taking account of handling

mortality. The estimates from the group effects model were also low. The robust design model suggested that temporary emigration was important in the study populations as the most parsimonious models all included some form of emigration. Survival estimates from this model are much higher than models not including temporary emigration. The handling mortality model provided strong support for a negative effect of the number of times large crayfish were caught on their survival. There was no significant effect for small or medium crayfish but the model nevertheless returned higher survival estimates for these size-classes compared to other models. This may be because the data set used for the handling mortality model did not include data from four sites where individuals had been handled an unknown number of times. Perhaps multiple handling did effect survival of small and medium sized crayfish but was not detectable using the model selection criteria. Handling appears to have an important effect on survival and the estimates from the model including it will therefore be used in future analysis.

5.4.4 Is growth and survival in *A. granulimanus* regulated by density?

5.4.4.1 Density-dependent regulation of growth

The rate at which the Von Bertalanffy growth function reaches the asymptote (growth parameter k) was slightly higher at low-density sites than at medium-density sites, which was slightly higher than that at high-density sites. This suggested that growth may be density-dependent in *A. granulimanus* but the difference was not significant. Using the multistrata model approach, a density effect on transition probability is included in the most parsimonious model again suggesting that growth may be density-dependent. The transition probability of crayfish from the small to the medium size-class is higher for low-density sites than for medium or high-density sites also providing weak support for density-dependent growth in *A. granulimanus*. However, the data suggest that the transition probability from the medium to the large size-class is higher at high-density sites than at low-density sites.

Stocking density affects the growth rate of captive lobsters (James *et al.* 2001) through competition for food. However, it has been suggested that density-dependent regulation of growth rates is much less important than that of survival or fecundity for wild crayfish populations (Momot & Gowing 1977). Because of lack of clear evidence, I do not include density-dependence in growth rates in the models developed in chapter seven.

5.4.4.2 *Density-dependent regulation of survival*

It was impossible to investigate the effect of density on survival using the data from this study as differences in survival between sites (Figure 5.1.2) were probably the result of differences in fishing mortality. Therefore it is necessary to look to the literature for evidence on whether survival is likely to be under density-dependent regulation. Only one study is available which investigates density-dependent survival in wild crayfish populations. Momot & Gowing (1977) show that survival of young of the year, juvenile and adult *Orconectes virilis* is regulated by density. However, density-dependent regulation of survival in crayfish populations is likely to be important and widespread. Density-dependent survival has been demonstrated in wild lobster populations (Addison 1986; Fogarty & Idoine 1986). In lobsters increased predation due to insufficient shelters may be the main cause (Addison 1986; Butler *et al.* 1997; Mercer *et al.* 2001), but direct cannibalism, particularly during the moult, probably also plays a role (Jones & Ruscoe 2001). Density has been shown to have a negative effect on survival in a number of studies of captive crayfish (Nystrom 1994; Jones 1995; Verhoef & Austin 1999). Aggressive interactions over access to shelters are common (Figler *et al.* 1999; Vorburger & Ribic 1999) and, like lobsters, crayfish are known to be cannibalistic (Jonsson 1992; Lodge & Hill 1994). Despite the lack of direct evidence, other authors consider density-dependent regulation of survival as an important regulatory mechanism of wild crayfish populations (Momot 1991; Anastacio *et al.* 1999) and I consider that it is likely to be important in *A. granulimanus*.

5.5 Summary

In this chapter I presented estimates of growth and survival from 22 months of mark-and-recapture data for *A. granulimanus* in the Ranomafana area. Growth rate and transition probabilities were investigated using two methods. The multistrata mark-and-recapture approach gave much lower estimates of growth than the approach of fitting a growth curve to repeated length measurements of individuals. Because the growth curve method was able to include data from many more sites, these estimates are based on more data and are therefore preferable. Survival was size-dependent, with larger crayfish showing higher survival than smaller ones. A number of different methods were used to estimate survival. Handling negatively affects survival of large crayfish, so a model adjusting for the number of times a crayfish was caught provides the best estimate of survival.

Comparing sites with varying density of large crayfish provided weak evidence of density-dependent regulation of growth but it was not significant and will not be included in future models. Density-dependence in survival could not be investigated from the data but evidence from the literature suggests that it is likely to be an important regulatory mechanism in wild crayfish population dynamics.

The growth and survival parameters from this chapter will be used to parameterise models of *A. granulimanus* population dynamics which I develop in chapter seven. Fecundity data are also necessary for such models. Chapter three has already demonstrated that fecundity in *Astacoides* species is size-dependent and that crayfish in the Ranomafana area breed just once a year. In the next chapter I investigate fecundity in *A. granulimanus* in more detail and look for evidence of density-dependent regulation. I also estimate the carrying capacity of *A. granulimanus* in rivers in the Ranomafana area.

Chapter 6

Estimating carrying capacity and density-dependence in fecundity of A. granulimanus

“Studies of the population dynamics of the various [Malagasy] crayfish species and the harvest practices of the local villagers will be essential for sustained harvest of this natural resource.” (Crandall 2004)



The size at which a female *A. granulimanus* becomes reproductive depends, to some extent, on the density of competitors.

6 *Estimating carrying capacity and density-dependence in fecundity of A. granulimanus*

6.1 Introduction

The carrying capacity of a population is its equilibrium size in the absence of harvesting or outside interference (Milner-Gulland & Mace 1998); alternatively, it can be defined as the abundance above which the population tends to decline (Akçakaya *et al.* 1999). A number of reasons make it difficult to estimate the carrying capacity of a natural population. Firstly, estimating population size is difficult and subject to large uncertainties (Seber 1973; Buckland *et al.* 1993). In addition, intrinsic dynamics may result in population fluctuations which mask the true carrying capacity (e.g. Clutton-Brock *et al.* 1997) or inter-annual variation in climatic conditions may mean populations do not stabilise (Fogarty *et al.* 1991; Aanes *et al.* 2002). Despite these difficulties, estimation of carrying capacity remains central to much of harvesting theory (Milner-Gulland & Mace 1998; Akçakaya *et al.* 1999).

Mark-and-recapture methods offer a framework for population estimation when a complete census is not possible (Seber 1973; Otis *et al.* 1978). Crayfish are suitable for mark-and-recapture studies as large numbers can be caught and processed in a relatively short period (Skurdal *et al.* 1992) and mark-and-recapture has been used to estimate population size for a number of wild crayfish populations (e.g. Morrissy & Caputi 1981; Brewis & Bowler 1983; Partanen & Penttinen 1995).

Fecundity is the mean number of eggs produced by a female in one breeding cycle. The fecundity of a species and its response to changes in density

affect its maximum population growth rate, which affects its vulnerability to exploitation (Robinson & Redford 1991; Kokko *et al.* 2001). The study of fecundity in crayfish has suffered due to inconsistency in measurement of reproductive output (with some studies reporting the number of eggs in the ovary, others the number of eggs successfully attached to the pleopods, and others the number of independent young) and failure to report the fecundity with reference to size (Austin 1998). Few studies are available which investigate density-dependent control of fecundity in wild crayfish populations (Reynolds 2002), despite the importance of such regulatory mechanisms for estimating sustainable levels of exploitation (Rhodes & Holdich 1982). Density-dependent control of fecundity and recruitment has been studied in just two wild crayfish species; *Orconectes virilis* (Momot 1977a; Momot 1977b; Momot & Gowing 1977) and *Astacus astacus* (Abrahamsson 1966).

In this chapter I estimate the number of *A. granulimanus* per unit length of river at unharvested sites to provide an approximation of carrying capacity. I use this parameter in chapter eight where I estimate the total number of crayfish available to harvesters from Vohiparara, from which I then estimate the number of crayfish that could theoretically be harvested sustainably in a year.

In chapter three I demonstrated that fecundity in *Astacoidea*, like that of all other crayfish which have been studied (Rhodes & Holdich 1982; Corey 1987; Austin 1998), shows a strong positive relationship with size. In this chapter I look at fecundity in *A. granulimanus* in more detail and investigate whether fecundity is likely to be regulated by density. I use this information in chapter seven where I develop a series of size-structured matrix population models to describe *A. granulimanus* population dynamics.

6.2 Methods

6.2.1 Carrying capacity (K)

To estimate the carrying capacity of *A. granulimanus* I calculated the mean number of each size-class found in streams identified as unharvested (see Figure 4.1.2) using mark-and-recapture analysis. I classified rivers and streams by stream order and estimated density separately for first and for second or third-order streams.

6.2.1.1 *Defining river order*

A river or stream's relative position in a drainage basin network can be defined by its order. First-order streams have no discrete tributaries, a second-order stream is formed where two first-order streams meet and so on (Figure 6.1).

The base maps, which I used to digitise rivers (see section 2.2.7), identified some streams as temporary. When I digitised the rivers and streams I classified streams as temporary or, for permanent streams, as first-order (headwater streams) to sixth-order (the largest river in the area: the Namorona).

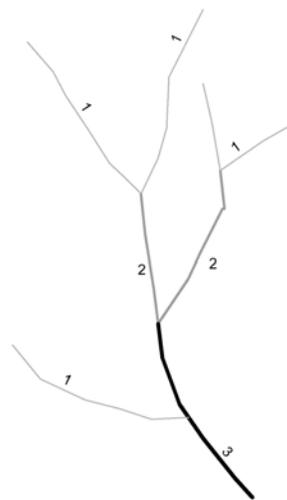


Figure 6.1 An example of a drainage basin with stream order assigned.

6.2.1.2 *Estimating carrying capacity*

We carried out mark-and-recapture at 17 sites which I considered unharvested (see Figure 4.1.2). I assumed that unharvested streams were at carrying capacity (see discussion in 6.4.1 below). Of these unharvested sites, nine were in first-order streams, six were in second and two were in third-order streams. I estimated the mean number of crayfish in 100 m length of river separately for first and for second or third-order streams, using a closed population model (Otis *et al.* 1978) with model averaging in programme MARK (see section 2.2.3.4). I compared the median number of crayfish in first-order and second or third-order streams using a Mann-Whitney U test.

Because the width of a river was not always a significant predictor of density (see chapter eight) I present the estimated number of crayfish found in 100 m stretch of river rather than density *per se*.

6.2.2 Fecundity

Mean fecundity of a population has two aspects: I) the proportion of females that are reproductive in a given year and, II) the number of eggs each reproductive female produces.

I investigated the effect of density on each aspect of fecundity using a Generalised Linear Model (GLM) or Iterated Reweighted Restricted Maximum Likelihood Model (IRREML). An IRREML was used in place of a GLM where there was significant repeatability (the magnitude of the effect more than two times the standard error) in a random factor. The estimated density of large crayfish at each site (estimated using a closed population model: see section 2.2.3.5) was entered as a covariate; site itself was treated as a random factor. Carapace length (CL) the first time an individual was recorded during the breeding season was a covariate.

Where there was a significant effect of density I plotted the shape of the density-dependent relationship for mean-sized females in the medium and large

size-classes. For the medium size-class the mean could be simply calculated from the upper and lower limit for the size-class (42.5 mm). Large is an open-ended size-class so the mean size was estimated by taking the average size of all females observed in that size-class ($n = 89$ females larger than 50 mm CL, 63.1 mm).

6.2.2.1 *The relationship between size and the proportion breeding*

I selected female crayfish larger than 22 mm CL caught between first August and 31 December (the peak reproductive period: see Figure 3.10; $n = 6189$) at sites where density was estimated. I used a binary response variable of whether or not an individual was reproductive in a GLM with binomial error structure to investigate whether density affected the proportion of females which were reproductive.

6.2.2.2 *The relationship between size and the number of eggs*

I selected *A. granulimanus* found bearing eggs at any site where density was estimated ($n = 291$). If an individual was caught more than once during the breeding season only the egg count from the first capture was included. The relationship between size and egg number is non-linear (see Figure 3.8) so I used \log_{10} of egg number as the response variable. Egg number may decrease during incubation due to egg loss following aggressive interactions, or fungal infections (Austin 1998; Rodriguez-Serna *et al.* 2000). To take account of this, I included the time since the start of the peak egg-laying time as a covariate in the model (Rhodes & Holdich 1982).

6.2.2.3 *Overall fecundity*

I plotted the relationship between overall fecundity and size for an *A. granulimanus* crayfish population at carrying capacity by multiplying the functions produced in 6.2.2.2 and 6.2.2.1. To demonstrate the shape of the density-dependent relationship, I plotted the relationship between mean fecundity and density for mean-sized females in the medium and large size-class.

6.3 Results

6.3.1 Carrying capacity (*K*)

6.3.1.1 Crayfish density

The mean crayfish density across first and second or third-order unharvested streams is given in Figure 6.2 below.

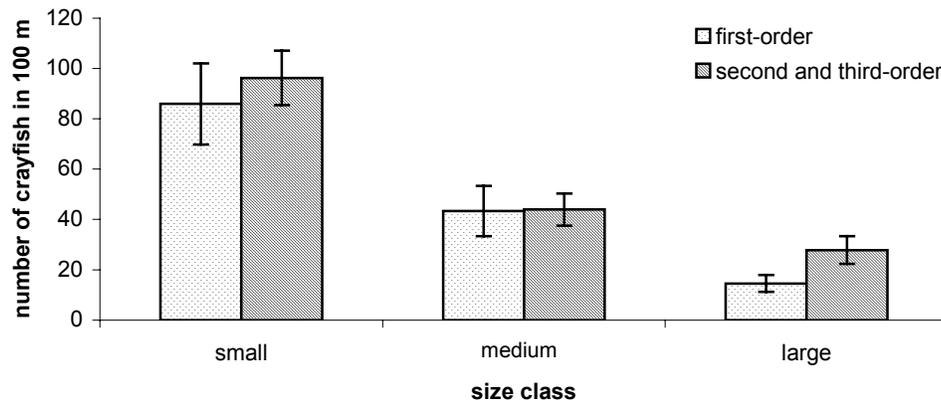


Figure 6.2 The estimated number of crayfish in 100 m of river at first and second or third-order unharvested streams.

There were more small and large crayfish in 100 m of second or third-order streams than there were in an equivalent length of first-order stream. However, these differences were not significant ($W = 77$, $p = 0.74$, $W = 62$, $p = 0.08$ respectively).

6.3.2 Fecundity

6.3.2.1 The relationship between size and the proportion breeding

Site did not show significant repeatability ($P > 0.05$) so a GLM was carried out. As expected, size was a significant predictor of the proportion of females which were reproductive ($F_{1,6187} = 1784.74$, $p < 0.001$). The density of large crayfish at a site was also a significant predictor ($F_{1,6187} = 34.25$, $p < 0.001$) and there was a significant interaction between these two covariates ($F_{1,6187} = 21.04$,

$p < 0.001$). The significant interaction between size and density suggested that the relationship between size and the proportion of females breeding was density-dependent, i.e. more females of a given size were reproductive at low-density sites than high-density sites. The results of the GLM are plotted in Figure 6.3, with the estimated proportion of females reproductive plotted by size for three example density levels.

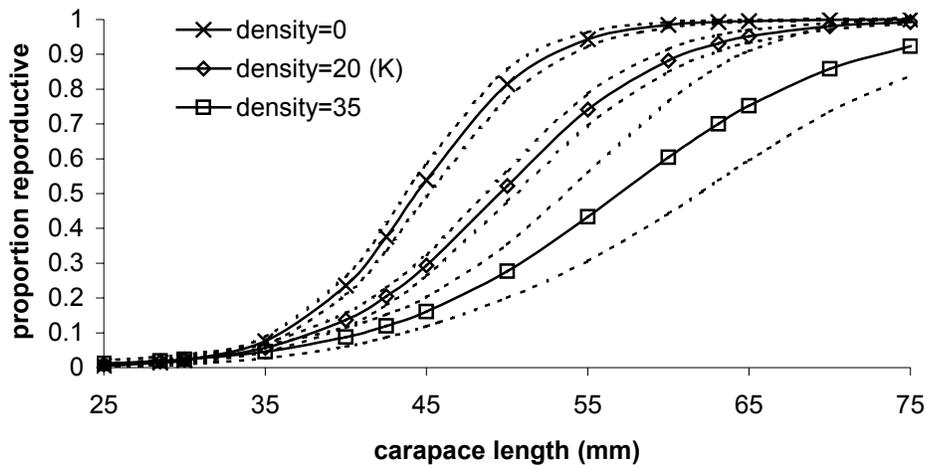


Figure 6.3 The relationship between the proportion of females which were reproductive and size for three example densities (0, 20 and 35 large crayfish in 100 m) predicted from the GLM described above. Error envelopes show 95% confidence intervals.

The relationship between the proportion of females which were reproductive, and density is plotted in Figure 6.4 for medium and large crayfish. Small crayfish did not reproduce so are not shown.

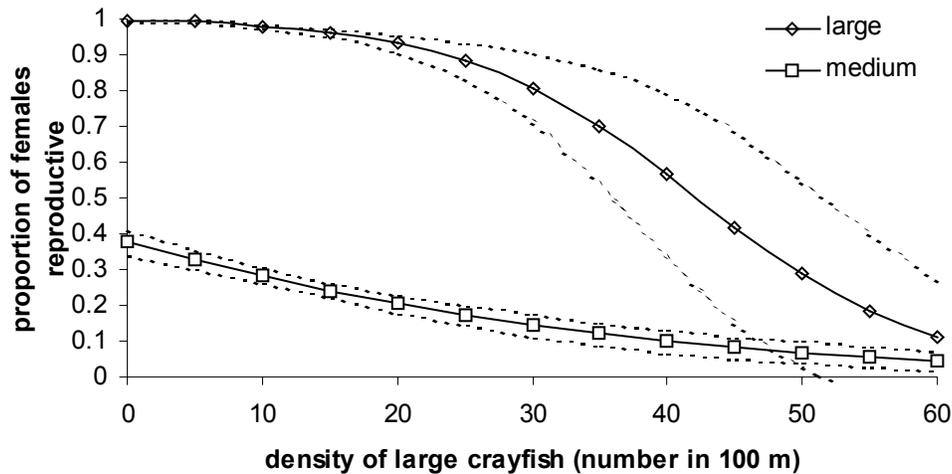


Figure 6.4 The relationship between the proportion of females which were reproductive and density (predicted from the GLM described above) for the medium and large size-class. Error envelopes show 95% confidence intervals.

6.3.2.2 *The relationship between size and the number of eggs*

Site showed no significant repeatability ($P > 0.05$) so a GLM was carried out. The minimal model described 45.2% of the variation. Size was the most significant predictor of the number of eggs carried by a breeding female ($F_{1,289} = 236.57$, $p < 0.001$). However days after the start of the breeding season was also significant ($F_{1,289} = 4.52$, $p = 0.03$) suggesting there was significant egg loss during the breeding season. Density had no significant effect on the number of eggs produced by an individual.

Figure 6.5 below shows the predictions from the GLM described above for 60 days after the start of the breeding season, i.e. the end of August. This was the time when eggs started to hatch (see Figure 3.10) so the plot represents realistic estimates of the number of eggs carried to hatching (assuming egg loss is linear with time).

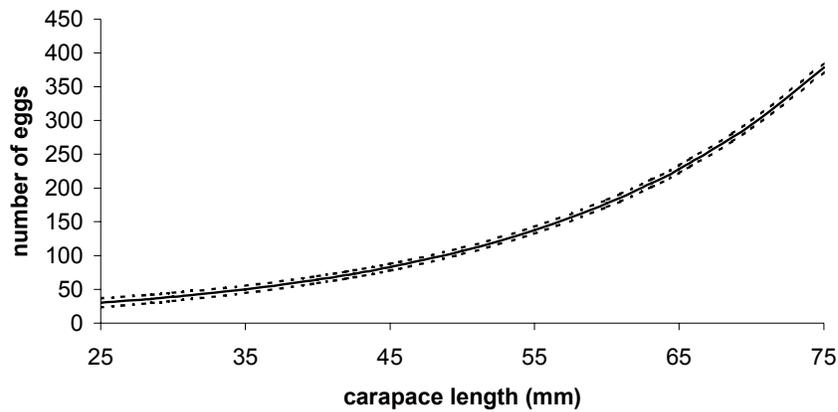


Figure 6.5 The relationship between size and the number of eggs for an individual egg-bearing female predicted using the GLM described in 6.3.2.2 with values estimated for 60 days after the start of the breeding season ($n = 291$). Error envelope shows 95% confidence intervals.

6.3.2.3 Overall fecundity

I combined the results from relationship between size and the proportion breeding at carrying capacity (6.3.2.1) and between size and the number of eggs (6.3.2.2) to give a function describing the relationship between size and overall fecundity for a population of *A. granulimanus* at carrying capacity (Figure 6.6).

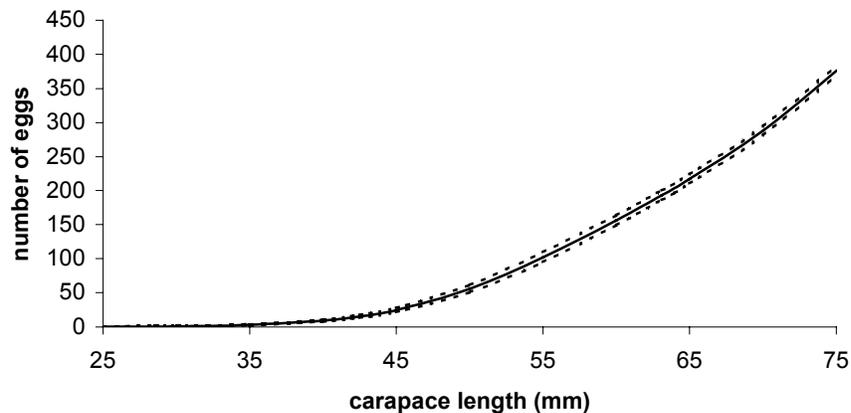


Figure 6.6 The relationship between size and overall fecundity (the mean number of eggs produced per female) for a population of *A. granulimanus* carrying capacity. Error envelope shows 95% confidence intervals.

The relationship between density and fecundity is plotted for medium and large size-class females in Figure 6.7.

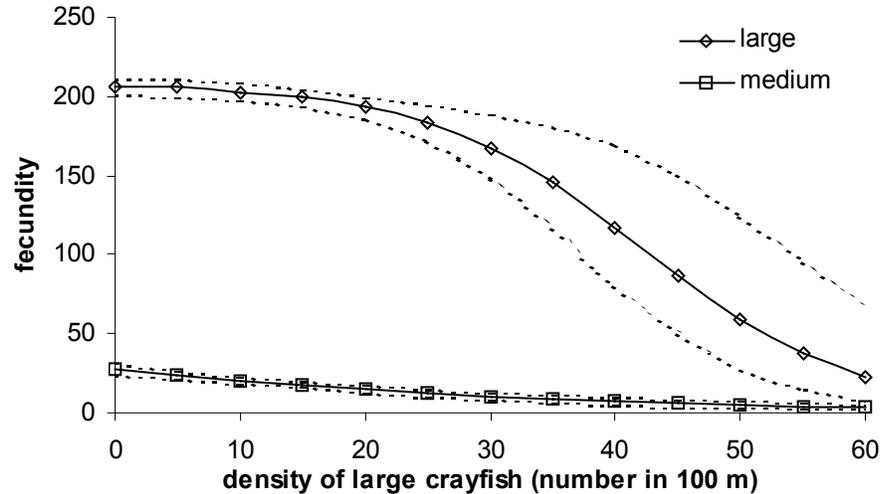


Figure 6.7 The relationship between density and fecundity for large and medium-sized crayfish. Error envelope shows 95% confidence intervals.

6.4 Discussion

6.4.1 The carrying capacity of crayfish

I estimated carrying capacity for *A. granulimanus* using a closed population model and mark-and-recapture data from 17 unharvested sites. The calculation depends on a number of assumptions which I discuss below.

6.4.1.2 *The transects were closed*

The mark-and-recapture model used (Otis *et al.* 1978) relies on the assumption of closure; that there is no birth, death, immigration or emigration during the sampling period. The assumption of zero mortality over the sampling period is probably justified due to the relatively high annual survival of these crayfish (see Figure 5.14) and the fact that the sampling period was only five days. The assumption of zero immigration or emigration is more difficult as crayfish could enter or leave the transect at the boundaries. Crayfish tend to be

relatively sedentary (see section 5.4.2.2) but it is likely some immigration and emigration occurred.

6.4.1.2 *Populations in unharvested rivers are at carrying capacity*

It is unlikely that any rivers in the Ranomafana area experience zero harvesting. However, I used conservative criteria to identify unharvested sites (see section 4.4.6.1) and it is likely that any harvesting at these sites would be very light. Whether or not unharvested populations of *A. granulimanus* are at carrying capacity is a difficult question. There are a number of situations where carrying capacity ceases to be a useful concept (Milner-Gulland & Mace 1998). These include where the population size is regularly reduced to very low levels by catastrophes so density-dependence is not acting, where the population lives in a highly variable environment and this variation masks any tendency of the population to stabilise, where the population is made up of a meta-population, or when a population can not reach an equilibrium due to unstable dynamics. I only have population estimates for a single point in time and so have no information on inter-annual fluctuations and how these may relate to variations in environmental conditions. In the absence of more information I use the mean density across a number of sites as an approximation of carrying capacity but acknowledge that this is based on limited data.

6.4.1.3 *The mark-and-recapture sites accurately reflect the area*

Species are not necessarily evenly distributed throughout their habitat. Differences in micro-habitats may affect their suitability for a species resulting in a patchy distribution (Emmons 1984). This makes it difficult to extrapolate from the density of a plot or transect to the whole study area (Williams *et al.* 2001). I estimated the mean number of crayfish per unit length of river, stratified by stream order, from 17 unharvested sites. To use this as an estimate for carrying capacity for the whole area assumes that the mark-and-recapture sites accurately reflect the range of densities found in the area and in the right proportions. Streams vary along their length and between tributaries in their rock

cover, substrate type and other habitat variables likely to be of importance to crayfish density (Lodge & Hill 1994). If mark-and-recapture sites were better on average than the available habitat then this would overestimate the number of crayfish and *vice versa*. I have no quantitative information on which to justify the assumption that the mark-and-recapture sites accurately represent the study area. However, I took care when selecting the mark-and-recapture sites to represent the range of habitat in approximately the proportions available and there were no obvious differences.

6.4.2 Density-dependent control of fecundity

In this study I found no effect of density on the relationship between size and the number of eggs carried by a reproductive female. However, the proportion of females carrying eggs showed a density-dependent response, with a higher proportion of females of a given size being reproductive at low-density than at high-density. This effect may be caused by one of two mechanisms: I) increased aggressive interactions and/or parasitism at high-density which may cause increased total egg loss, or II) females at high-density withholding reproduction until they reach a larger size. It is impossible to separate these two possible mechanisms by which density may mediate fecundity as a female found without eggs may have spawned and suffered total egg loss or may not have spawned. Egg loss during brooding is well known from many captive and wild studies of crayfish. The mechanism is mostly thought to be due to aggressive contacts (Pursiainen *et al.* 1987; Woodcock & Reynolds 1988; Taugbol & Skurdal 1990), but infections and parasitism cause egg loss during incubation (Austin 1998; Rodriguez-Serna *et al.* 2000) and such problems could also increase with density. Total egg loss has been observed in captive white-claw crayfish *Austropotamobius pallipes* (Rhodes & Holdich 1982) and in the signal crayfish *Pacifastacus leniusculus* (Mason 1977) but no measure of its frequency in wild populations is available.

6.4.3 Are *A. granulimanus* biennial breeders?

Figure 6.3 shows that as crayfish size increases, individuals are more likely to reproduce. The probability of reproducing increases quite slowly with age, with only a proportion of females of most sizes reproducing each year. This pattern could be due to two underlying causes: individual females may become reproductive at different sizes, perhaps due to differences in quality. Alternatively, individuals may not breed every year, with the frequency of reproduction increasing with size. Female noble crayfish *Astacus astacus* are known to spawn in alternate years (Skurdal & Qvenild 1986; Huner *et al.* 1991). One New Zealand parastacid, *Parastacoides tasmanicus*, is a biennially breeder throughout its life (Hamr & Richardson 1994).

In this study we recaptured 240 females in the 2002/2003 breeding season which we had caught during the 2001/2002 breeding season. I used a GLM to investigate the factors predicting egg bearing in the second season. As expected, size was the most important predictor of whether an individual was found carrying eggs in the second year ($F_{1,238} = 5.83$, $p < 0.001$). Seven females found with eggs in the first year did not have eggs in the second year but in general females found with eggs in the first year were significantly more likely to be found with eggs in the second year ($F_{1,238} = 2.28$, $p = 0.02$) indicating that there were quality differences between females. These results do suggest that whether an individual successfully carries eggs depends both on its size and individual quality. However it remains unclear whether individuals make reproductive decisions on whether to spawn or not based on their quality or that some individuals are more likely to suffer total egg loss than others.

6.5 Summary

In this chapter I estimated carrying capacity for *A. granulimanus* by calculating the mean number of crayfish per unit length of river across 17 sites exposed to very low harvesting pressure. I also demonstrated that fecundity of *A. granulimanus* is under density-dependent regulation. This regulation occurs through an increase in the proportion of females reproducing at low-density rather than through a change in the number of eggs born by breeding females.

This chapter and chapter five have provided the parameters necessary to parameterise a population model. In chapter seven I develop a series of size-structured matrix population models of *A. granulimanus* population dynamics to investigate what harvesting strategy would provide the greatest yields. In chapter eight I use the estimate of carrying capacity to estimate whether the crayfish harvest around the harvesting village of Vohiparara may be sustainable under current conditions.

Chapter 7

Modelling a harvested population of *A. granulimanus*: what sizes should harvesters take?

“Very large and fine eels are caught in the rivers, as well as crayfish of a kind peculiar to Madagascar.” (Sibree 1915)



Women from Vohiparara harvesting crayfish.

7 Modelling a harvested population of A. granulimanus: what sizes should harvesters harvest?

7.1 Introduction

Overharvesting of exploited resources is undesirable for conservationists and harvesters alike as at low population sizes the risk of extinction through stochastic processes is increased and the yield is decreased (Beverton 1998; Kokko *et al.* 2001). Successful management of a harvested resource requires an understanding of how the resource responds to exploitation (Milner-Gulland & Mace 1998). Models of population dynamics are useful tools both to investigate the underlying dynamics of an exploited species and to select between management alternatives (Burgman & Possingham 2000). Matrix population models (Leslie 1945) are commonly used in wildlife management and conservation biology (e.g. Cattán & Glade 1989; Nantel *et al.* 1995; Pertierra *et al.* 1997; Anderson & Putz 2002; Chaloupka 2002). Size or stage-structured matrix population models (Lefkovich 1965), extensions of the age-based Leslie matrix, are used where vital rates are more closely associated with an organism's characteristics other than age (e.g. size or developmental stage) or where age cannot easily be established (Caswell 2001).

Population modelling can suffer from a number of uncertainties due to I) a lack of understanding of the processes regulating the population, II) inherent stochasticity in ecological systems, and III) errors in parameter estimation (Chatfield 1995; Ludwig 1999; Harwood 2000; Calder *et al.* 2003). The form and strength of density-dependence is often an important uncertainty in the processes regulating the population. Density-dependence is central to harvesting theory (Hilborn *et al.* 1995; Kokko & Lindstrom 1998), with its form and strength

having a large influence on population growth rates (Ginzburg *et al.* 1990) and therefore vulnerability to harvesting (Fogarty *et al.* 1991). Unfortunately quantifying density-dependence remains extremely difficult (Ginzburg *et al.* 1990; Shenk *et al.* 1998), due to both the lack of long-term data sets using consistent methods and the problem of separating density-dependence from fluctuations in vital rates due to a variable environment (Pollard *et al.* 1987; Lande *et al.* 2002). Where adequate information on density-dependence is not available, information from related species can be used (Burgman *et al.* 1993) and various functional forms incorporated into a suite of models and the effect on the population dynamics investigated (Runge & Johnson 2002).

All biological systems are stochastic. For example, vital rates and population carrying capacity are likely to fluctuate with climatic variation (Milner-Gulland & Mace 1998). Improved computing power has led to a rapid increase in stochastic population modelling (Beissinger & Westphal 1998; Reed *et al.* 2002), which is helpful in making uncertainty explicit in model construction. An important reason for incorporating stochasticity in harvesting models is that it will result in more conservative conclusions as population growth rates in a variable environment are lower than the deterministic growth rate (Levins 1969; Lande *et al.* 1994), even if the mean parameter values are the same. However where no information on inter-annual variation is available, only deterministic analysis is possible (Fieberg & Ellner 2001).

Uncertainty in some parameter estimates will be relatively unimportant if that parameter contributes little to population growth rate. Elasticity analysis (Kroon *et al.* 1986) is a useful tool for investigating the relative contribution of parameters to the population growth rate; vital rates with high elasticity demand greater accuracy of estimation than those with low elasticity. Elasticity analysis has also become popular for identifying vital rates that have a disproportionate influence on population growth rates and can therefore be targeted for conservation management or control (Benton & Grant 1999). A harvest focusing on a size-class with low survival elasticity is likely to be more sustainable than a

harvest which focuses on a size-class with high survival elasticity. Elasticities bear a direct relationship to reproductive values - an individual's expected contribution to future generations (Fisher 1930). McArthur (1960) suggested that harvesting should generally focus on individuals with the smallest reproductive value, as this will minimise the impact the harvest has on population growth.

Population models have been extensively used to investigate the optimum level of harvesting (e.g. Hudson & Dobson 2001; Aanes *et al.* 2002; Brodziak 2002; Skonhott *et al.* 2002; Freckleton *et al.* 2003). In populations regulated by intrinsic (density-dependent) processes, the maximum sustainable yield (MSY) is obtained when the population is kept at the density at which the population growth rate is maximised. The concept of management for MSY, central to fisheries science from the 1950s to the mid-1970s (Punt & Smith 2002), has been much criticised (Larkin 1977; Mangel *et al.* 2002), one reason being its failure to account for uncertainty. However, despite its many problems, MSY remains a useful concept, although it now tends to be used as a maximum limit of exploitation rather than a target for management, and uncertainty is often explicitly taken into account (Punt & Smith 2002).

The choice of harvesting strategy is very important as it will influence both the sustainability and the productivity of the harvest. There are three major classes of harvesting strategy: constant quota (a fixed number of individuals are harvested), constant proportion (a fixed proportion of the population is harvested), and threshold (where all excess individuals above a critical population size are immediately harvested; Lande *et al.* 1995). Constant quota strategies are dangerous as harvesting at a level higher than MSY leads to rapid population collapse (Milner-Gulland & Mace 1998; Sutherland 2001). Constant proportion strategies are much safer as a slight increase in harvest rate results in a decrease in population size and a corresponding fall in harvest level. Threshold harvesting tends to be the best option in terms of maximising both annual yield and, in stochastic models, cumulative yield before extinction (Lande *et al.* 1995). However, threshold strategies result in a very high variance in annual yield, with

all harvesting ceasing in some years, and so such strategies are socio-politically unacceptable in many practical situations (Milner-Gulland & Mace 1998).

Crustaceans show indeterminate growth where size is not necessarily closely related with age. Moreover, it is extremely difficult to know the age of wild crustacean populations due to the lack of retained hard parts (Belchier *et al.* 1998; Hartnoll 2001). As a result, size-structured population models are better than age-structured ones for modelling the population dynamics of crustaceans. Matrix models have been used to inform harvest strategies in number of crustacean species, e.g. blue crab *Callinectes sapidus* (Miller 2001) and Tasmanian rock lobster *Jasus edwardsii* (Punt & Kennedy 1997). However, few population models of crayfish have been built. The CRISP (Crayfish and Rice Integrated System of Production) model of the introduced red swamp crayfish *Procambarus clarkii* in Portuguese rice fields (Anastacio *et al.* 1999) is perhaps the only example.

In this chapter I present a series of size-structured matrix population models of *A. granulimanus*, which vary in the way in which density-dependence is incorporated. I use the models to investigate what size structure should be harvested to produce the largest overall harvest in terms of biomass. I modelled constant proportion harvesting, one of most common forms of harvest to include in structured populations models (Caswell 2001). Data collection was carried out in only two consecutive years, giving a single estimate of transition probabilities and no measure of inter-annual variation. As no information was available on temporal variation in parameter estimates, I do not incorporate stochasticity into the models. It is essential to validate any population model using data not used in model construction (Lindenmayer *et al.* 2001; McCarthy *et al.* 2001). No validation was possible for the way the models behaved away from carrying capacity. However, I compared the population structure predicted by the density-dependent model (and the density-independent models at carrying capacity) to that observed in wild unharvested populations as a simple test of how well the models describe the population.

7.2 Methods

7.2.1 Model structure

I built a size-structured matrix population model and parameterised it using field data on *A. granulimanus*. Body size was split into four classes: young of the year (YOY) < 22 mm CL, small (22-34.9 mm CL), medium (35-49.9 mm CL), and large (> 50 mm CL; see section 2.2.3.3). *Astacoides* are seasonal breeders (see Figure 3.10) so I used a birth pulse model (Caswell 2001). YOY enter the population in January and have either died or reached the small size-class (22-35 mm CL) by the time of the census, immediately before the next instantaneous breeding episode. YOY do not therefore appear in the matrix and fecundity (F_i) is the mean number eggs produced per female (E_i) multiplied by the survival of YOY to the end of the first year (Φ_1). I only modelled female population dynamics since crayfish are polygynous maters (Reynolds 2002) meaning males are unlikely to limit population growth except at very low numbers (Kokko *et al.* 2001). At each time step an individual can either remain in class i with probability P_i or, if it grows sufficiently, move to stage $i+1$ with probability G_i .

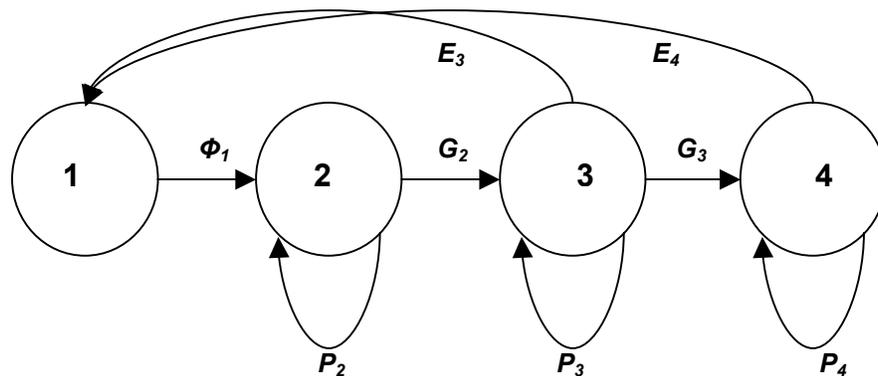


Figure 7.1 Size structured life-cycle graph for *A. granulimanus*. The nodes represent YOY (1), small (2), medium (3), and large (4) individuals. P_i is the probability of staying in the same node, G_i is the probability of moving to the next node, E_i is the mean number of eggs produced per female and Φ_1 is the survival of young to the end of the first growing season.

Matrix elements P_i , G_i and F_i were incorporated in a transition matrix \mathbf{A} . Projections were made over one year corresponding to a December pre-breeding

census. The size and structure of the population at time t is described by vector $\mathbf{n}(t)$. At each time step the transition matrix (\mathbf{A}) was multiplied by the vector $\mathbf{n}(t)$ such that $\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t)$

$$\text{Where } \mathbf{A} = \begin{bmatrix} P_2 & F_3 & F_4 \\ G_2 & P_3 & 0 \\ 0 & G_3 & P_4 \end{bmatrix} \text{ and } \mathbf{n}(t) = \begin{bmatrix} n_2 \\ n_3 \\ n_4 \end{bmatrix}$$

The asymptotic population growth rate λ is given by the dominant eigenvalue of matrix \mathbf{A} (Caswell 2001). I ran model simulations using the programme Unified Life models (ULM; Legendre & Clobert 1995).

7.2.2 Model parameters

The parameters obtained from the fieldwork (Table 7.1) can be used to derive the matrix elements P_i (Equation 7.1) and G_i (Equation 7.2).

$$\text{Equation 7.1} \quad P_i = \phi_i - (\phi_i \times \gamma_{ij})$$

$$\text{Equation 7.2} \quad G_i = \phi_i \times \gamma_{ij}$$

where ϕ_i is survival of stage i and γ_{ij} is the survival-dependent transition probability from stage i to stage j .

Fecundity F_i can be estimated from the number of eggs per female (E_i) multiplied by survival from the egg to the end of the first year (ϕ_1). To estimate the number of female eggs produced E_i must be divided by two (assuming a 1:1 sex ratio at hatching; Equation 7.3).

$$\text{Equation 7.3} \quad F_i = \frac{E_i}{2} \times \phi_1$$

It was not possible to obtain ϕ_1 from the field data as individuals less than 22 mm CL were not marked individually (see section 2.2.3.3). I obtained this parameter by assuming that unharvested populations were at equilibrium ($\lambda = 1$). I found the value of ϕ_1 where $\lambda = 1$ using the pop tools addin in Microsoft Excel.

Table 7.1 The parameters and their source.

vital rate	mean	SEMs	data source
survival from the egg to the end of the first year, Φ_1	0.035		see above
small crayfish survival, Φ_2	0.517	0.044	chapter five
medium crayfish survival, Φ_3	0.517	0.044	chapter five
large crayfish survival, Φ_4	0.703	0.122	chapter five
small to medium transition, γ_{23}	0.468	0.035	chapter five
medium to large transition, γ_{34}	0.281	0.099	chapter five
no. of eggs per medium ♀ E_3	15	1.5	chapter six
no. of eggs per large ♀ E_4	193	2.7	chapter six

7.2.3 Density-independent model

I used the mean parameter values in Table 7.1 above to build a density-independent model: model 1.

7.2.3.1 Model validation

To test the general predictions of the model I compared the predicted size-structure (the right eigenvector of the deterministic matrix; Caswell 2001) with that observed at the 17 mark-and-recapture sites considered unharvested (see Figure 4.12). All the parameters in Table 7.1 above, with the exception of Φ_1 , have associated estimation error. To investigate the error in the model estimate of stable age structure, simulations were carried out in programme R (R 1.8.1). At each iteration parameters were drawn from normal distributions with means and standard deviations as given in Table 7.1 above. Survival estimates were bounded so that $0 < \Phi_i < 1$, and transition probabilities so that $0 < \gamma_i \leq 1$. For each combination of randomly-chosen parameter estimates, Φ_1 was chosen to give a stable population ($1 < \lambda < 1.00001$). After 500 iterations the mean and standard error of the stable age structure had stabilised and were compared with that observed in wild unharvested populations.

7.2.3.2 *Stable size-structure and reproductive value*

The right eigenvector of the deterministic matrix is the stable age structure (see above). The left eigenvector gives the reproductive value of the size-classes in a transition matrix (Caswell 2001). This is a measure of the expected contribution of individuals to the ancestry of future generations (Fisher 1930).

7.2.4 Density-dependent models

A density-dependent matrix model can be written:

$$\mathbf{n}(t+1) = \mathbf{A}_n \mathbf{n}(t)$$

where the subscript indicates that the matrix elements a_{ij} depend on the population vector \mathbf{n} . Each stage may contribute differently to density.

There is only weak evidence of density-dependent control of growth in *A. granulimanus* (see section 5.4.4.1) so density-dependence was not incorporated in transition probabilities. Evidence for density-dependent regulation of mean egg number produced per female is available (see Figure 6.7). It was not possible to test for density-dependence in survival using the data in this study. However, this is likely to be an important regulator of crayfish populations (see section 5.4.4.2). The only available study on density-dependent survival in crayfish (Momot & Gowing 1977) was used to inform the density-dependence and a number of alternatives investigated.

7.2.4.1 *Types of density-dependence*

I incorporated two types of density-dependent function. Linear density-dependence (Equation 7.4; model 2) and non-linear density-dependence (Equation 7.5), with regulation operating either far from carrying capacity ($c < 1$; model 3) or close to carrying capacity ($c > 1$; model 4):

Equation 7.4

$$a_i = A \left[1 - \left(\frac{n_t}{K} \right) + B \right]$$

Equation 7.5

$$a_i = A \left[1 - \left(\frac{n_t}{K} \right)^c + B \right]$$

where K is the carrying capacity, n_t is the population size at time t , B is the parameter value when $n_t = K$, A and B are constants and c is a shape parameter. The shapes of the three forms are shown in Figure 7.2.

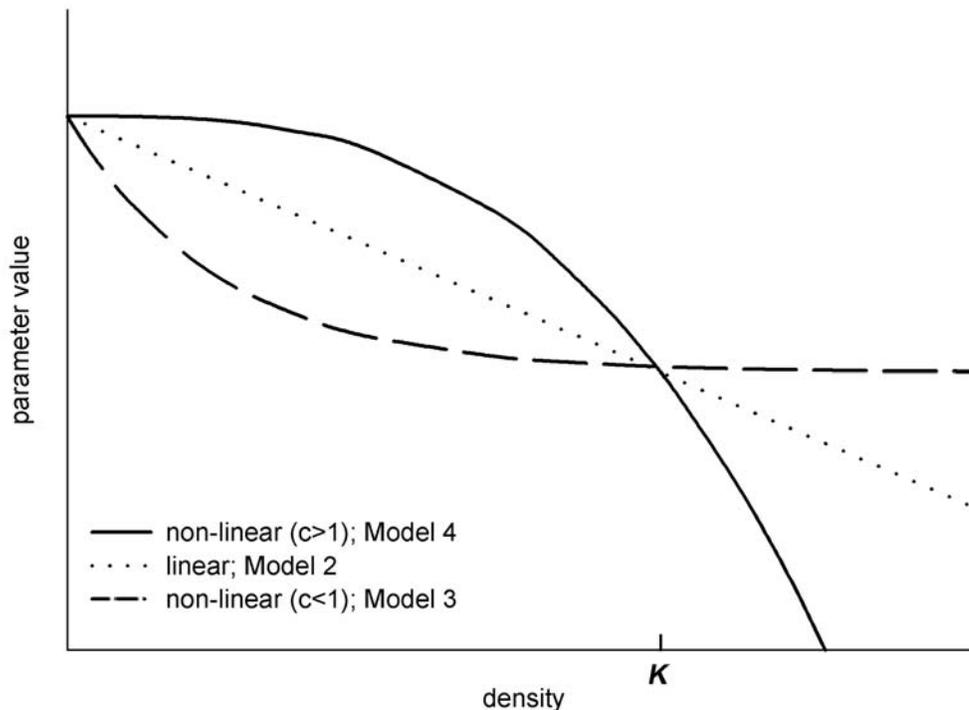


Figure 7.2 The three forms of density-dependence modelled.

I set carrying capacity arbitrarily at 10,000 large crayfish and calculated the number of individuals in other size-classes using the stable age structure of an unharvested population.

7.2.4.2 *Varying how and where in the life-cycle density dependence acts*

I ran a number of alternative models to investigate the result of assumptions on where in the life cycle density-dependence acts and how the size-classes contribute to regulation. In all models survival of smaller crayfish was assumed to be under density-dependent control as crayfish are cannibalistic

(Lodge & Hill 1994) In one set of models (set a) density-dependence was incorporated into survival of YOY (Φ_1), small (Φ_2) medium (Φ_3), and large (Φ_4) crayfish with the biomass of crayfish the same size or larger being taken as the appropriate measure of density regulating the parameter. Larger crayfish are behaviourally dominant (Figler *et al.* 1999) and therefore likely to contribute more strongly to density-dependence. The mean carapace length of each size-class was converted to individual mass using equation 4.1 in chapter four and hence overall biomass. The models in set b were similar to set a except that density-dependence was not incorporated in the survival of large crayfish (Φ_4) as their survival was so high at carrying capacity that it may not be strongly regulated. In the next set of models (set c) density-dependence is incorporated in all size-classes but is regulated by the number of crayfish of the same size or larger. In the final set of models (set d), density-dependence for YOY and small survival (Φ_1 and Φ_2) was regulated by the number of medium and large crayfish and the survival of medium and large crayfish (Φ_3 and Φ_4) was regulated by the biomass of crayfish of the same size or larger. This final subset of models assumed that regulation of YOY and small crayfish was likely to be through direct predation so any larger crayfish is a potential predator but that regulation of medium and large crayfish survival acts through competition over access to shelters or food resources. Biomass is therefore a more suitable measure of density than number. Table 7.2 below describes the 13 models run.

Table 7.2 The models developed in this chapter. Models vary by the form of density-dependence (ρ -dep.), where in the life-cycle it acts and what it is regulated by.

model name	type of ρ-dep.	ρ-dep. acts on survival of:	ρ-dep. regulated by:
model 1	none		
model 2a	linear	$\Phi_1, \Phi_2, \Phi_3, \Phi_4$	biomass of crayfish same size or larger
model 2b	linear	Φ_1, Φ_2, Φ_3	biomass of crayfish same size or larger
model 2c	linear	$\Phi_1, \Phi_2, \Phi_3, \Phi_4$	no. of crayfish same size or larger
model 2d	linear	$\Phi_1, \Phi_2, \Phi_3, \Phi_4$	no. of crayfish same size or larger (Φ_1, Φ_2), biomass of crayfish same size or larger (Φ_3, Φ_4)
model 3a	non-linear, $c < 1$	$\Phi_1, \Phi_2, \Phi_3, \Phi_4$	biomass of crayfish same size or larger
model 3b	non-linear, $c < 1$	Φ_1, Φ_2, Φ_3	biomass of crayfish same size or larger
model 3c	non-linear, $c < 1$	$\Phi_1, \Phi_2, \Phi_3, \Phi_4$	no. of crayfish same size or larger
model 3d	non-linear, $c < 1$	$\Phi_1, \Phi_2, \Phi_3, \Phi_4$	no. of crayfish same size or larger (Φ_1, Φ_2), biomass of crayfish same size or larger (Φ_3, Φ_4)
model 4a	non-linear, $c > 1$	$\Phi_1, \Phi_2, \Phi_3, \Phi_4$	biomass of crayfish same size or larger
model 4b	non-linear, $c > 1$	Φ_1, Φ_2, Φ_3	biomass of crayfish same size or larger
model 4c	non-linear, $c > 1$	$\Phi_1, \Phi_2, \Phi_3, \Phi_4$	no. of crayfish same size or larger
model 4d	non-linear, $c > 1$	$\Phi_1, \Phi_2, \Phi_3, \Phi_4$	no. of crayfish same size or larger (Φ_1, Φ_2), biomass of crayfish same size or larger (Φ_3, Φ_4)

7.2.4.3 *The strength of the density-dependence in survival*

I used the strength of density-dependence in survival of the crayfish *Orconectes virilis* (Momot & Gowing 1977) to inform the strength (the difference between Φ_i at $n = K$ and $n = 0$) of density-dependence in *A. granulimanus* survival and the shape of the curve (parameter c) in model 3. Density-dependence was incorporated into survival of YOY (Φ_1) and small (Φ_2), medium (Φ_3) and large (Φ_4) crayfish using the appropriate relationship from Momot and Gowing (YOY survival, juvenile survival, adult survival and adult survival respectively; Figure 7.3). For models 2 and 4 the strength of density-dependence was taken from the slope of a linear regression. For model 3 the strength of density-dependence and the shape parameter c was taken from fitting the non-linear equation (Equation 7.5) using the solver function in Microsoft Excel. The shape parameter c for model 4 was arbitrarily set at 2.5, as a value greater than 3 produced a biologically unrealistic rate of population growth rate resulting in stable limit cycles (May 1976). The fit of the two curves was compared using Akaike Information Criteria AIC; in each case there was no significant difference between the fit of the linear and non-linear curve ($\Delta AIC < 2$; Burnham & Anderson 1998).

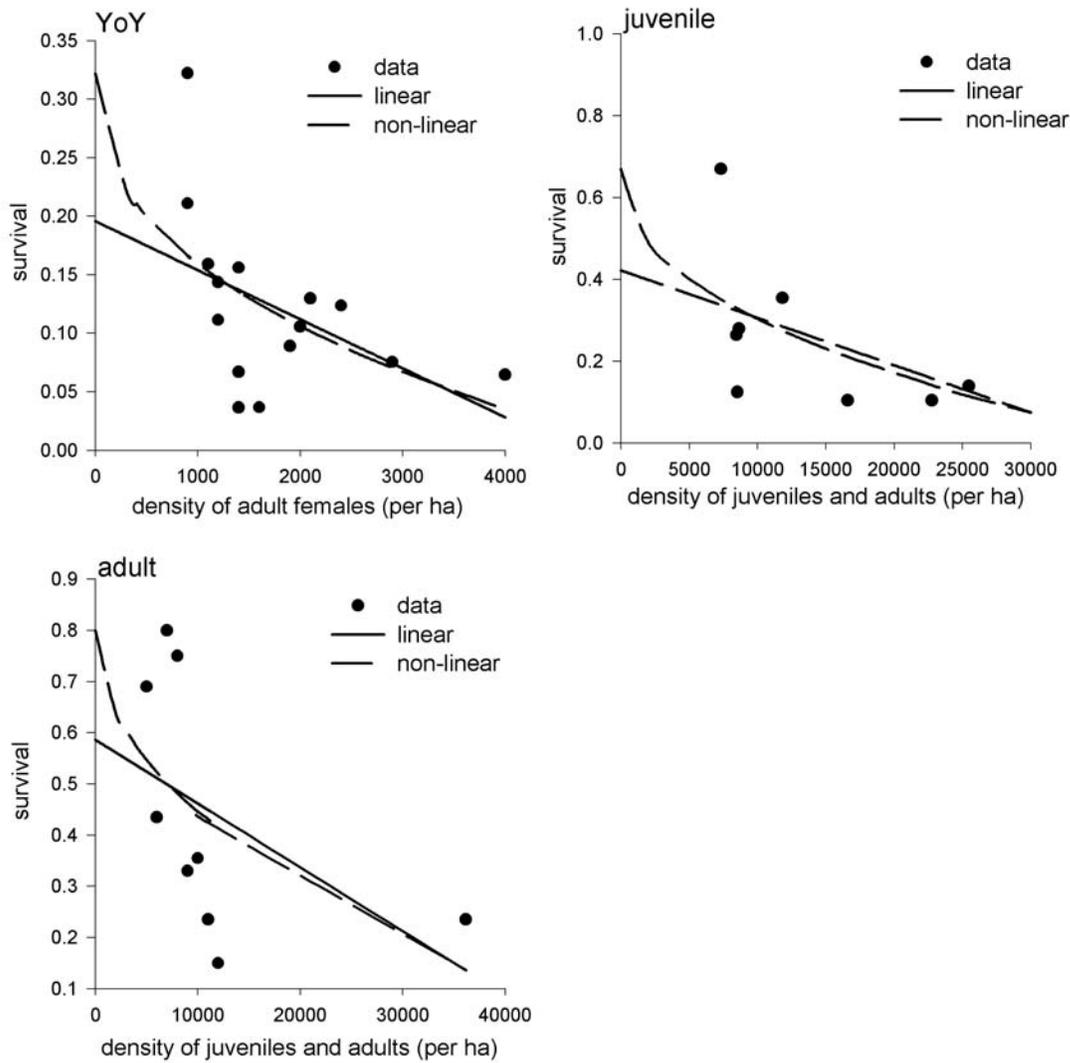


Figure 7.3 The relationship between density and survival for YOY, juvenile and adult *O. virilis* (data from Momot & Gowing 1977).

7.2.5 Elasticity analysis

Elasticity analysis estimates the effect of a proportional change in the vital rates on population growth rate λ (Benton & Grant 1999). The elasticity, e_{ij} , of λ with respect to matrix element a_{ij} is given by the partial derivative (Equation 7.6) from the Leslie population matrix (Kroon *et al.* 1986).

$$\text{Equation 7.6} \quad e_{ij} = \frac{a_{ij} \partial \lambda}{\lambda \partial a_{ij}} \frac{\partial \log \lambda}{\partial \log a_{ij}}$$

The elasticity e_{ij} is therefore the slope of the log of λ plotted against log a_{ij} (Caswell 2001).

In density-dependent populations at equilibrium $\lambda = 1$ by definition, thus the effect of small changes in parameter values cannot be examined by investigating changes in λ . Instead, elasticity analysis for density-dependent models must examine whether or not a variant form would invade a resident population at equilibrium (Benton & Grant 1999). The rate at which the variant invades is given by the invasion exponent (Rand *et al.* 1994). For populations with a stable equilibrium, i.e. without chaotic dynamics, density-dependent elasticity, e_{ij} , with respect to matrix element a_{ij} are equivalent to the standard elasticities for the projection matrix evaluated at the equilibrium point (Grant & Benton 2000).

7.2.6 The strategy which produces the largest sustainable yield

I simulated constant-proportion harvesting, where harvesters remove a constant proportion h_i of the individuals present in size-class i each year. The harvest was removed just prior to reproduction. The proportion of each size-class harvested was varied from 0 to 1 at intervals of 0.1 for each size-class while holding the proportion of the other two classes constant. I found the total biomass harvested by each of the resulting strategies by converting number of crayfish harvested in each size-class to mass using equation 4.1. For each model I found

the harvest strategy which resulted in the largest sustainable yield (i.e. a yield which did not result in a negative population growth rate λ).

To test whether biomass represented the true economic value of crayfish, we showed a cooked crayfish of various sizes (35, 42.5, 52 and 62 mm CL) to ten villagers in Vohiparara and asked them to estimate the price. The value increased linearly with mass ($F_{1,39} = 312.8$, $r^2 = 0.89$, $p < 0.001$) and the price of a crayfish of mean size in the medium size-class (42.5 mm CL, 33.9 g) was half that of a mean-sized crayfish in the large size-class caught in Vohiparara (52 mm CL, 61.2 g). This justifies using biomass as a surrogate for economic value.

7.3 Results

7.3.1 Density-independent model (model 1)

7.3.1.1 Model validation

The stable size structure observed across 17 unharvested sites shows a good fit to that predicted from the deterministic model providing general support for the model and parameter estimates (Figure 7.5).

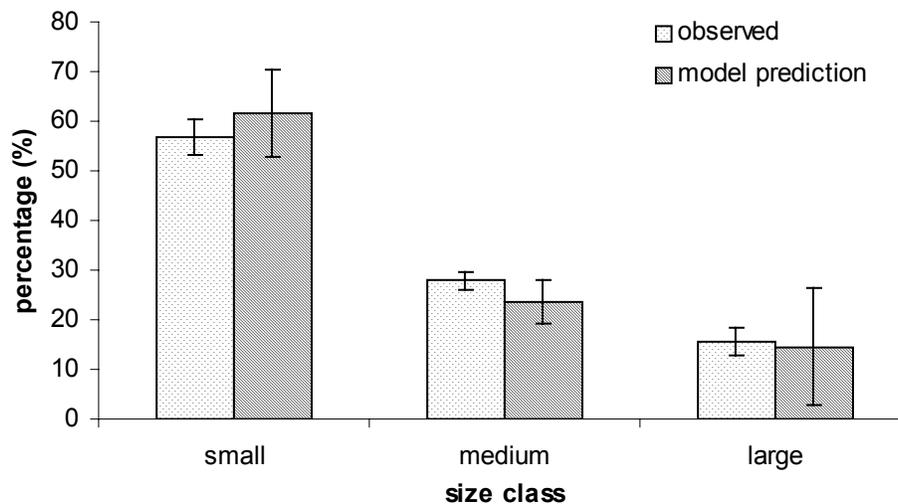


Figure 7.5 The stable size-structure predicted from model 1 compared with that observed at unharvested sites. Error bars shows SEMs.

7.1.1.7 Stable size structure and reproductive value

The stable size structure and reproductive value predicted by model 1 are shown in Figure 7.6. Large individuals have a much higher reproductive value than smaller individuals, due to the increase in fecundity with size.

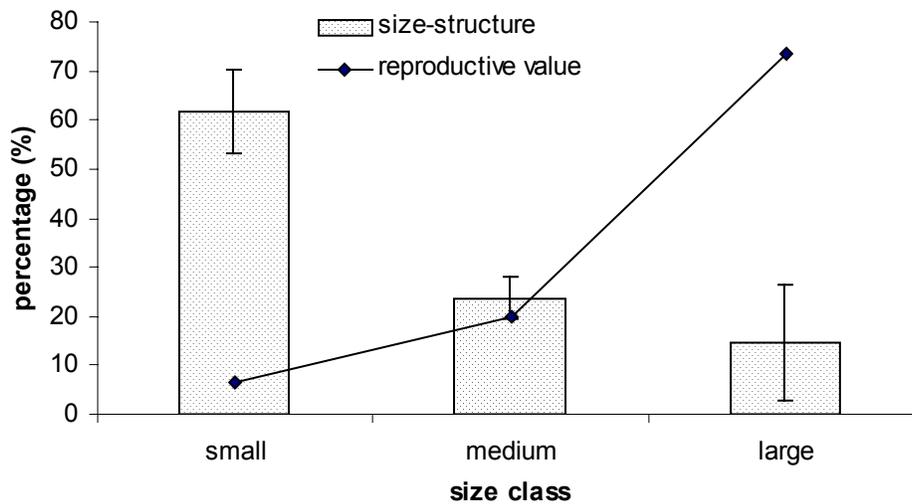


Figure 7.6 The stable size-structure and reproductive value of size-classes estimated from model 1.

7.3.2 Elasticity analysis

The elasticities of the density-independent model (model 1; Figure 7.7) suggest that proportional changes in survival of large crayfish have the largest impact on population growth rate λ .

$$1 = \begin{bmatrix} 0.065 & 0.024 & 0.147 \\ 0.171 & 0.107 & 0 \\ 0 & 0.147 & 0.345 \end{bmatrix}$$

Figure 7.7: The elasticity of the transition matrix in model 1.

The density-dependent elasticities of models 2, 3 and 4 are given in Figure 7.8 below. They show the same general pattern as that seen in the elasticities of the density-independent model.

$$\begin{aligned}
2a &= \begin{bmatrix} 0.064 & 0.023 & 0.144 \\ 0.166 & 0.099 & 0 \\ 0 & 0.143 & 0.363 \end{bmatrix} & 2b &= \begin{bmatrix} 0.064 & 0.025 & 0.146 \\ 0.171 & 0.102 & 0 \\ 0 & 0.146 & 0.356 \end{bmatrix} & 2c &= \begin{bmatrix} 0.061 & 0.023 & 0.141 \\ 0.164 & 0.098 & 0 \\ 0 & 0.142 & 0.371 \end{bmatrix} \\
2d &= \begin{bmatrix} 0.061 & 0.223 & 0.142 \\ 0.165 & 0.099 & 0 \\ 0 & 0.142 & 0.368 \end{bmatrix} & 3a &= \begin{bmatrix} 0.063 & 0.024 & 0.145 \\ 0.169 & 0.100 & 0 \\ 0 & 0.145 & 0.333 \end{bmatrix} & 3b &= \begin{bmatrix} 0.064 & 0.025 & 0.146 \\ 0.171 & 0.102 & 0 \\ 0 & 0.146 & 0.346 \end{bmatrix} \\
3c &= \begin{bmatrix} 0.062 & 0.024 & 0.144 \\ 0.168 & 0.099 & 0 \\ 0 & 0.144 & 0.359 \end{bmatrix} & 3d &= \begin{bmatrix} 0.062 & 0.0234 & 0.144 \\ 0.167 & 0.102 & 0 \\ 0 & 0.144 & 0.357 \end{bmatrix} & 4a &= \begin{bmatrix} 0.059 & 0.021 & 0.141 \\ 0.162 & 0.098 & 0 \\ 0 & 0.141 & 0.377 \end{bmatrix} \\
4b &= \begin{bmatrix} 0.063 & 0.024 & 0.146 \\ 0.170 & 0.106 & 0 \\ 0 & 0.146 & 0.346 \end{bmatrix}
\end{aligned}$$

Figure 7.8 The density-dependent elasticities of the density-dependent models 2-4. Elasticities were estimated at the equilibrium point where $\lambda = 1$.

In all cases survival of large crayfish is the most important parameter contributing to population size, especially in models regulated by number not biomass (models c).

7.3.3 The harvest strategy which produces the largest yield

Figure 7.9 shows, for each of models 2a, b, c and d, the shape of the relationship between biomass produced and the proportion of medium and large crayfish harvested for three different levels of harvesting of small crayfish; 0%, 40% and 80%. For example, the first row, of Figure 7.9 shows that under model 2a, if no small crayfish were harvested, the maximum biomass was obtained where 100% of large and 30% of medium were harvested. If 40% of small were harvested then the maximum yield occurred when 30% of medium and 30% of large were harvested, but this yield was lower than that obtained when no small crayfish were harvested. If 80% of small were harvested all yields were very much reduced. The pattern was similar for all models, with higher yield when harvesting concentrated on larger size-classes.

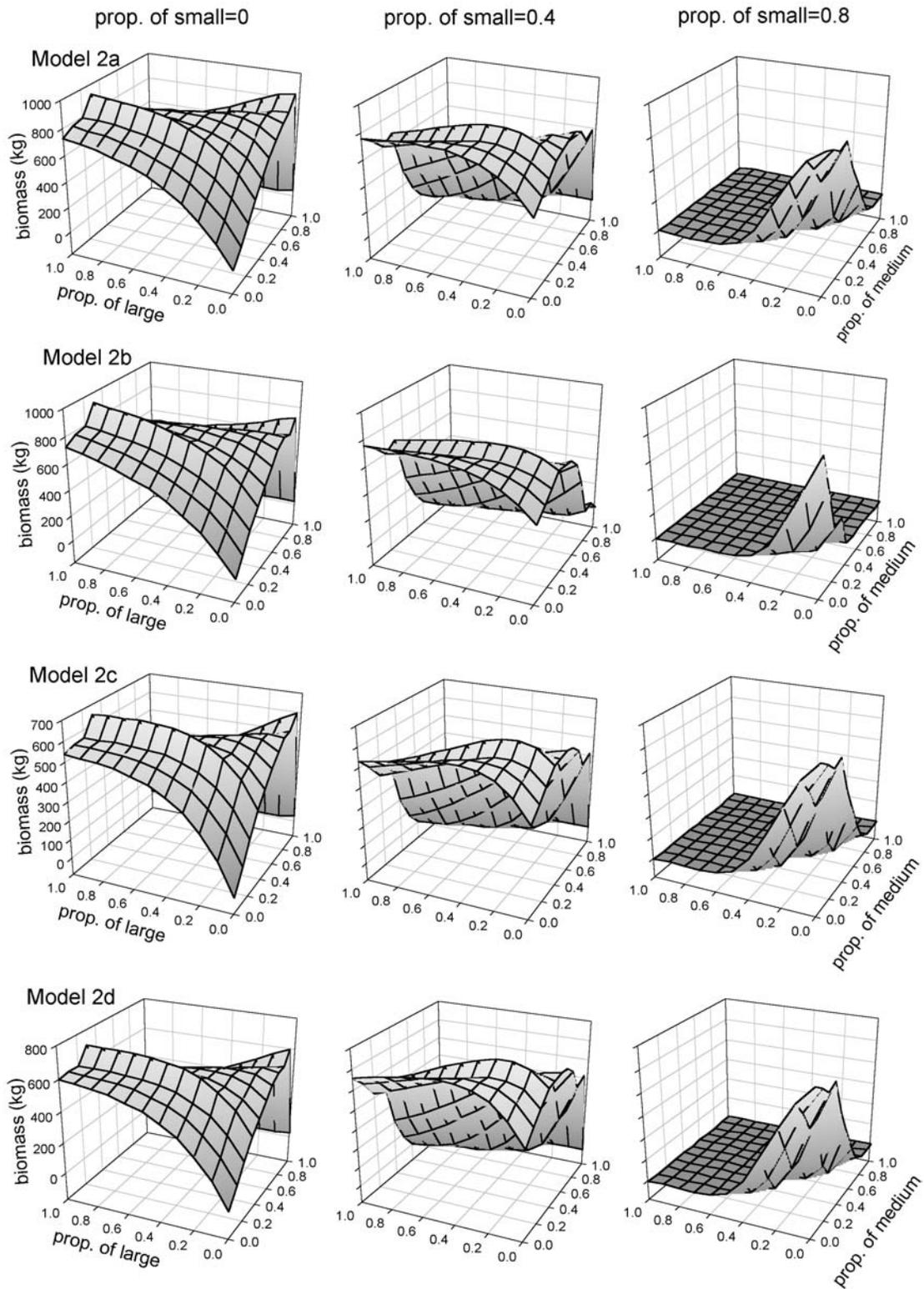


Figure 7.9 The yield in biomass (kg) predicted for various offtake rates for models 2a, b, c and d.

Figure 7.10 shows the predicted yield under the same harvesting strategies for models 3a and 4a only. The patterns were broadly similar but as Figure 7.11 below shows, the highest yield in terms of biomass for model 4 occurred with some limited harvesting of small crayfish.

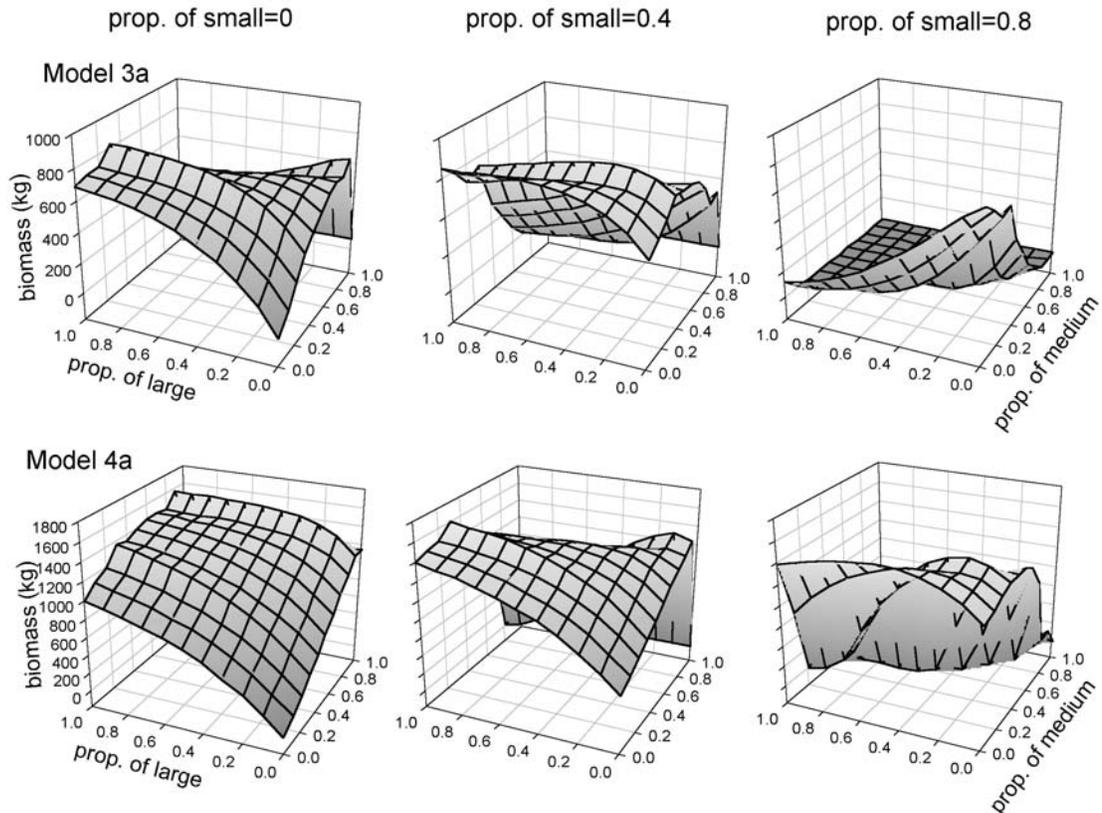


Figure 7.10 The yield in biomass (kg) predicted for various offtake rates for model 3a and 4a.

The harvesting strategy which produced the maximum yield for the different models is shown in Figure 7.11 below. Models 4c and 4d produced extremely unstable dynamics so a maximum offtake could not be calculated. For the rest of the models the pattern was similar; the highest yields were found with little harvesting of small crayfish and heavy harvesting of the largest size-class. Where density-dependence was regulated entirely or partly by number rather than biomass (models c and d), maximum yield was associated with removing a lower proportion of large crayfish than for models where density-dependence was regulated by biomass.

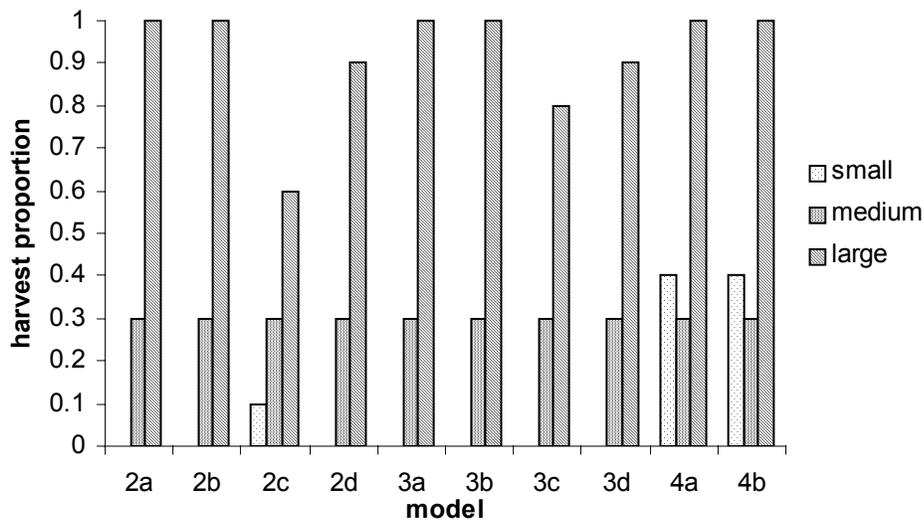


Figure 7.11 The harvesting proportions which yield the highest biomass for each model.

7.4 Discussion

7.4.1 Model verification

The predictions of population models are seldom tested with field data that were not used to build the model although this is an essential step to evaluate the usefulness of the model (McCarthy *et al.* 2001; Lindenmayer *et al.* 2003). I compared the size structure predicted by the density-independent model (built using vital rate data collected from unharvested populations of *A. granulimanus*) with the population structure observed at unharvested sites. These showed good fit suggesting that the deterministic model describes the population structure at carrying capacity. It was not possible to validate the density-dependent models' behaviour away from the carrying capacity, as although approximate harvest levels are known for the area around Vohiparara, offtake could not be linked closely enough to specific locations to use this as a test.

7.4.2 Elasticity analysis

Elasticity analysis showed that the population growth rate λ is most sensitive to changes in survival of large crayfish. This is unfortunate given that

this parameter has the highest uncertainty (a high coefficient of variation see Table 7.1) associated with it. The general pattern in the elasticities is the same for all models tested: the highest elasticity is for large crayfish survival and the lowest for survival and stasis of small crayfish. This suggests that reducing the survival of small crayfish would have a less negative influence on population growth rate than reducing the survival of large crayfish.

Elasticity analysis has become a popular way to prioritise conservation management (Wootton & Bell 1992; Crowder *et al.* 1994; Ratsirarson *et al.* 1996). However, there are important limitations to its usefulness. Elasticities are concerned with the effect of infinitesimally small changes in a parameter value whereas management may change a vital rate substantially. How well elasticity analyses predict the response of population growth to a perturbation in a parameter value will depend on the linearity of the response in λ to changes in vital rates over the relevant values (Mills *et al.* 1999). In addition, vital rates are not equally amenable to change and the relative cost of management interventions should be taken into account as well as simple elasticities (Green 2002). In the case of harvesting a structured population, the relative economic value of size-classes must also be considered (Kokko *et al.* 2001).

7.4.3 Optimal harvesting strategy

Naïve consideration of the elasticities and reproductive values produced by the models would suggest that harvesting should focus on small individuals as these have least influence of population growth rate. However, the results of all the models suggest that the largest sustainable harvest, in terms of biomass, can be produced by focusing on larger crayfish. Part of the reason for this discrepancy is the large difference (ten times) in the mass of a large crayfish relative to a small crayfish. In addition, in most of the models tested (sets a, b and d) the large size-class has a disproportionate influence on population regulation as density-dependence is assumed to act wholly or largely through biomass and large crayfish are much heavier than smaller ones. Removal of

large crayfish is therefore necessary to allow maximum possible increases in survival and fecundity to obtain the maximum productivity. Where density-dependence is regulated by number not biomass (model c), the maximum harvest is obtained when fewer of the large size-class are removed (Figure 7.10). These results emphasize the care that must be taken when using elasticity analysis to inform management decisions (Mills *et al.* 1999; Kokko *et al.* 2001).

The model outputs presented in this chapter should be interpreted with care. The maximum biomass offtake possible should not be taken as a precise estimate but rather as an indicator of which harvesting strategies produce the highest sustainable offtake under the various assumptions considered. The analysis is essentially looking for the MSY but as many authors have stressed, the MSY is seldom sustainable under real conditions. MSY should be used as an absolute limit of extraction rather than a target for management (see section 7.1). The message from the models is that, if density-dependent regulation occurs in the way in which it is assumed in the models tested, harvesters should focus on larger individuals to maximise yield. This conclusion will hold even if the strength of density-dependence varies. It depends only on the assumption that density-dependence is due to the effects of large crayfish and that large crayfish are disproportionately valuable. The assumptions made about the shape and strength of density-dependence are discussed below.

The harvesting community of Vohiparara do tend to harvest large crayfish in preference; their catch is made up disproportionately of medium size crayfish with few small and large (see Figure 4.5).

7.4.4 The assumptions concerning density-dependence

7.4.4.1 Regulation of growth and fecundity

I found no strong evidence for density-dependent regulation of growth in *A. granulimanus* (see section 5.4.4.1) so I did not incorporate it in the models. This finding agrees with the one study of density-dependent regulation in wild

crayfish (Momot & Gowing 1977), which found that fecundity and survival, but not growth, were under density-dependent control. Anastacio *et al.* (Anastacio *et al.* 1999), in their model of population dynamics of the red swamp crayfish *Procambarus clarkii*, assumed that density-dependence acted mostly on survival and not on growth. The shape of the density-dependent relationship for fecundity in *A. granulimanus* was demonstrated in Figure 6.7 and was used to inform the models.

7.4.4.2 *Regulation of survival*

Information concerning the strength and shape of density-dependent control of survival of *A. granulimanus* is completely lacking. The literature suggests that density-dependent regulation of survival is likely to be important in crayfish (see section 5.4.4.2) but I found only a single study which quantified this. The strength of density-dependence was therefore taken from an unrelated crayfish, *O. virilis*, the only species for which density-dependent survival has been quantified. Density-dependence may act differently on closely related species so this approach must be taken with care and the uncertainty in the strength of density-dependence remembered when interpreting the results. If the strength of density-dependence in *A. granulimanus* is lower than in *O. virilis* then the predicted yields will be higher than those achievable in reality, whereas if density-dependence is stronger, true yields may be larger.

7.4.4.3 *Which model is the most realistic?*

In some of the models (sets a and b) density-dependence is regulated by the biomass of competing size-classes, rather than by number (set c). This is the approach taken in the only other crayfish population model published to date (Anastacio *et al.* 1999). Regulation by biomass seems justified, particularly for the larger size-classes. Larger crayfish are competitively dominant (Figler *et al.* 1999; Vorburger & Ribí 1999) and density is likely to influence survival through cannibalism and direct conflict over access to resources such as food and shelter (Taugbol & Skurdal 1992; Saez-Royuela *et al.* 2001) where relative size will be

important. In models in set d, survival of YOY and small crayfish is regulated by the number of medium and large crayfish while survival of medium and large crayfish is regulated by biomass. This may be the most suitable model as regulation of YOY or small crayfish is likely to be mainly through direct predation so any larger crayfish is a potential predator. For medium and large crayfish, on the other hand, density-dependence acts through competition over access to shelters or food resources and biomass is therefore more suitable than number.

Due to its simplicity, linear density-dependence (models 2) is commonly included in population models, although it is unlikely to represent biological reality (Caswell 2001). There was no significant difference in the fit of the linear model and the non-linear model with density-dependence acting far from the carrying capacity to the data for *O. virilis*. However, the non-linear model results in the most conservative estimates of sustainable offtake, so should be favoured. Model 4, where density-dependence acts close to carrying capacity, resulted in an extremely high rate of population growth rate at low population size leading to chaotic dynamics under harvesting (May 1976). This is biologically unrealistic and so I do not consider these models in the following chapter.

7.4.5 Limitations

7.4.5.1 *Individuals were grouped together in arbitrary size-classes*

Matrix models require the population to be divided into discrete classes (based on age or size). Ideally classes would group only individuals with similar demographic rates (Vandermeer 1978; Moloney 1986) but if classes are divided too finely data are too sparse to allow estimation of parameters. The size-frequency distribution of *A. granulimanus* was continuous (see Figure 2.5), with no obvious size-classes. The size-classes selected for modelling were therefore arbitrary, the only criteria being sufficient animals in each size-class to allow parameters to be estimated. Recent advances in continuous-state discrete-time modelling (Easterling *et al.* 2000) avoid the problem of arbitrary classes. So far

few studies have applied these 'integral projection models' but they are likely to become much used.

7.4.5.2 *Environmental stochasticity was not modelled*

Ideally data on vital rates should be collected over a number of years and stochasticity due to fluctuating environmental conditions modelled explicitly (Fieberg & Ellner 2001). In this study data collection was only carried out in two consecutive years, giving a single estimate of transition probabilities and no measure of inter-annual variation. No information on which to estimate environmental stochasticity was available so only deterministic models were built. Density-independent factors are likely to play important roles in the population dynamics of some crustaceans particularly in recruit survival (Botsford 1986; Caddy 1986). Species without planktonic larval stages are likely to be less vulnerable to environmental fluctuations and subject to lower levels of recruitment variability than species with planktonic larval stages (Fogarty *et al.* 1991). Crayfish exhibit relatively extended parental care, with the young carried by the mother for a number of moults after hatching; variability in recruitment is therefore likely to be lower than for other decapods (Fogarty *et al.* 1991). However all populations are affected by environmental variation and temperature (Karplus *et al.* 1998; Perez *et al.* 1998; Verhoef *et al.* 1998; Verhoef & Austin 1999), food availability (Brewis & Bowler 1983) and rainfall (Robinson *et al.* 2000; Acosta & Perry 2001) may all affect populations of *A. granulimanus*. Stochasticity will tend to reduce the predicted sustainable yield (Lande *et al.* 1994) and increase the probability of stock collapse (Fogarty & Idoine 1986). If stochasticity is correlated across vital rates within years, sustainable yield will be decreased further (Fieberg & Ellner 2001). The way in which stochasticity is incorporated and its strength will affect absolute predictions but will not generally change the rank order of management options (Fieberg & Ellner 2001; Ellner & Fieberg 2003; Kaye & Pyke 2003). The central recommendation from this study—to harvest larger individuals to maximise yield—is therefore useful, but little faith should be put in the absolute estimates of maximum outputs possible.

5.4.6 How useful is the modelling approach?

Only two years worth of data collection was carried out for this study resulting in a single set of transition parameters. Limited data sets are a common problem in building population models, particularly for species of conservation concern (Fieberg & Ellner 2001). There is a danger that producing a model creates the appearance of greater certainty than is due (Burmaster & Anderson 1994) and if data are too limited the predictions of population models should be treated with extreme caution and possibly even ignored (Coulson *et al.* 2001). In this study good estimates are available for survival, growth and fecundity parameters but no information is available on how these parameters vary temporally or how survival may be regulated by density. These uncertainties must be remembered when interpreting the results of the model.

That said, there is often significant value in simply building a model as it clarifies assumptions, integrates knowledge from available sources, forces rigorous reasoning, and can guide further data collection (Burgman & Possingham 2000). One of the clear outcomes from this study is our lack of knowledge of how density-dependence acts in wild crayfish populations. The difficulties in detecting density-dependence from a sequence of population estimates are well known (Hassell 1986) and further advances in our understanding of population regulation are likely to come from experimental tests (Fogarty *et al.* 1991). Density manipulation experiments are very difficult, but have been used successfully to investigate density-dependent survival (Keeley 2001) and fecundity (J. Gascoigne & R. N. Lipcius in prep.). Further such studies are necessary to reduce the uncertainty in models of population harvesting. However, it must be considered whether the effort required, relative to the value of the resource, makes such work a justified use of scarce conservation funds (Hockley *et al.* in press).

7.5 Summary

In this chapter I developed a series of size-structured population models of *A. granulimanus*, parameterised with information on survival, growth and fecundity presented in the previous two chapters. No information was available on density-dependent control of survival in *A. granulimanus* so I developed a number of models which differed in the way in which density regulated survival and in which size-classes were under density-dependent control. I used the models to investigate what proportion of each size-class should be harvested to provide the maximum sustainable yield in terms of biomass. The models are simple and do not explicitly take uncertainty in parameter estimation and the effects of environmental stochasticity into account. The results should therefore be treated with caution. All the models suggest that harvesting should focus on larger crayfish.

In the next chapter I use these models to investigate the likely sustainability of the current offtake rate of crayfish from the harvesting village of Vohiparara.

Chapter 8

Is crayfish harvesting in RNP sustainable at the current level?

“Efa ela mihintsy no nisaka orana izahay, efa fomban-drazanay io.”

“We have always collected crayfish; it is our tradition.” (Elder in Vohiparara)



Interviewing elders about perceived trends in harvest intensity and stock abundance provided useful information on the sustainability of the harvest.

8 *Is crayfish harvesting in RNP sustainable at the current level?*

8.1 Introduction

Wild meat and fish are important resources to local communities living in and around tropical forests throughout the developing world (Pimentel *et al.* 1997; Bennett & Robinson 2000; Milner-Gulland & Bennett 2003). Many such resources have been sustainably exploited for hundreds of years, or even millennia, but as human populations have increased, traditional resource management systems have broken down and new technologies have been introduced and many harvested species have become overexploited (see references in Robinson & Bennett 2000). This is a serious problem both to the communities who depend on the resources (Davies 2002; Milner-Gulland & Bennett 2003) and to those concerned with biodiversity conservation. There is therefore enormous interest in assessing the sustainability of extraction systems by communities in tropical forests. Unfortunately recognising whether a harvest is sustainable or not is problematic (Hilborn *et al.* 1995; Milner-Gulland & Akçakaya 2001). A pervasive problem in identifying overexploitation is that sustainable exploitation is dependent upon a growing population so it is necessary to reduce the population below its carrying capacity to take advantage of density-dependent increases in survival or productivity (Kokko *et al.* 2001). It is a common error to show that exploitation has reduced population density below its unexploited level and then infer that the harvest is unsustainable (Robinson & Redford 1994; Sutherland 2001).

There are many possible ways of assessing whether a harvest is sustainable, although the lack of data on exploited species in tropical forests is a consistent problem for each of them (Robinson & Redford 1994). The simplest approach is to compare the population density between harvested and

unharvested sites (Robinson & Redford 1994). However, sites may vary naturally in their density due to physical differences (Emmons 1984) and, as mentioned above, reduced density through harvesting does not necessarily indicate an unsustainable harvest. Monitoring changes in density at a single site over time is more useful; ongoing decline, or sudden stock collapse, indicates unsustainable exploitation. This method, commonly used in western fisheries (Shepherd *et al.* 2001; Myers & Worm 2003) requires information on trends in population size over time, seldom available for exploited species in developing countries (Robinson & Redford 1994 but see Silva & Strahl 1991). It is generally easier to monitor changes in harvests than to monitor populations (Sutherland 2001), and where temporal information on catches are available, trends in Catch Per Unit Effort (CPUE) can be used to indicate the sustainability of a harvest (e.g. Vickers 1991). However, this approach is fraught with confounding errors such as changes in technology or in the area exploited, and a stable CPUE may indicate either sustainable exploitation, or that decreases in abundance are compensated for by increased efficiency (Robinson & Redford 1994; Sutherland 2001). Comparing the age-structure of exploited and unexploited populations has been proposed as another way of measuring the sustainability of a harvest but since methods of aging individuals and the demographic information to interpret such age-structures are not available for most exploited tropical species, the method has very limited application (Robinson & Redford 1994).

Many recent studies aimed at assessing the sustainability of extraction of wildlife resources in tropical forests estimate offtake and compare this with what the population could theoretically produce. Simple algorithms, such as the Robinson and Redford index (Robinson & Redford 1991), which require few parameters and give crude estimates of sustainable yields, are commonly used to provide such theoretical maximum offtakes in studies of bushmeat harvesting in tropical forests (Fa *et al.* 1995; Muchaal & Ngandjui 1999; Alvard 2000; Robinson & Bennett 2000). However, such indices may be poor at maximising offtake for a given risk of overexploitation (Milner-Gulland & Akçakaya 2001): a serious cause for concern as hunting is a vital economic activity for many tropical

people. Size-structured population models will tend to perform better than crude indices, particularly where the value of individuals of different size varies (Boot & Gullison 1995; Kokko *et al.* 2001; Milner-Gulland & Akçakaya 2001).

In this chapter I investigate the sustainability of the harvest of *A. granulimanus* in Ranomafana National Park (RNP) using two methods. I use the first two of Bennett and Robinson's criteria for ecological sustainability (see section 1.2 and Bennett & Robinson 2000), as there is not sufficient information on the role of crayfish in river ecosystems to judge whether harvest levels affect crayfishes' ecological function. Firstly, in what I term the comparative approach, I compare the population density and structure of the three size-classes across sites exposed to different levels of harvesting. To interpret these results it is necessary to know what has happened to the harvest over time. I use interviews with elders in the heavily harvesting village of Vohiparara to establish how long crayfish have been harvested in the area and the likely trend in the level of harvesting effort over time. Secondly, in what I call the modelling approach, I use the size-structured density-dependent population models developed in chapter seven to estimate the maximum sustainable yield from various areas surrounding Vohiparara village and compare this with the true offtake from Vohiparara in the year 2003/2004 and the area available to the harvesters.

8.2 Methods

8.2.1 The comparative approach

8.2.1.1 *Population estimates*

Between November 2001 and April 2003, we carried out five consecutive days of mark-and-recapture at 79 sites across a range of harvesting intensities (see Figure 2.3). The level of crayfish harvesting in the Ranomafana area is strongly affected by local taboos (*fady*; see section 4.3.1.2). The sites were within the area harvested by the non-*fady*, heavily harvesting villages of Sahavondronana (six sites) or Vohiparara (31 sites), or in *fady* areas (37 and five

sites accessed from the *fady* villages of Bevoahazo and Andemaka respectively; Figure 8.1).

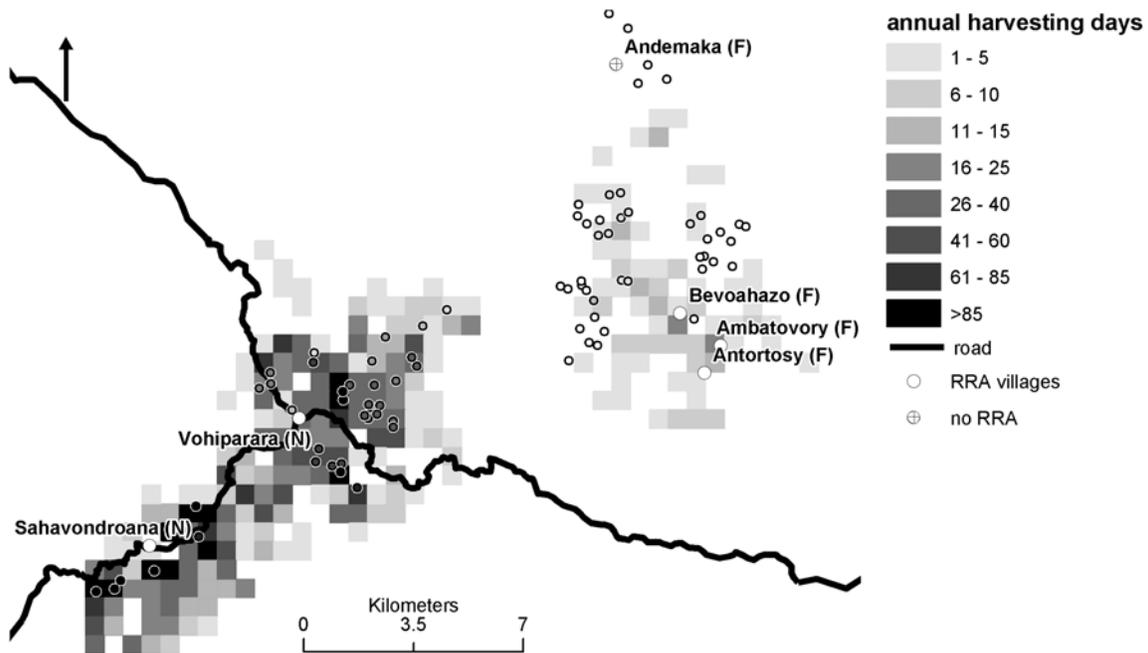


Figure 8.1 The study area showing mark-and-recapture sites and nearby villages. Villages which are *fady* for commercial crayfish harvesting are marked (F) and non-*fady* villages are marked (N).

The number of small (22-34.9 mm CL), medium (35-49.9 mm CL) and large (> 50 mm CL) crayfish was estimated at each site using model averaging in a closed population model framework in programme MARK (see section 2.2.3.5).

8.2.1.2 *Habitat variables*

At each site, consisting of 100 m length of river, we recorded habitat variables so the effect of habitat variability could be controlled for and the effect of harvesting on population size investigated. Habitat variables measured were: river width every 10 m, river depth at 0.5 m intervals across the stream every 10 m of its length, and percentage cover of small (< 0.2 m longest length), medium (0.2-1m) and large (> 1m) rocks for each 10 m section. We gave a bank score out of 20 for each 10 m section of river based on the number of metres of each side of bank which were suitable for burrowing, i.e. had an adequately steep soft substrate. I averaged these bank scores and the scores for percentage cover of

the various rock types over the 10 sections to give a mean value per site for each measure. We took measurements between November and April so it was necessary to standardise depth measurements for rainfall. We measured a sub-sample of the rivers (33/79) between three and six times throughout the year. I built Generalised Linear Models (GLMs) using mean monthly rainfall statistics (see Figure 2.2), for both maximum depth ($r^2 = 0.69$) and average depth ($r^2 = 0.80$), using site as a factor and mean monthly rainfall as a covariate. For the GLM describing maximum depth, both rainfall ($F_{1,154} = 5.22$, $p < 0.001$) and site ($F_{78,154} = 11.64$, $p < 0.001$) were significant. Similarly for the GLM predicting average depth both rainfall ($F_{1,154} = 8.02$, $p < 0.001$) and site ($F_{78,154} = 8.89$, $p < 0.001$) were significant. I used the GLMs to predict maximum depth and average depth for all sites for a standardised month with mean rainfall.

8.2.1.3 *The effect of harvesting on the size and structure of populations*

To investigate what factors affected the size and structure of crayfish populations found at sites, I built GLMs for each size-class (small, medium and large) separately. Population size of each size-class, as estimated from programme MARK, was entered as the response variable, square root transformed where necessary to ensure normally-distributed residuals of the minimal model. Habitat variables (mean river width, mean depth, maximum depth, % cover of small, medium and large rocks, and bank score) and a surrogate for harvesting intensity were entered as predictors. I used two surrogates for harvesting intensity:

- I) Distance from, and type of, the nearest village:

The study area contains sites which are in within the harvesting distance of heavily-harvesting, non-*fady*, villages and others which are out of the maximum range of harvesters and effectively accessible only from *fady* villages. The distance from the nearest village was entered as a covariate and the area (*fady* or non-*fady*) entered as a factor. Distance was the straight-line distance from the nearest village measured using ArcGIS 8.3.

II) Number of harvesting days, from the interview data:

The number of harvesting days at each mark-and-recapture site was estimated using the data from the Rapid Rural Appraisal (RRA) interviews carried out in five villages (see section 4.2.5). We did not do interviews in Andemaka so harvest intensity was not known for the five sites close to this village and they were therefore excluded from the analysis.

8.2.1.3 *The history of crayfish harvesting in Vohiparara*

We carried out interviews to investigate the history of crayfish exploitation in the area (see section 2.2.6.2). We used a historical matrix (Freudenberger 1998) with a group of ten elders and other villagers to investigate how long the village had been in its current position and general trends in the number of crayfish harvesters. Important events in recent village history (in 1958 and 1980) and the present (2001) were used as reference points. The group discussed each question (e.g. the number of people in the village) and placed beans on the matrix to indicate relative trends. Only in the case where elders were asked to estimate the number of people in Vohiparara did the beans relate to something tangible: in this case households. In response to other questions the beans indicated relative trends only. The results appearing on the matrix were often less important than the discussion which surrounded the placing of the beans.

During RRA interviews with harvesting households in Vohiparara, we asked some harvesters their opinion on trends in crayfish availability since the establishment of the Park in 1991. These data are not quantitative but give an impression of harvesters' perception of temporal changes in crayfish abundance.

8.2.2 The modelling approach

8.2.2.1 *The models*

In chapter seven I developed a number of models to describe the population dynamics of *A. granulimanus*. Here I use two sets of these models which differ in the form of density-dependence: linear density-dependence (models 2) and non-linear with density-dependence acting far from the carrying capacity (models 3; see Table 7.2). I did not use models 4 (with density-dependence acting close to carrying capacity) in this chapter, as they were likely to overestimate sustainable yield (see section 7.4.4.3). Each model included a number of sub-models which differ in where in the life cycle density-dependent regulation of survival occurs, and in the relative contribution of the various size-classes to regulation (sub-models a-d; see Table 7.2). In total I used eight models in this chapter (models 2a-d and 3a-d).

8.2.2.2 *Estimating the number of crayfish available*

To estimate the carrying capacity of crayfish available to harvesters from Vohiparara, I estimated the length of rivers of each type (temporary streams, first-order, second-order, etc: see Figure 6.1) available within various distances of Vohiparara using ArcGIS 8.3 (see Figure 8.2). I estimated the number of crayfish available in unharvested first, second and third-order streams by multiplying the length available by the estimate of the number of crayfish per km in each size-class for each type of stream (see Figure 6.2). We did not carry out mark-and-recapture in what are marked on the maps as temporary streams or in rivers larger than third-order, so no estimates of population size in these rivers were available. I therefore used information on the density of crayfish in first, second and third-order streams and made two sets of assumptions: conservative and generous, as to the number of crayfish per unit length in temporary and fourth, fifth and six-order streams.

I consider temporary streams first. The maps from which the rivers were digitised were made from aerial photographs and the presence of small streams on the map, and their classification as permanent or temporary, was mostly inferred from topography; it is unlikely to be perfectly accurate. We verified in the field that streams marked as temporary tended to be smaller than those marked as permanent and some were only flowing seasonally, although permanently wet with standing water and saturated soil. Such streams, despite being small were likely to hold important populations of crayfish. Other streams marked as temporary on the map were equivalent in size to many first-order streams, while still others which existed on the ground did not appear on the map. Under the conservative set of assumptions, I assumed that temporary streams had half the number of crayfish per km found in first-order streams. Under the generous assumptions, I assumed temporary streams had the same number of crayfish per km as first-order streams.

Similarly mark-and-recapture was not carried out in rivers larger than third-order. The number of large crayfish tended to be higher in second and third-order streams than in smaller first-order streams (see Figure 6.2); in addition, the number of medium crayfish was dependent on the width and number of large crayfish on the depth of rivers (see Table 8.1 and Table 8.2 below), both of which increase with river order. This suggests that there were more crayfish per unit length in large rivers than in smaller ones. Under the conservative assumptions I therefore assumed that fourth, fifth and sixth-order rivers had twice the number of crayfish as second and third-order streams. Under the generous assumptions I assumed that fourth, fifth and sixth-order rivers had five times the density of second and third-order streams.

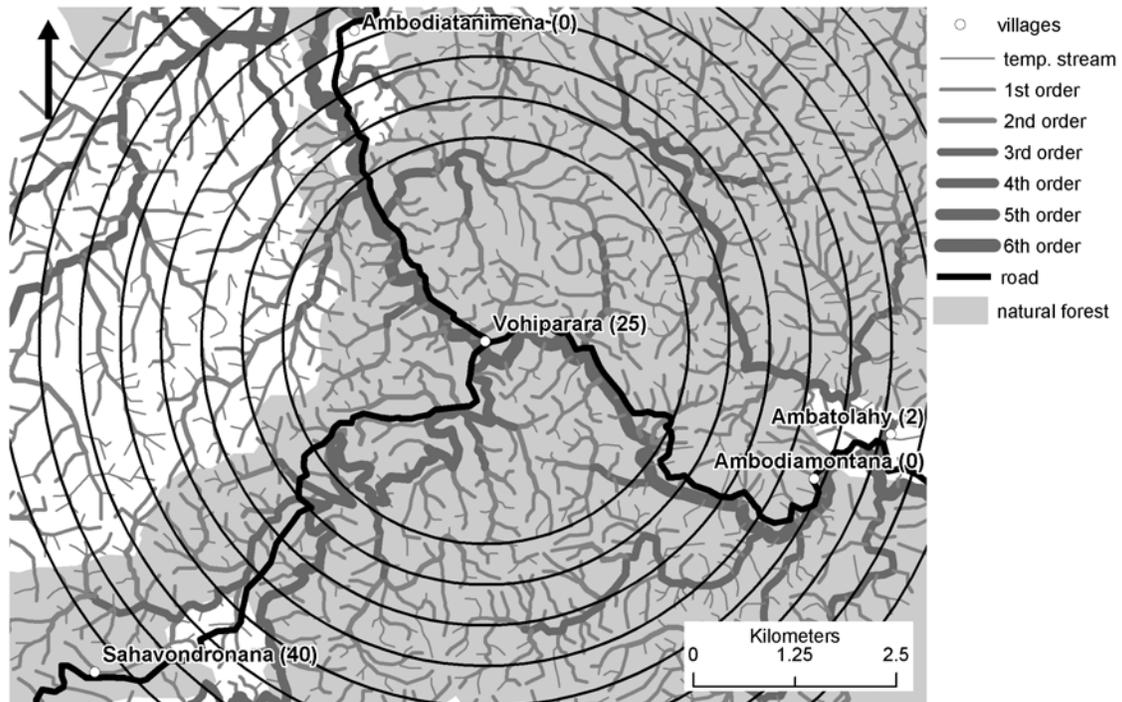


Figure 8.2 The rivers surrounding Vohiparara within distances from the village marked as circles of 2.5 to 6.0 km radius at 0.5 km intervals. Other villages in the area are also shown, with the number of harvesting households in brackets (see Figure 4.2).

8.2.2.3 *The relationship between the size-structure caught and distance travelled*

All harvested sites were unlikely to receive equal number of visits from harvesters; therefore the size structure and the structure of what was harvested was likely to vary between sites. To test this, I investigated the relationship between distance from the village and I) the mean carapace length (CL) of batches, and II) the proportion of crayfish in a batch which were large (> 50 mm CL), using 442 batches of crayfish measured in the daily interviews (see section 2.2.6.3) for which all the necessary information was available. I fitted a linear function to the relationship between average carapace length of crayfish in a catch and distance from Vohiparara and a binomial function to the proportion of large crayfish caught with distance from Vohiparara.

8.2.2.4 *The number of crayfish harvested each year in Vohiparara*

The total number of *A. granulimanus* harvested in Vohiparara in 2003/2004 was 51,017; 5% of these were small, 75% medium and 20% large (see section 4.3.2.1). This corresponded to 2550 small, 38,250 medium and 10,200 large crayfish. As the harvest was not taken from a single population, exposed to identical harvesting and therefore with the same age structure, I converted the harvest into biomass of economically sized crayfish (medium or large) for ease of comparison between offtake and predicted sustainable yield. The mean mass (estimated from equation 4.1) of large crayfish (68.2 g) was twice that of medium crayfish (34.0 g). Harvesters in Vohiparara therefore collected 1996 kg of economically sized crayfish in the year 2003/2004.

As small crayfish are very abundant (67% of the population at carrying capacity) and made up a tiny proportion of the harvest (5%; see section 4.3.2.1) I do not consider them in the results presented. However, under all the models tested, more than 2550 small crayfish could have been harvested sustainably.

8.2.2.5 *The area needed to provide the observed harvest sustainably*

I ran each model using the carrying capacity of crayfish in successively larger areas around Vohiparara, expanding these by 0.5 km radius at each step. Harvesters use methods (fishing with sticks with worms tied to the end and turning over large rocks) that are selective for larger crayfish. I assumed that the techniques were equally successful for medium or large crayfish thereby catching an equal proportion of the crayfish present in each size-class. I assumed that a much lower proportion (50 times lower) of the small crayfish present were encountered with the method. I assumed that any crayfish caught was harvested regardless of size. I ran simulations in programme ULM (Legendre & Clobert 1995) and found the maximum sustainable yield for each starting population size for each model.

8.2.2.6 *The area available to harvesters from Vohiparara*

The maximum distance travelled by crayfish harvesters from Vohiparara was 6.3 km (see Figure 4.6). However to assume that all the area within a 6.3 km radius of Vohiparara was available exclusively to harvesters from Vohiparara would be to ignore the presence of other harvesting communities in the area. I used information on the spatial arrangement of other villages and their involvement in crayfish harvesting, to estimate an approximate area of forest to which Vohiparara harvesters had essentially exclusive access.

8.3 Results

8.3.1 The comparative approach

8.3.1.1 *Distance to village as a surrogate for harvest intensity*

Controlling for the effect of significant habitat variables, there were significantly fewer large crayfish in non-*fady* areas (those sites likely to be influenced by commercial crayfish harvesters) than in *fady* areas (Figure 8.3c; Table 8.1). There was no significant effect of the distance from the nearest village, suggesting that large crayfish were equally depleted at all distances (up to 5.8 km, the maximum distance of a mark-and-recapture site from a non-*fady* village in this study). The number of medium crayfish at a site was not influenced by the distance to the nearest village or whether it was in area influenced by *fady* or non-*fady* villages (Figure 8.3b; Table 8.1) i.e. there appeared to be no influence of harvesting on the number of medium-sized crayfish at a site. There was a weak positive relationship between distance from the nearest village and the density of small crayfish. However there were more small crayfish at sites potentially impacted by commercial harvesting villages than in sites in areas where the nearest villages are *fady* for crayfish harvesting (Figure 8.3a; Table 8.1).

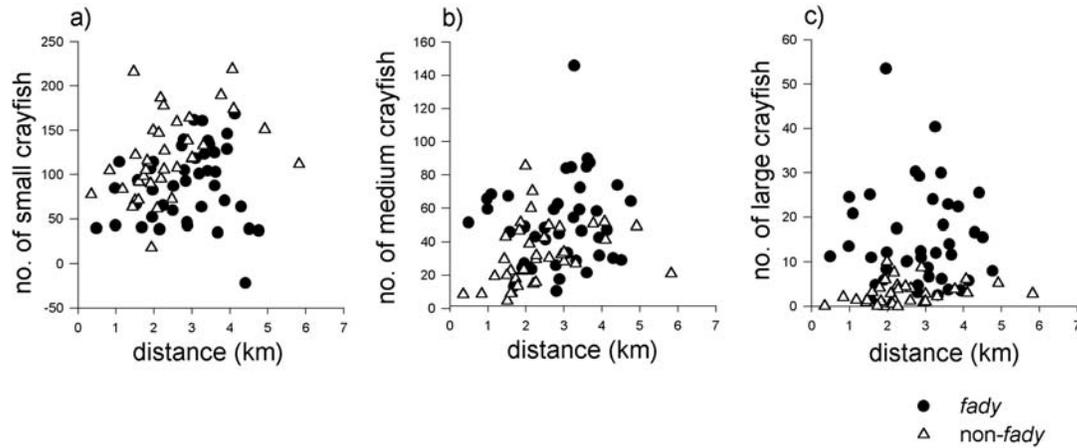


Figure 8.3 The relationship between the number of (a) small, (b) medium and (c) large crayfish per site and distance from the nearest village in *fady* (circle) and *non-fady* (triangle) areas, adjusted for the effect of significant habitat variables (see Table 8.1).

Other variables which had a significant influence on the number of crayfish at a site (Table 8.1) were: average stream width (small and medium crayfish), percentage cover of big rocks (small crayfish) and percentage cover of small rocks (small and large crayfish).

Table 8.1 GLM of the factors affecting population size of small, medium and large crayfish using distance from, and type of, the nearest village as a surrogate for harvesting intensity. The response variable is the number crayfish in a 100 m transect (square root transformed in the analysis of large crayfish). The minimal model comprised only significant terms, $n = 79$ sites. Significant terms are shown in bold.

explanatory terms		small ($r^2 = 0.47$)		medium ($r^2 = 0.14$)		large ($r^2 = 0.52$)	
<i>name</i>	<i>d.f.</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
ave. depth (cm)	1	2.43	0.123	1.24	0.271	1.80	0.183
max. depth (cm)	1	1.71	0.195	1.34	0.232	2.58	0.112
ave. width (m)	1	11.90	0.001	13.13	<0.001	2.04	0.982
% cover of large rocks	1	6.98	0.011	1.37	0.246	0.25	0.618
% cover of medium rocks	1	1.17	0.283	2.77	0.100	0.00	0.982
% cover of small rocks	1	19.5	<0.001	1.45	0.232	17.92	<0.001
bank score	1	0.00	0.123	0.27	0.608	0.71	0.403
distance from village (km)	1	4.96	0.029	1.01	0.319	0.32	0.571
<i>fady</i> / <i>non-fady</i> area	1	13.38	<0.001	1.65	0.203	63.99	<0.001
<i>minimal model</i>		<i>effect</i>	<i>SEM</i>	<i>effect</i>	<i>SEM</i>	<i>effect</i>	<i>SEM</i>
constant		39.6	22.1	20.95	6.30	4.65	0.30
ave. width (m)		25.75	5.47	7.53	2.08	/	/
% cover big rocks		-3.28	1.24	/	/	/	/
% cover small rocks		6.28	1.49	/	/	-0.146	0.0345
distance from village (km)		0.0108	0.00511	/	/	/	/
<i>fady</i>		0	0	/	/	0	0
<i>non-fady</i>		37.20	11.30	/	/	-2.10	0.26

8.3.1.2 Interview data as a surrogate for harvest intensity

Controlling for other significant variables, there was a significant negative effect of the number of harvester days on the number of large crayfish found at a site (Figure 8.4c; Table 8.2). However, the number of annual harvesting days at a site did not significantly predict the number of small or medium crayfish (Figure 8.4a,b; Table 8.2).

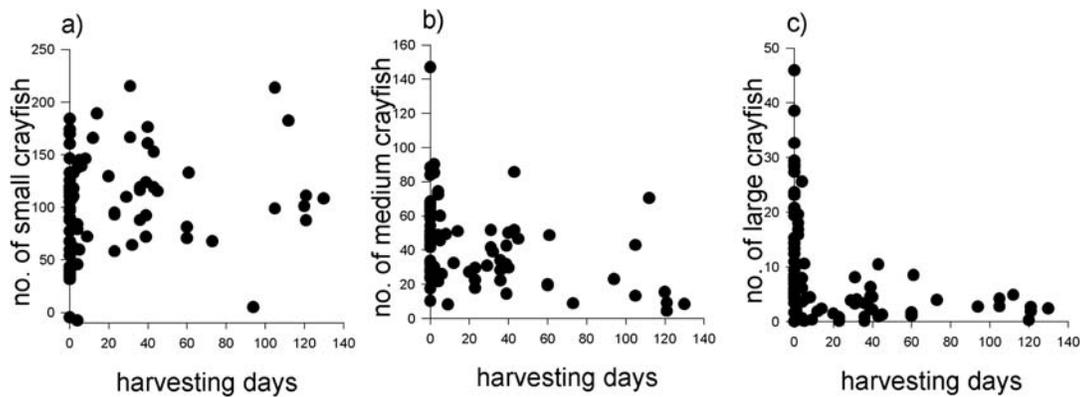


Figure 8.4 The relationship between the number of small (a), medium (b) and large (c) crayfish per site and annual number of harvesting days at that site, adjusted for the effect of significant habitat variables (see Table 8.2).

Other variables which had a significant influence on the number of crayfish at a site (Table 8.2) were: maximum stream depth (large crayfish), average width (small and medium crayfish) % cover of big rocks (small crayfish) and % cover of small rocks (small and large crayfish).

Table 8.2 GLM of the factors affecting population size of small, medium and large crayfish using number of harvester days (from interview data) as a surrogate for harvesting intensity. The response variable is the number of crayfish in a 100 m transect (square root transformed in the analysis of large crayfish). The minimal model comprised only significant terms, $n = 74$ sites. Significant terms are shown in bold.

explanatory terms		small ($r^2 = 0.46$)		medium ($r^2 = 0.16$)		large ($r^2 = 0.33$)	
<i>name</i>	<i>d.f.</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
ave. depth (cm)	1	1.31	0.257	1.57	0.214	2.76	0.101
max. depth (cm)	1	1.44	0.235	2.23	0.140	5.41	0.023
ave. width (m)	1	16.5	<0.001	14.89	<0.001	2.93	0.091
% cover of large rocks	1	8.06	0.006	1.49	0.226	2.09	0.153
% cover of medium rocks	1	1.84	0.179	3.34	0.072	0.56	0.457
% cover of small rocks	1	24.8	<0.001	0.48	0.492	6.27	0.015
bank score	1	0.01	0.909	0.45	0.506	1.33	0.252
harvester days	1	0.96	0.331	1.99	0.163	18.56	<0.001
<i>minimal model</i>		<i>effect</i>	<i>SEM</i>	<i>effect</i>	<i>SEM</i>	<i>effect</i>	<i>SEM</i>
constant		13.10	17.90	19.37	6.14	3.107	0.465
max. depth (cm)		/	/	/	/	0.0313	0.0134
ave. width (m)		21.40	5.27	7.78	2.02		
% cover big rocks		-3.83	1.54	/	/		
% cover small rocks		7.81	1.35	/	/	-0.104	0.0414
harvester days		/	/	/	/	-0.0176	0.00429

8.3.1.3 *The history of crayfish harvesting in Vohiparara*

The historical matrix produced with elders from Vohiparara is shown in Figure 8.5.

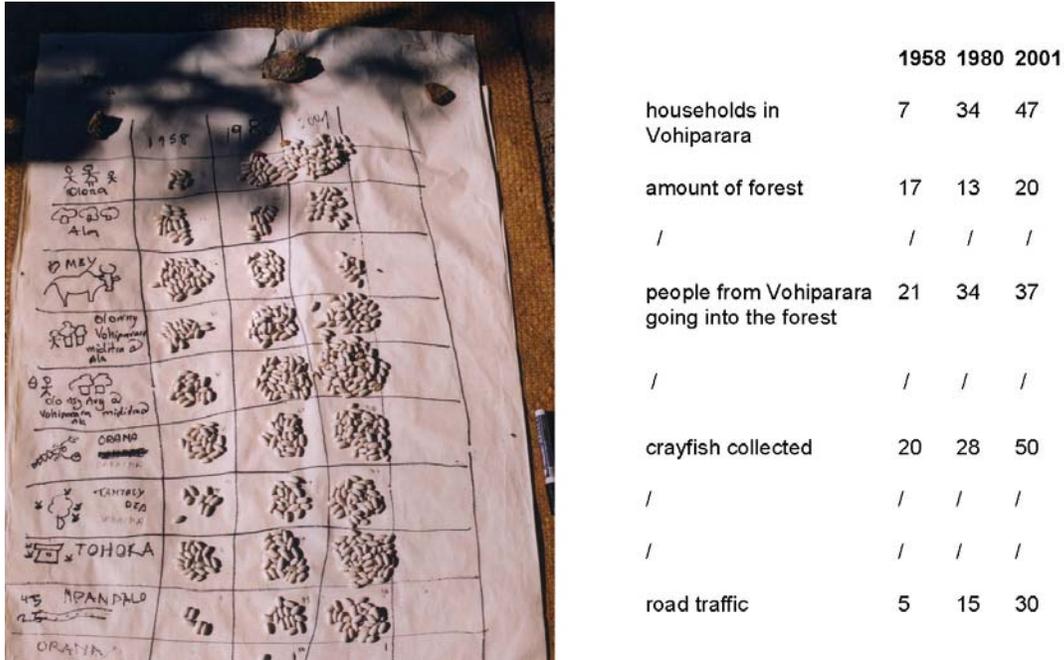


Figure 8.5 The results of the historical matrix carried out with a group of approximately ten people, most elders, in Vohiparara in January 2002. For simplicity, only terms discussed in the text are translated in the panel on the right.

Vohiparara moved to its present site from its former location slightly to the north, approximately 70 years ago. The population increased greatly between 1958, when there were approximately 7 households, and 1980, when there were about 34. Population growth rate was much less between 1980 and the present; today the village is home to 47 households (Figure 8.5). By 1958 commercial timber logging operations had started working in the area. This peaked in the 1980s and ceased with the establishment of Ranomafana National Park in 1991, indicated on the matrix by less forest cover in 1980 relative to 1958 and 2001.

Crayfish have been exploited in Vohiparara for as long as anyone can remember, probably since people first came to the area. One middle-aged crayfish harvester, who started aged 15, said that his father, grandfather and his

father before him had collected crayfish. However, in the past, crayfish were collected for subsistence use only. Sometime between 1958 and 1980 collecting crayfish for sale became important, part of a general shift in the village economy away from reliance on agriculture to dependence on selling forest products. This is indicated by an increase in the number of Vohiparara people going to the forest between 1958 and 1980 on the historical matrix; this number apparently did not increase between 1980 and 2001 (Figure 8.5).

The above question indicated that the number of people using the forest has stayed relatively constant since 1980, Unfortunately the historical matrix did not provide us with direct information on the change in number of crayfish harvesters through time. The question ‘how many people harvested crayfish as their primary source of income at each point in time?’ was not answered and a rather different question discussed: that of the number of crayfish harvested per year. The increase recorded on the historical matrix in the number of crayfish collected between 1980 and 2001 cannot be interpreted as being due to an increase in pressure as the discussion on this question was dominated heavily by one man who was trying to make a point that there are more crayfish available today than in the past.

The elders reported that the number of road users has increased steadily since 1958. This may be significant as it could represent a substantial increase in the market for crayfish between 1980 and 2001. However when asked directly if the market for crayfish has grown they said that in the 1980s, during the peak period of timber extraction, there were also many people in the area buying crayfish and there was no general agreement as to whether the market for crayfish has grown since 1980.

During individual interviews with harvesters we attempted to establish whether the size and abundance of crayfish has changed during the decade since the establishment of the National Park. There was no general agreement between harvesters and a wide range of opinions were expressed. A few stated

that it is harder finding crayfish today than in the past. However, others reported that their family have always lived off crayfish and there has always been the same number of crayfish available. Most harvesters agreed that they have to go far into the forest to get very large crayfish. Opinions were divided as to how long this has been the case but it was generally acknowledged that it has been so for some time, probably since before the Park was set up in 1991.

8.3.2 The modelling approach

8.3.2.1 *Estimating the number of crayfish available*

The length of streams and rivers available within distances from 2.5 to 6.0 km of Vohiparara is shown in Figure 8.6a. Figure 8.6b shows the estimated number of large crayfish at carrying capacity found within the various radii of Vohiparara under conservative and generous assumptions about the density of crayfish in streams for which density information is not available.

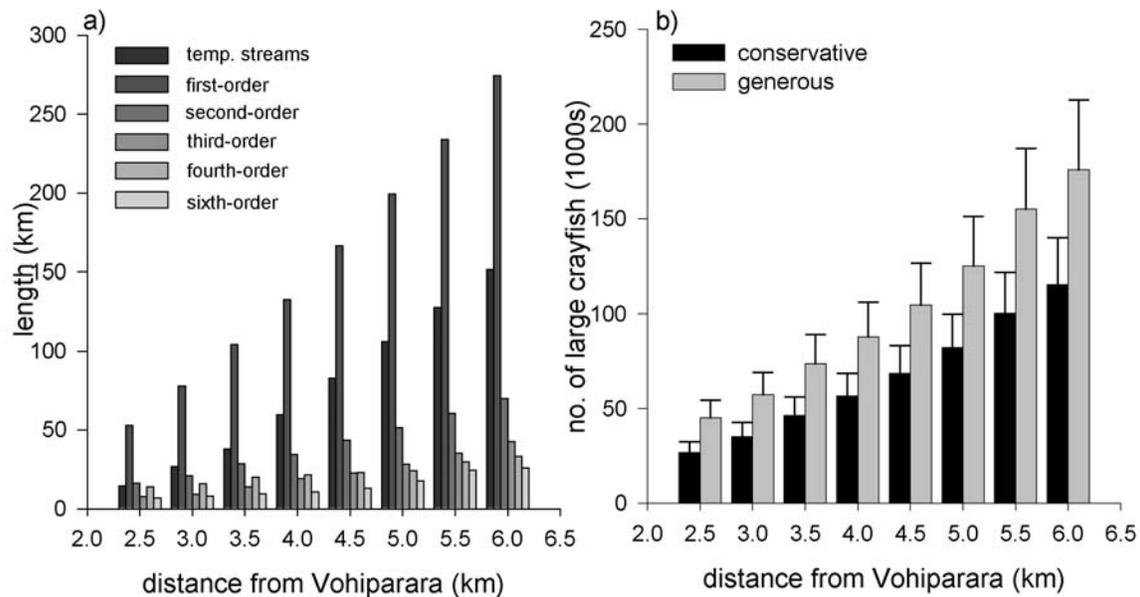


Figure 8.6 The length of streams and rivers (a) and the carrying capacity of large crayfish under conservative and generous assumptions regarding the density of crayfish in streams (b) available within various distances of Vohiparara. Error bars show SEMs.

8.3.2.2 *The relationship between the size-structure caught and distance travelled*

Measurements of batches of crayfish caught by harvesters brought to the daily interviews in Vohiparara (see section 2.2.6.3) show that harvesters tended to find more large crayfish further from the village. Both the proportion of large crayfish in a batch ($F_{1,441} = 90.39$, $p < 0.001$; Figure 8.7a) and mean carapace length ($F_{1,441} = 37.26$, $p < 0.001$, $r^2 = 0.078$; Figure 8.7b) increased with distance from Vohiparara.

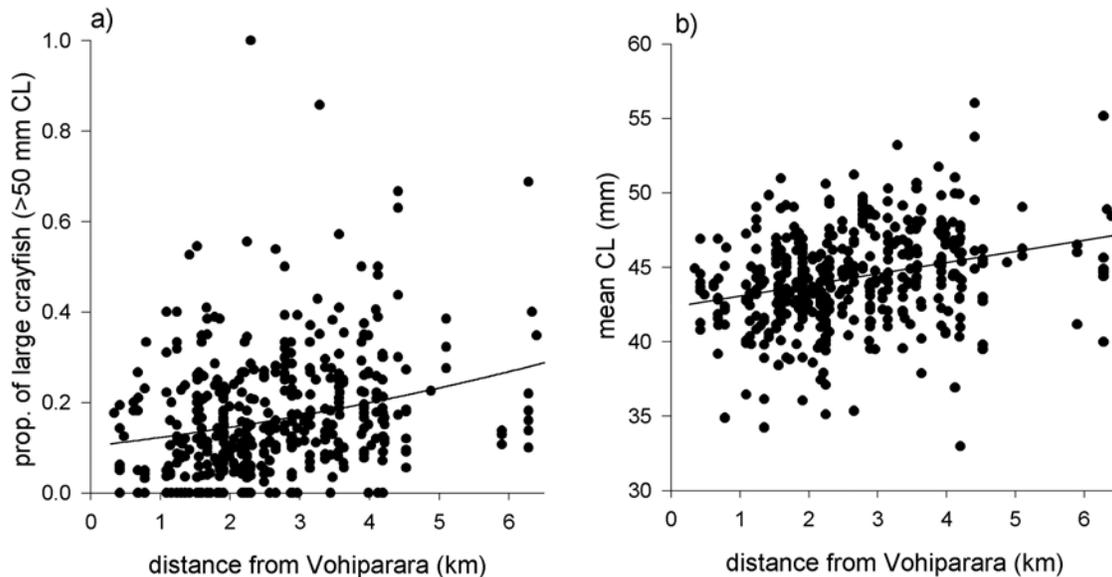


Figure 8.7 The relationship between distance from Vohiparara and (a) the proportion of large crayfish in batches and (b) the mean carapace length of batches.

However, the slopes of the relationships were very shallow and distance from Vohiparara explained only a small amount of the variance. So although harvesters found larger crayfish the further they travelled, this effect was very weak. For example moving 6.3 km away from Vohiparara was associated with a mean change in carapace length of less than 5 mm.

8.3.2.3 *The area needed to provide the observed harvest sustainably*

Figure 8.8a below shows the biomass of economically important crayfish (medium or large) that could be sustainably harvested from the area within certain distances of Vohiparara under the different models, with the conservative estimate of carrying capacity. This is compared to the biomass harvested by Vohiparara in the year 2003/2004. Figure 8.8b shows the same information but using the generous assumptions concerning carrying capacity. Models 2 (with linear density-dependence) suggest a higher sustainable harvest than models 3 (density-dependence acting away from carrying capacity). Models where density-dependence is operated by biomass (a and b) show greater yields than those operated, at least in part, by number (c and d). Under generous assumptions (model 2a and b, with generous assumptions concerning carrying capacity), the Vohiparara crayfish harvest of 2003/2004 could have been obtained sustainably within an area enclosed by a radius 3.5 km from Vohiparara. Under the most conservative assumptions (model 3c with conservative assumptions concerning carrying capacity) an area within a 5.5 km radius of Vohiparara would have been necessary.

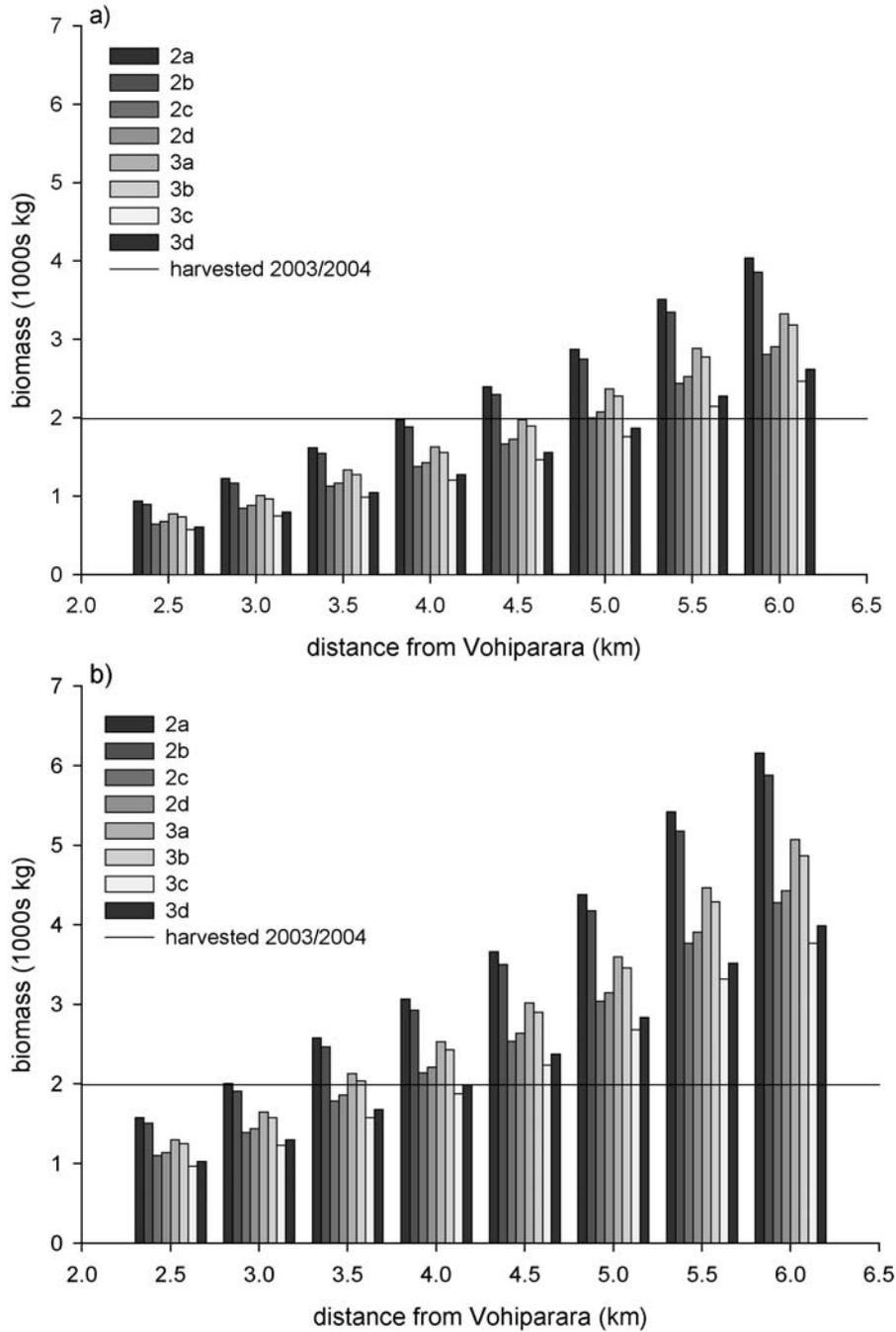


Figure 8.8 The maximum biomass yield of medium and large crayfish for the various models with (a) more generous, and (b) more conservative estimates of carrying capacity, compared with the offtake by harvesters from Vohiparara in 2003/2004 (horizontal line).

8.3.2.4 *The area available to harvesters from Vohiparara*

The four closest villages to Vohiparara (Amboditanimena [4.1 km], Ambodiamontana [4.1 km], Ambatolahy [5.1 km] and Ambodiriana [6.0 km]) carry out very little harvesting (Figure 8.9). Amboditanimena and Ambodiamontana have no households commercially harvesting crayfish and Ambatolahy has just two part-time harvesters (see section 4.3.1.1). However, the village of Sahavondronana, just over 6.2 km to the west of Vohiparara, is heavily reliant on crayfish harvesting (see section 4.3.1). The village of Ambalakindresy (10 km north of Vohiparara) also harvests crayfish, although the village was not visited in this study and the level of harvesting there is unknown. It is difficult to know what effective area is available exclusively to harvesters from Vohiparara but the nearest site to Vohiparara that Sahavondronana harvesters reported harvesting at during the RRA interviews was 3.1 km from Vohiparara.

Taking this information into account I estimated that Vohiparara harvesters had exclusive access south of the major Namorona river up to 3.1 km from Vohiparara, and that beyond this point harvesters from Sahavondronana impact the forest (Figure 8.9). North of the Namorona I assume that Vohiparara harvesters have essentially exclusive access up to 5.5 km away, with some limited harvesting by the part-time harvesting households in Ambatolahy and some subsistence collecting close to the village of Amboditanimena. Beyond 5.5 km harvesters from Ambalakindresy may impact the forest. This gives a total area of 58 km²: equivalent to a circle of radius 4.3 km from Vohiparara village.

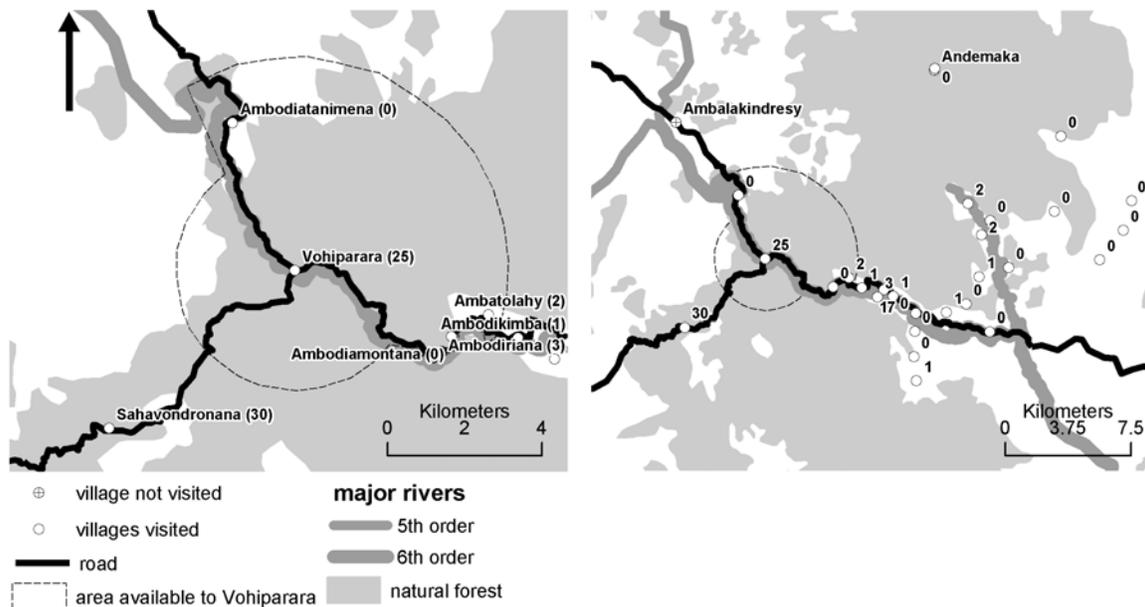


Figure 8.9 The villages surrounding Vohiparara showing the approximate number of households involved in commercial crayfish harvesting in parentheses.

8.4 Discussion

8.4.1 The comparative approach

8.4.1.1 Does harvesting affect crayfish population density and structure?

The two surrogates for harvesting intensity I used gave similar results. In both analyses the number of large crayfish at a site was negatively affected by harvesting intensity whereas no affect was detected on the number of medium-sized crayfish. One of the surrogates (distance from the nearest village and whether it was *fady* or not) suggested that small crayfish are more abundant under harvesting: there were significantly more small crayfish in non-*fady* (commercially harvesting) areas than *fady* areas. This could indicate a density-dependent response of higher survival or faster growth of young of the year and small crayfish at harvested sites where larger crayfish have been removed. However, this result was not seen using the other surrogate of harvest intensity, and so should be treated with caution.

8.4.1.2 *The accuracy of the surrogates of harvest intensity*

The harvest level at each site could not be known perfectly. However two independent surrogates were available as a measure of harvest intensity: I) a measure combining distance from the nearest village and whether it was a *fady* or non-*fady* area (i.e. likely to be exposed to commercial harvesting or not), and II) a measure of annual number of harvesting days at a site based on the interview data carried out in the five villages most likely to impact on the sites. The first assumes that harvesting is more intense close to settlements rather than further away. This assumption makes intuitive sense as the costs (in terms of travel time) are lower for harvesting at near sites, and many studies have shown hunting pressure is much greater closer to communities (e.g. Mittermeier 1991; Muchaal & Ngandjui 1999). Using distance to the nearest village only (rather than some measure such as population size within a given distance) makes sense in the local context as the RRA data suggested clearly that the sites in non-*fady* areas (the 37 sites close to Sahavondronana or Vohiparara) are likely to be influenced only by the nearest of those villages. The sites close to Bevoahazo (37 sites) could in principle be affected by any of the nearby villages (Bevoahazo, Antortosy, Ambatovory) but since crayfish harvesting in the forest is very low by any of these villages (see Figure 4.12) it is unlikely that these villages impact the sites. The five Andemaka sites are very close to the village and therefore Andemaka people are likely to be the main harvesters. The sites in *fady* areas (Bevoahazo and Andemaka sites) are far enough away from Vohiparara or Sahavondronana to be unaffected by harvesters from these villages (see Figure 4.6).

The straight-line distance to a village from a site is, however, not the only factor likely to affect harvest intensity at the site. Sites which are hard to get to due to lack of paths or difficult river crossings may receive less harvesting than expected, as will sites which are close to tombs. Using the interview data as a surrogate for harvesting intensity should account for these preferences and may therefore be preferable.

Both of the surrogates of harvest intensity do not take account of harvesting by outsiders. The forest to the north-east of Bevoahazo is sporadically used by illegal gold-miners (see section 4.3.4). The miners are likely to eat crayfish when camped in the forest, but their numbers are few and therefore their impact is likely to be relatively small. A potentially more important error would be if harvesters from distant harvesting communities such as Ambalakin-dresy occasionally harvest at the sites to the north of Bevoahazo. However, excluding these sites from the analysis does not affect the results and I am confident that most of the variation in harvesting intensity between sites was captured by my surrogates.

8.4.1.3 Is crayfish harvesting sustainable in the Ranomafana area?: conclusions from the comparative approach

The mark-and-recapture study suggests that the density of large crayfish is reduced under harvesting by the villages of Vohiparara and Sahavondronana, but the density of small and medium crayfish is unaffected (and the density of small crayfish may even be higher under harvesting). Medium-sized crayfish currently make up 75% of the catch in Vohiparara. If such medium-sized crayfish have formed the basis of the harvest for some time, this would imply that the harvest has been sustained. However, if the harvest has recently increased, this pattern could simply mean that large crayfish have been removed and only now are harvesters turning their attention to medium crayfish and soon this size-class will also be depleted. The interview data are therefore essential to the interpretation of the results of the mark-and-recapture study. I use three lines of evidence below to argue that the crayfish harvest in Vohiparara is likely to be at equilibrium.

- I) Crayfish have been harvested commercially for more than 20 years

The interview data presented in this chapter suggest that commercial crayfish harvesting has been important in Vohiparara since between 1958 and 1980. This agrees with the findings of other researchers who worked in the area

in the early 1990s. By 1990, when Alex Deghan interviewed villagers in Vohiparara, nearly 100% of households were involved in either harvesting or selling crayfish and they had been harvesting commercially for approximately 30 years (Deghan 1990). Our historical matrix with elders in Vohiparara suggests that although the number of households in the area has increased, there were already approximately 34 by 1980 (compared with 47 today; see Figure 8.5). Deghan estimated that crayfish provided 75% of the income to the village and, although this value should not be taken as an accurate estimate, it indicates that commercial crayfish harvesting was very important by 1990. He found similarly high levels of harvesting in Sahavondronana. Ferraro (1994) carried out extensive interviews with households in both Vohiparara and Sahavondronana in 1990 and 1991; his study confirms that crayfish selling was a principle source of income for both villages at that time.

II) Large crayfish were already depleted close to Vohiparara and Sahavondronana before 1990

By 1990 the abundance of large crayfish had declined in both Vohiparara and Sahavondronana, when compared to some unspecified time in the past (Ferraro 1994). Interviews with harvesters in Vohiparara in this study gave mixed opinions on whether the abundance of crayfish is changing. However, they tended to agree that there were more large crayfish some time in the past, probably before the establishment of the Park in 1991.

III) The distance travelled to harvest sites by harvesters from Vohiparara has not changed

Harvesters in Vohiparara reported in 1990 that they travelled approximately 3 km to harvest sites (Deghan 1990). The mean harvest distance today is 2.4 km and 75% of trips fall within 3.1 km of the village (Figure 4.6). The estimate from Deghan's study is unlikely to be very precise (as it is based on villagers' own estimates of distance and it is difficult to estimate distance

travelled in forest), but it does indicate that there has not been a major increase in travel distance by harvesters over the last 14 years.

If large crayfish were already depleted in the areas around Vohiparara and Sahavondronana before 1990, yet the distance travelled to harvest sites has not increased, medium crayfish are likely to have been the focus of harvesting for at least 14 years. The fact that no effect of harvesting on their density is detectable today suggests that the population is in equilibrium and the current harvest may be sustainable.

8.4.2 The modelling approach

8.4.2.1 Could the 2003/2004 harvest have been sustainably harvested within the area available to harvesters from Vohiparara?

Under the conservative assumptions concerning the density of crayfish in streams for which we do not have data, only two of the models, those with linear density-dependence regulated by biomass, suggest the harvest obtained by Vohiparara harvesters in 2003/2004 could be harvested sustainably within the area available to Vohiparara. However, under the more generous set of assumptions concerning the density of crayfish, all the models suggest the harvest would have been sustainable.

8.4.2.2 Assumptions concerning crayfish density

The area necessary to obtain sustainably the volume of crayfish harvested by Vohiparara in 2003/2004 depends on the assumptions concerning the number of crayfish per unit length in rivers for which this was not measured. Below I discuss the two sets of assumptions I made (conservative and generous). I suggest that the conservative set of assumptions were indeed conservative and the true numbers of crayfish in streams for which we did not have estimates may more closely meet the generous assumptions.

Under the conservative assumptions I assumed that temporary streams held half the number per unit length of first-order streams. This is conservative as many streams so marked on the maps were indistinguishable on the ground from first-order streams where we had carried out mark-and-recapture. In addition many temporary streams present on the ground were not marked on the maps, resulting in an underestimate of the length of this habitat available.

Under the conservative assumptions I assumed that the number of crayfish per unit length in fourth, fifth and sixth-order streams was twice that in second and third-order. The relationship between river width and the amount of crayfish habitat will depend several things, such as rock cover, and is not necessarily dependent simply on area. However, fourth, fifth and sixth-order streams were larger and therefore generally would have had more habitat and so more crayfish. This was supported by the fact that more medium crayfish per unit length were found in wider streams (see Table 8.1 and 8.2). In addition, more large crayfish were found in second and third-order streams than in the smaller first-order streams (see Figure 6.2).

8.4.2.3 *Limitations of the approach*

As discussed in section 7.4.5 there are many uncertainties surrounding the models. The type of density-dependent regulation is entirely unknown. Although I present a range of models, varying in the shape and where and how in the life cycle density-dependence acts, the strength of density-dependence is based on that observed in a study of an unrelated crayfish species which may show different regulatory mechanisms. In addition, no information is available on temporal variation in, and any correlation between, vital rates. Even if the vital rates recorded accurately represent the mean for the population, temporal variation, especially if correlated, will reduce the level of the sustainable harvest (Lande *et al.* 1994; Fieberg & Ellner 2001).

The indiscriminate use of sustainability indices to assess whether a harvest is sustainable has been criticised by a number of authors (Slade *et al.*

1998; Milner-Gulland & Akçakaya 2001). Many of the criticisms apply in part to this study and are discussed in turn.

I) Market surveys, often used to estimate offtake (e.g. Fa *et al.* 1995), can seriously underestimate true offtake because of informal sales or home consumption, or wastage at the point of capture (Milner-Gulland & Bennett 2003). In this study annual offtake was estimated by recording what harvesters brought to the village. Harvesters came to the project house to record their catches before selling the crayfish, meaning subsistence harvesting should in theory be captured (but see section 4.4.1). Wastage at the point of harvest would be missed in this study but is unlikely to be high for crayfish as they are caught by hand rather than in traps in which many animals die and rot before being collected (Muchaal & Ngandjui 1999).

II) Ignoring source-sink dynamics can lead to under or over-estimating the sustainable harvest in an area depending on the harvest intensity in the surrounding area (Novaro *et al.* 2000; Salas & Kim 2002). The area surrounding Vohiparara is likely to be exposed to less harvesting than Vohiparara, particularly in the large area of forest to the east of the village. These areas could in principle act as sources, increasing the sustainable harvest to Vohiparara above that estimated here. However, crayfish are not very mobile (Hazlett *et al.* 1974; Robinson *et al.* 2000), and most of the less harvested area drains eastwards, rather than westwards into the Vohiparara rivers, so it seems unlikely that source-sink dynamics will increase the sustainable harvest significantly. In addition in the face of uncertainty it is prudent to make conservative assumptions; assuming no inflow from the less harvested areas is conservative.

III) Necessary population parameters (e.g. density, age at first reproduction, and annual number of young) are often unavailable for the target population and are taken from the literature, zoo populations or even estimated using extrapolation from species with a similar body size (Robinson & Redford 1991). In this study parameters necessary for the model (density, survival,

fecundity and growth) were not estimated in the exact area for which the sustainable harvest was being modelled as it was necessary to know the carrying capacity and survival of individuals and these could not be established from harvested populations (as they will be below carrying capacity and survival will be affected by the harvest). However the unharvested sites chosen were close (<15 km) to the area for which harvest was being modelled, at similar altitude, and with no perceivable differences in habitat.

8.4.2.4 *Is crayfish harvesting sustainable in the Ranomafana area?: conclusions from the modelling approach*

The results of the modelling suggest that the harvest taken by villagers in 2003/2004 may be sustainable given the area to which harvesters have access. The principle caveats to this conclusion is that it depends on the use of deterministic models, which do not take into account stochastic variation in vital rates, and that the models used hinge on a number of untested assumptions concerning the strength and shape of density-dependence in *A. granulimanus*. The models are useful in supporting the general conclusions from the mark-and-recapture study that the current harvest may be sustainable but they also suggest that the current harvest may be close to the sustainable limit.

8.4.3 Interpretation of the evidence

I suggest the following interpretation of the data presented in this chapter. In the past the economy of Vohiparara was based on subsistence farming with some forest product collection for household use. Between 1958 and 1980 the villagers started to rely more on collecting and selling forest products, particularly crayfish, for their livelihood. Under this change in harvesting pressure the larger crayfish were rapidly fished out, resulting in a more productive population (due to increased survival and fecundity of smaller crayfish). The population now appears to be in equilibrium again with this more productive size-structure. When harvesters today report that there were more large crayfish in the past, they are probably remembering a time before the new equilibrium was reached. The

tentative conclusions of the various lines of evidence suggest that current harvesting may be sustainable under current conditions but that harvesters, at least in Vohiparara, may be taking close to the sustainable limit for the system.

8.4.4 What about other crayfish species?

In this chapter I ask the whether crayfish harvesting in RNP is sustainable at the current level. However, all the data presented considers only one species of crayfish in the area: *A. granulimanus*. This is justified by the fact that *A. granulimanus* is the most important economically, making up more than 95% of the catch in Vohiparara (section 4.3.2.1). However *A. betsileoensis* is also targeted to some extent and may be threatened by overharvesting. *A. betsileoensis* do not reproduce until they reach a larger size than *A. granulimanus* (Figure 3.9) and a lower proportion of *A. betsileoensis* than *A. granulimanus* harvested would have already reproduced (section 4.3.2.1). *A. betsileoensis* is much less common than *A. granulimanus*. Where a rare species is hunted along with a more common species, the vulnerable species may be harvested beyond the point where exploitation would otherwise cease to be profitable (Clayton *et al.* 1997; Wilkie & Godoy 2001; Rowcliffe *et al.* 2003). Multi-species harvesting of *A. betsileoensis* alongside the more common *A. granulimanus*, and the fact that *A. betsileoensis* does not reproduce until a larger size, may mean *A. betsileoensis* is much more threatened by overharvesting than *A. granulimanus*. *A. betsileoensis* was described by Hobbs (1987) as “probably the most ornate of any extinct or extant species of crayfish”. Further work on this large and beautiful crayfish species is a priority.

8.5 Summary

In this chapter I presented the results of two methods for assessing the sustainability of crayfish harvesting in the Ranomafana area. First, I used mark-and-recapture to compare the population size and structure across 79 sites exposed to a wide range of harvesting intensity: from unharvested sites deep in the forests in an area where the villagers are *fady* for crayfish harvesting, to sites close to the heavily harvesting villages of Sahavondronana and Vohiparara. Large crayfish were less abundant at harvested sites but there were no detectable difference in the abundance of medium and small crayfish. Most of the current harvest in Vohiparara comprises these medium crayfish. This evidence, combined with historical information suggesting that commercial crayfish harvesting has been important in Vohiparara and Sahavondronana at least since the 1980s, implies that the current harvest may be sustainable.

Chapter 9

Discussion

“Raha tany misy vato sy ala sady misy rano, dia misy peopeoka, fa rehefa lasa ny ala, lasa koa ny peopeoka.”

“If there is forested land with rocks and water, there are crayfish, but when the forest goes, the crayfish go.” (Elder from Vatofotsy)

“Ny oran-maintso efa tsy misy koa satria efa lany ny ala”

“There are no more crayfish because there is no more forest” (Elder from Amboahoanana)



Villages such as Amboahoanana to the east of the park have experienced great deforestation in the last 20 to 30 years. No crayfish are found in their streams today.

9 Discussion

Harvesting of wildlife resources for food, medicine and building materials, is vitally important to the livelihood of millions of people in developing countries (Balick & Mendelsohn 1992; Edwards 1996; Pimentel *et al.* 1997; Robinson & Bennett 2000). Such resources are particularly important to poorer households (Appasamy 1993; Gunatilleke *et al.* 1993; Hegde *et al.* 1996; Cavendish 2000), or as natural insurance to smooth incomes during difficult times (Godoy *et al.* 2000; Pattanayak & Sills 2001). Unfortunately overexploitation of wildlife resources is a serious problem and has resulted in some exploited species being threatened with extinction (Robinson & Redford 1991; Hilton-Taylor 2000; Oates *et al.* 2000). Both biological and socio-economic factors affect the likely sustainability of a harvest system (Bennett & Robinson 2000; Kokko *et al.* 2001).

Astacoides, the genus of crayfish endemic to Madagascar, has been harvested for food at least since early colonial times (Sibree 1915; Monod & Petit 1929). Today crayfish are an important source of protein and income to people throughout the eastern highlands of the country (Dehgan 1990; Raberisoa *et al.* 1996; Guilhaume 1999; Freudenberger 2002). However, there has been concern that the harvest is unsustainable (Dehgan 1990; Ferraro 1994; Crandall 2004). In this thesis I have addressed the question of the sustainability of the crayfish harvest in and around Ranomafana National Park (RNP) using ecological and socio-economic methods.

9.1 Key Findings of the thesis

9.1.1 Six crayfish taxa are found in RNP

Six taxa, comprising four species (two forms of *A. betsileoensis*, *A. caldwelli*, two forms of *A. crosnieri* and *A. granulimanus*) of crayfish are found in RNP. These were identified from more than 30,000 individual crayfish caught and

released during this study (chapter three). This finding contradicts earlier reports that all six described species of *Astacoides* inhabit the area (Dixon 1992)

9.1.2 The taxa in the Ranomafana area vary in their vulnerability to threats

Some taxa (notably a form of *A. crosnieri* which is found only in swampy forest rich in *Pandanus* spp., and *A. betsileoensis* which is found only in large, deep rivers above 1000 m in the Park) show restricted habitat requirements. Taxa become reproductive at different sizes, with *A. betsileoensis* becoming reproductive at a larger size than the other taxa in the area. These differences between taxa will affect their vulnerability to habitat loss and to exploitation (chapters three and four).

9.1.3 Crayfish are very important to some people in the RNP area

Commercial crayfish harvesting is very important to only a relatively small proportion of villages in the Ranomafana area, but subsistence harvesting occurs in most communities (chapter four). Within the villages where commercial harvesting occurs, crayfish are very important, particularly to the poorer households. The 25 harvesting households in one harvesting village, Vohiparara, earned approximately \$2074 from harvesting in 2003/2004; this is very significant in the context of local incomes (more than 88% of rural people in Fianarantsoa province live on less than \$170 a year; INSTAT 2002). Poorer households, particularly those headed by women, depend most heavily on crayfish harvesting.

9.1.4 Harvesting focuses on one species: *A. granulimanus*

The crayfish harvest in the Ranomafana area focuses on one species, *A. granulimanus*. This species makes up 95% of the catch in the harvesting village of Vohiparara (chapter four). *A. betsileoensis* and *A. caldwelli* are also harvested where available, but are much less common and so make up a lower percentage of the catch. *A. crosnieri* are very seldom harvested due to their small size,

muddy taste (*fofom-potaka*) and the difficulty of harvesting in their swampy habitat.

9.1.5 Density-dependent regulation may be important

Fecundity of *A. granulimanus* is regulated by density; the proportion of females which are reproductive increases with decreasing density (chapter six). There was some evidence from the data that growth may also be density-dependent but this effect was not significant. The effect of density on survival could not be investigated from the data but evidence from the literature suggests that survival of crayfish is likely to increase when the density of large crayfish is reduced (chapter five). Such density-dependence will increase the resilience of crayfish to exploitation.

9.1.6 Harvesting of *A. granulimanus* may be sustainable

The harvest of *A. granulimanus* in the Ranomafana area may be sustainable under current conditions. There are fewer large crayfish at sites exposed to heavy harvesting but this study found no effect of harvesting intensity on the density of medium-sized crayfish (the size-class which currently dominates the catch). Evidence from interviews and previous studies in the area (Dehgan 1990; Ferraro 1994) suggest that large crayfish were already depleted in the areas around the harvesting villages of Vohiparara and Sahavondronana before 1990, yet the distance travelled to harvest sites has not increased since then. Medium-sized crayfish are therefore likely to have been the focus of harvesting for at least 14 years and the fact that there is no detectable effect of harvesting on their density today suggests that the population is in equilibrium and that the current harvest may be sustainable. However, population models suggest that the harvest, at least in Vohiparara which was studied in detail, may be close to the limit of sustainability (chapter eight).

9.1.7 More work is needed on *A. betsileoensis* to assess its threat status

A. betsileoensis is found only in large rivers. Such rivers in the Ranomafana area have been invaded by an introduced predatory fish, the Asian snake-head *Channa striata*, which eats crayfish (chapter three). *A. betsileoensis* also reproduces at a larger size than other crayfish in the area, making it potentially more vulnerable to recruitment overfishing than *A. granulimanus* (chapter four). Harvesters collect *A. granulimanus* and *A. betsileoensis* together, meaning *A. betsileoensis* may continue to be harvested at densities where it would cease to be profitable if harvested alone (chapter eight). I suggest that more work is needed on this large and beautiful species to assess its threat status and vulnerability to exploitation.

9.2 The sustainability of crayfish harvesting in the Ranomafana area

9.2.1 What might happen in the future?

The main question in this thesis is whether crayfish harvesting in the Ranomafana area is sustainable. My conclusion is that the harvest appears to be sustainable under current conditions but that the offtake by harvesters in Vohiparara may be close to the maximum of what is sustainable. A harvest that is only just sustainable now may well become unsustainable should local conditions change. Therefore it is important to consider how changes in the socio-economic conditions of the Ranomafana area might affect the sustainability of the harvest.

The human population of the Ranomafana area is increasing (Korhonen *et al.* in press) and human population growth tends to lead to increased harvesting of wildlife resources (Bennett & Robinson 2000; Davies 2002 but see Bulte & Horan 2002). Changes in the level of the harvest will also depend on changes in the costs and benefits of crayfish harvesting in the area. Harvest costs will rise if increased availability of alternative employment increases the opportunity cost of

harvesting (Wilkie & Godoy 2000; Milner-Gulland & Bennett 2003) or if the current ban on crayfish harvesting within the Park boundaries is enforced (Clayton *et al.* 1997). The benefits from harvesting will increase if the market price increases. The likely influence of future development on markets for crayfish in the Ranomafana area depends on a multitude of factors (Wilkie & Godoy 2001; Milner-Gulland & Bennett 2003) and so is very difficult to predict. The price depends currently on local demand but improvements to the transport infrastructure could open up new markets by allowing crayfish to be exported to the provincial or even national capital, thus raising the price locally (Shanley *et al.* 2002; Marshall *et al.* 2003).

The primary local market for crayfish in the Ranomafana area is villagers buying crayfish to eat as a sauce (*laoka*) with their rice, and middle-class Malagasy passing through the area buying crayfish as a snack. Tourists currently represent a relatively small market. Whether crayfish are a superior good (consumption increases as income increases) or inferior good (consumption decreases as income increases) will affect the market if the region develops (Wilkie & Godoy 2001). I did some preliminary work to investigate preferences for crayfish relative to alternative foods. I showed pictures of different foods (various domestic meats, crayfish, lemur, fish, beans and greens) to villagers, middle-class Malagasy and tourists, and asked them to rank foods in order of preference. The results, not presented here, suggested that crayfish are an inferior good to villagers who prefer domestic meat especially pork, beef and duck. This suggests that increases in local villager's wealth will not increase their crayfish consumption. However, tourists and middle-class Malagasy rank crayfish highly meaning that markets for crayfish may grow if tourism to the area increases and/or improvement of the transport system allows export of crayfish to the cities.

Crayfish harvesting is not a preferred activity in the Ranomafana area (Peters 1998b and chapter four) and the high transaction costs associated with meeting market demand for many non-timber forest products means they are

less likely to be attractive to those emerging from poverty and those with alternative wealth-generating options than for extremely poor people (Arnold & Perez 2001). If economic development provides alternatives to poor villagers currently engaged in crayfish harvesting, the rising opportunity costs may be enough to reduce the pressures on crayfish stocks.

9.2.2 Crayfish conservation in Ranomafana National Park

The primary aim of Madagascar's national parks is the protection of biodiversity and ecosystem function (Anonymous 2004; Randrianandianana *et al.* 2004). Park managers have a difficult task because such aims may conflict with traditional use of the forest by local people (Peters 1998b; Ferraro 2002). Fortunately crayfish harvesting, at least of the most common species *A. granulimanus*, seems to be sustainable under current conditions in the Ranomafana area. However, harvesting may threaten the rarer *A. betsileoensis*. This species may also be threatened by the introduced Asian snake-head *Channa striata*. Park managers should consider further work to assess the vulnerability of *A. betsileoensis*.

Although the harvest of *A. granulimanus* may be sustainable under current conditions, Park managers could consider promoting practices to reduce the risk of overexploitation as socio-economic conditions change. The Park management has been carrying out environmental education in villages surrounding the Park since the early 1990s, including promoting the practice of not harvesting crayfish with eggs. This has had little success, at least in Vohiparara where villagers continue to harvest crayfish with eggs (see below). This may be in part because the Park rules remove the rights of local communities to manage their resources, the result being that a long-term view is not favoured at the village level. Under COAP (*Code de Gestion des Aires Protégées*), the recent law defining management of protected areas in Madagascar, (law no. 2001/05); it is possible for communities and the Park authorities to agree ZUCs (*Zone d'Utilisation Contrôlée*). These are areas where a specific village gains extraction rights to

certain resources in a defined area of forest subject to certain restrictions. ZUCs may be useful in the context of crayfish harvesting in Ranomafana National Park as secure rights may promote improved management by harvesting communities. I argue that strict enforcement of the official ban on crayfish harvesting in the Park would not be the best use of scarce conservation resources as it would damage relations with local communities, divert resources away from more immediate issues, such as avoiding *tavy* (slash-and-burn agriculture) within the Park, and may have little ecological benefit as the current harvest, at least of *A. granulimanus*, is sustainable.

9.3 This study in the context of the ‘sustainability debate’

There has been a tendency in the past to see poor rural communities living in and around forests as ‘noble savages’, living in balanced harmony with their surroundings. This view has been rebuffed a number of authors (Redford 1991; Buege 1996; Grande 1999) and there is now increasing recognition that such people are not innate conservationists and most cases of apparent ‘conservationism’ are in fact the result of people maximising their economic returns as predicted by optimal foraging theory (Alvard 1993; Alvard 1994).

When considering non-timber forest product harvesting in developing countries, scholars are divided into three camps as to whether such exploitation is sustainable; those who still believe in the noble savage and assume local people manage the forest sustainably, those who say they do not, and those who say sustainable exploitation is the result of special conditions that must be identified in each case (Godoy *et al.* 1993). As discussed in 1.3 there are a number of well-understood socio-economic and biological factors which favour or disfavour sustainable exploitation. The idea that we can generalise, e.g. that all indigenous exploitation is sustainable, may be attractive but a case by case assessment looking at both the socio-economic and ecological circumstances of each harvest is probably necessary.

9.4 Could promoting community-based management of crayfish aid conservation in Madagascar?

There is growing interest among conservation decision makers in Madagascar in promoting forest product harvesting by communities as an incentive for retaining forest cover (Anonymous 2004; Erdmann 2004b). The life-history of *A. granulimanus*, with its high fecundity and density dependent regulation of survival and fecundity (chapters five, six and eight), makes it relatively amenable to sustainable harvesting (chapter eight). However, in common with studies in a number of other countries (Godoy *et al.* 2000; Coomes 2004), Erdmann (2004b) suggests that revenues from forest products alone are unlikely to outweigh the value from timber or conversion to agriculture in Madagascar. This is because of both the scattered nature of forest products in the forest, and poorly developed markets (Arnold & Perez 2001; Wong *et al.* 2001). I agree with this conclusion and do not consider that promoting crayfish harvesting, through working to increase markets, is a sensible option for conservation managers in Madagascar to pursue. This is because I) the value generated from sustainably harvested crayfish, even if improved markets were found, is unlikely to exceed the value that could be obtainable from other land uses (Godoy *et al.* 2000), and II) promoting new markets would change the dynamics of the harvest and may result in unsustainable exploitation (Bennett & Robinson 2000).

Although I do not believe that crayfish harvesting should be promoted as a conservation tool, it is important that conservation managers recognise that crayfish are, in many places, an important economic resource as well as an important element of Madagascar's biodiversity. Allowing harvesting of forest products, such as crayfish, could also help reduce the opportunity costs of forest conservation, which is currently borne by local people (Ferraro 2002; Balmford & Whitten 2003). Devolving forest management to the community level could promote sustainable management procedures. Communities and

conservationists have worked together in some parts of Madagascar to develop local laws (*dina*) to control and manage access to locally important natural resources (Rakotoniaina & Randriamanampisoa 1999; Durbin *et al.* 2004). The legal framework to recognise such devolution of responsibility for management of natural resources to the local level is defined in the GELOSE (*Gestion Locale Sécurisée*) law (no. 96-0125) and the simpler system under the GCF (*Gestion Communautaire Forestier*) law (no. 97-017; Josserand 2001; Anonymous 2002). A number of communities in Madagascar have successfully obtained legal rights to manage their forest resources (Winterbottom 2001; LDI 2002; Garreau & Manantsara 2004).

A number of management tools may be useful to protect crayfish stocks from overexploitation (discussed below) and could be implemented and enforced at the local level. Which tool is suitable will depend on local conditions and should be selected by the communities concerned. Such locally managed rules have the potential to directly benefit communities and so be locally enforced where communities have a strong interest in the persistence of the resource and have long-term rights. However, there are some situations where local management and locally enforced *dina* are unlikely to offer adequate protection of crayfish as an element of Madagascar's biodiversity. For example if further research identifies *A. betsileoensis* as threatened by overharvesting, external protection may be required to prevent its overexploitation as it is probably not in itself an important enough resource to make community management a viable option.

9.5 Managing crayfish populations for sustainability

Under the terms of the agreements being set up to transfer responsibility for forest management from the Département des Eaux et Forêts to local communities (Josserand 2001; Anonymous 2002; LDI 2002) communities are expected to set rules to ensure forest resources are exploited sustainably. There

is therefore a lot of interest in management tools which could reduce the risk of overexploitation of harvested species.

The importance of protecting crayfish brood stock to maximise the productivity and sustainability of a fishery has been stressed by a number of authors (Momot 1977b; Skurdal & Taugbol 1994). This is recognised in Malagasy law, which only allows harvesting of crayfish larger than 100 mm total length (45 mm CL; regulation number 2.233-MAP/FOR, 22 December 1960 Article 6). However this law is not currently enforced and its existence is not widely known, even among conservation officials. There are a number of possible management tools which could be used to protect crayfish brood stock. I discuss each of these in turn and comment on their practicality and relative ease of enforcement in the Malagasy context.

9.5.1 Size limits

Setting minimum size at such a level to ensure that females have spawned at least once before they are harvested is a common management tool for crayfish populations in Europe (Skurdal & Taugbol 1994). The current legal size for crayfish harvesting in Madagascar of 100 mm total length (equivalent to approximately 45 mm CL) may be suitable for *A. granulimanus* as by this size more than 40% of females breed in a given year (Figure 3.9). However, not until 140 mm total length (65 mm CL) do 40% of *A. betsileoensis* become reproductive meaning a larger minimum size may be required to protect this species from overexploitation. Size limits are relatively easy to enforce as enforcement can take place at the point of sale (in a market). Although this will not stop people harvesting undersized crayfish for home consumption, it could be a useful mechanism where commercial harvesting is important.

9.5.2 No-take zones

No-take zones (areas from which any harvesting is banned) have become an important tool in the management of marine resources (Boersma & Parrish

1999). The theory behind no-take zones is that they protect spawning stocks, increasing recruits to adjacent fishing grounds through emigration thus enhancing fisheries (Roberts & Polunin 1993). Recent empirical work suggests that no-take zones can indeed improve marine fish catches (Roberts 1995; Roberts *et al.* 2001; Halpern & Warner 2002; Gell & Roberts 2003). It has been suggested that fully protected core areas of forests may act in a similar way by providing a source to re-supply animal populations in nearby harvested areas (Bennett & Robinson 2000; Salas & Kim 2002; Milner-Gulland & Bennett 2003). However, knowledge of metapopulation dynamics and dispersal patterns is essential in defining whether such no-take zones will effectively improve local catches and, if so, where they should be situated (Lipcius *et al.* 2001). Even the most basic information on dispersal and metapopulation dynamics is not available for crayfish in Madagascar, but the strong relationship between size and fecundity suggests that no-take zones may be a useful way of increasing recruitment in heavily fished areas. However, no-take zones in forest would be difficult to enforce as it would be impossible to identify the origin of catches once they enter the market, and monitoring in the forest would be required.

9.5.3 Leaving crayfish with eggs

The simplest method of protecting brood stock and so reducing the risk of overexploitation is for harvesters to leave crayfish with eggs. To this end ANGAP have been carrying out environmental education in many of the villages in the periphery of RNP, since the early 1990s. Villagers are aware of the benefits of leaving crayfish with eggs but continue to harvest them. Two issues must be considered when encouraging harvesters to leave crayfish with eggs: I) many villagers express a strong preference for crayfish with eggs saying they are fatter and tastier (*matavy sady matsiro*), and II) the peak egg laying period (July to October) overlaps with the 'hungry period' of food scarcity (approximately August to December). Enforcing a ban on harvesting crayfish with eggs would be relatively difficult as villages may simply scrape off eggs before bringing them to market.

9.5.4 Constraining fishing methods

Depending on the fishing method, females may be relatively unsusceptible to harvesting thus providing some automatic protection to the brood stock. In an experimental crayfish fishery, Momot (1977b) found that females entered traps much less frequently than males as they were less mobile and tended to inhabit deeper water. Female *A. granulimanus* are less susceptible to the capture methods used by harvesters in Vohiparara; the ratio of females to males brought to the daily interviews by harvesters was 1:1.14 ($n = 12,628$, $\chi^2_1 = 53.2$, $p < 0.001$). This could be because female crayfish with eggs are less likely to respond to baited sticks than are male crayfish. In some areas harvesters reportedly use spades to dig for crayfish rather than tempting them out of holes with baited sticks. Such a method is likely to offer no protection to the brood stock and, in addition, destroys habitat. Banning such destructive harvesting practices, although difficult to enforce, may aid the sustainability of the harvest.

9.6 Habitat loss: the most serious threat?

In this thesis I have focused on the threat to crayfish in Madagascar from overexploitation. However, during my work in Madagascar I became increasingly aware that habitat loss is a significant threat to *Astacoides*. In chapter three I demonstrated that *A. granulimanus*, although widespread and abundant in the Ranomafana area, is dependent on forest habitat. This is in contrast to an earlier report based on a much briefer study by Dixon (1992), which suggested that they might be tolerant of altered habitat. The dependence of *A. granulimanus* on forest is reflected in one of its local names: the forest crayfish (*oran'ala*). In the deforested area to the east of the Park, *ray aman-dreny* (elders) in the villages of Amboahoanana and Vatofotsy (see Figure 2. 3) reported that crayfish (probably *A. granulimanus*) had been extirpated between ten and 40 years ago, depending on the watershed. The *ray aman-dreny* blamed the loss of crayfish on the loss of the forest through *tavy* (see quotations at the start of this chapter). We searched

the rivers on the deforested watersheds surrounding the villages and confirmed they are devoid of crayfish.

Most work on Malagasy crayfish to date has taken place in the Ranomafana area (Dehgan 1990; Dixon 1992) where, thankfully, there is still plenty of forest and where harvesting of crayfish is an obvious activity. This has led to a bias in the literature stressing the importance of overexploitation as a threat relative to deforestation. Crandall (2004) suggests that because slash-and-burn activities in Madagascar tend to be below 900 m and crayfish occur between 800 m 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 is slower at higher elevations where access is difficult (Nicoll 2004), habitat loss is a serious problem throughout the eastern rainforests of Madagascar. Much forest above 800 m has been, and continues to be, lost (Gade 1996; Brand *et al.* 2002; Dufils 2004; Freudenberger 2004). Although so far very little information on the subject is available, I consider habitat loss to be a very significant threat to crayfish in Madagascar and of more immediate concern than overharvesting.

9.7 Conclusions

Malagasy crayfish have been harvested for food in the Ranomafana forests probably since people came to the area some hundreds of years ago. Crayfish provide important protein and income to many communities surrounding the Park; these people are very poor and have few alternative income sources. Fortunately the harvest, at least of the most common species in the area *A. granulimanus*, appears to be sustainable under current conditions, although it may be close to the limits of sustainability. Little information is available to assess the threat to other crayfish species in the Ranomafana area but the less common *A. betsileoensis*, with its large size at first reproduction, and possible vulnerability to the Asian snake-head *Channa striata*, may be more threatened. Management tools, which may be useful to reduce the risk of overexploitation of crayfish include a minimum size limit, no-take areas, a ban on harvesting crayfish with eggs, or a ban on digging for crayfish with spades. Where responsibility for management of forest resources is being transferred to local people, such tools could be promoted to help communities manage crayfish stocks sustainably. Allowing the harvest would help to reduce the opportunity costs of forest conservation borne by local people.

Although some *Astacoides* populations may be threatened by overharvesting, this alone is unlikely to cause extirpation or extinction. However, habitat loss may be a real threat to the persistence of some species, especially those limited to a specific forest type. In conclusion I add my voice to the many who stress the value and importance of Madagascar's remaining, but highly threatened, eastern rainforests.

Glossary

Malagasy terms used in the text	definition
<i>Asotry</i>	the season from March to May when the rice harvest starts
<i>Betsileo</i>	the dominant ethnic group in the west of RNP
<i>Dina</i>	local law, <i>dina</i> can be recognised by national Malagasy law
<i>Fady</i>	something which the ancestors have forbidden and made taboo. <i>Fady</i> may be a property of a place, an individual or to a group such as a family.
<i>Fahavaratra</i>	the hot, stormy months from December to February
<i>Hofa forest</i>	natural forest in waterlogged areas, rich in <i>Pandanus</i> species.
<i>Laoka</i>	a sauce containing greens, beans, meat or fish eaten with rice for a main meal
<i>Lohatoana</i>	the warm, dry months from September to December
<i>Mpanjaka</i>	the traditional leader in a <i>Tanala</i> village, in some villages his role is mostly ceremonial
<i>Ray aman-dreny</i>	the group of senior and respected elders who make village decisions
<i>Ririnina</i>	the cold months from May to August
<i>Tapaka</i>	abandoned rice fields which have been allowed to re-grow
<i>Tanala</i>	the dominant ethnic group in the eastern part of RNP. The word <i>Tanala</i> literally means 'of the forest'
<i>Tavy</i>	slash-and-burn (swidden) agriculture

Abbreviations

abbreviations used in the text	definition
ANGAP	Association pour la Gestion des Aires Protégées (Madagascar's national park service)
CL	carapace length (measured from the tip of the rostrum to the end of the carapace)
CJS	Cormack-Jolly-Seber
GLM	General Linear Model
GPS	global positioning system
ICDP	Integrated Conservation and Development Project
NTFP	Non-Timber Forest Product
RNP	Ranomafana National Park
RRA	Rapid Rural Appraisal
SEM	Standard error of the mean

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