Effects of native forest and pastoral land use on the population dynamics and trophic role of the New Zealand freshwater crayfish *Paranephrops planifrons* (Parastacidae)

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Preface

Tales from the Frond: Crayfish reflections of a bygone era

Imagine yourself in New Zealand hundreds of years ago, when the moa roamed the dense forests and the enormous Haast eagle, with a 3m wingspan, soared above looking for its meal. If you escaped becoming a mid-morning snack, you would have to look down beneath all this to see where our story lies. In streams beneath the forest canopy, hiding under stones, logs and fern fronds lay the humble crayfish. A crayfish or koura, as it is known by its Maori name in New Zealand, was probably spending its day back then as it does today. Trying to look like dead tree fern leaves and trying to avoid being eaten.

A traditional Maori way of fishing for koura was to place a tree fern frond into the water and wait for the koura to climb in amongst it, before lifting the frond out with its tasty harvest aboard. Today, I stand sweating in thick black waders in the middle of a stream with a 600-volt Electric Fishing machine strapped to my back, holding nets and electrical anodes in the water. I triumphantly scoop another look-a-like koura out of the water only to discover that it is a piece of dead tree fern. Oh, the cruel irony.

But New Zealand today is not as it was when moas roamed the land. Through human inhabitation, particularly the recent European colonisation, the landscape has changed dramatically. Once predominantly forest, New Zealand is now predominantly farmland. So what happens when the shady stream you've been sitting in, with plenty of leaves as shelter and food, suddenly becomes a hot and silty drainage channel? What happens when you've spent hundreds, perhaps thousands of years perfecting the art of looking like a dead tree fern leaf, and they take all the tree ferns away from you?

This is what I have spent cold, dark nights with a headlamp and 600 volts trying to find out. In remnant forest we can catch a glimpse of how life must have been for koura. By comparing the life histories, habitat and diet of koura in native forest streams with those of koura in pasture streams, we can see how crayfish have coped with their changed environment. Luckily, koura have been remarkably adaptable. As omnivores they have been able to change their main food source to capitalise on the more abundant invertebrate fauna in pasture streams. Koura can be equally as resourceful in finding shelter. It is not uncommon to find a koura making a home for itself in an abandoned beer can. Unfortunately, there is a downside. Despite the well-meaning intentions of lazy beer drinkers, there now seem to be fewer of my little friends.

Lab experiments have led me to believe that koura are unusually intelligent yet annoyingly fickle creatures. Their preference for animal food has driven some koura to "beg" to be fed as I enter the room. To have a crayfish standing upright, tapping on the glass and gesticulating wildly at you, is really rather unsettling. I am glad that the finer points of crayfish semaphore escape me, otherwise I might be quite offended.

So why do crayfish excite my curiosity? They are not going to provide a cure for cancer or ozone depletion (well probably not). They are not even very good pets. Their Alcatraz-defying escape abilities and voracious appetites mean you often find them dried up in mid-stride on the way to the refrigerator. Who cares that, despite major changes to the streams they live in, they have been able to adapt and alter the way they get energy from the environment?

Well, aside from being very tasty, it could be because they are integral members of stream foodwebs. They are leaf processors, invertebrate consumers, a food source for native fish, and the ultimate recyclers, scavengers of dead animals. Or, it could be that, unlike the moa and the Haast eagle, the koura are intriguing because they have made it through to today. There is a lesson in that. If you dress like a tree fern, carry a beer can.

Stephanie Parkyn

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Abstract

Deforestation and conversion to pasture of over 50% of land area has affected the water quality, physical habitat, and fish and benthic invertebrate communities of New Zealand streams, but the impact of land use change on crayfish populations is unknown. The population dynamics, growth, and diet of crayfish in Waikato pastoral streams were compared to crayfish inhabiting native forest streams to determine whether conversion to pasture has adversely affected crayfish populations and whether the change in land use has affected their role in the stream community.

Crayfish densities were greater in native forest streams due primarily to greater juvenile recruitment. Crayfish populations in pastoral streams exhibited much greater growth than in native forest streams, but their longevity was shorter. Reproductive maturity occurred after 1 year in pasture streams, as opposed to 2 years in the native forest streams, and consequently juvenile crayfish endured only one winter period, where greatest mortality occurred, before reproducing. Temperature was the primary factor influencing the faster egg development and greater growth rates of juvenile *P. planifrons* in pasture sites, although food source may also have been a significant factor. Crayfish in pasture streams consumed more invertebrates than in native forest streams where leaf detritus dominated stomach contents. In laboratory growth experiments, invertebrate food sources increased the moult increment of juvenile crayfish and decreased the length of the intermoult period, whereas conditioned leaf litter did not promote growth and was not assimilated into body tissue. Warmer water temperatures decreased the length of the intermoult period, but had no effect on the size of moult increment.

Crayfish annual production estimates did not differ between land use, as a consequence of higher crayfish densities in native forest streams and faster growth of crayfish in pasture streams, suggesting that the overall success of the crayfish populations in pasture streams was similar to native forest streams. However, the removal of riparian trees (particularly the loss of their root systems) seems to have undermined the stability of habitat available to crayfish. Habitats of crayfish in native forest streams were primarily tree roots, undercut banks, and accumulations of woody debris. Deforestation has resulted in the loss of many of these habitats, and cobble substrates, macrophytes and terrestrial vegetation growing within the stream, now provide important habitats for crayfish in pasture streams. Crayfish in pasture streams were not as resistant to a major flood disturbance as those in native forest streams, suggesting that the habitats in these pasture streams did not provide stable refugia. Furthermore, the rate of recovery of a crayfish population in one pasture stream following the flood was very slow indicating that *P. planifrons* does not exhibit resilience traits and is dependent on stable refugia to persist during floods.

Crayfish were identified as top invertebrate predators in these hill-country streams despite omnivorous feeding habits that allowed crayfish to exploit a variety of food resources. Crayfish in native forest streams had greater volumes of leaf detritus in their gut contents than those in pasture streams. However, stable carbon and nitrogen isotope analyses and bioenergetic studies of the trophic basis of crayfish production identified aquatic invertebrates as the major energy source for crayfish growth in both native forest and pasture streams. Snails, mayflies and chironomids were the most important taxa to crayfish diet particularly in native forest streams, but by acting largely as a predator of a wide range of invertebrate taxa in pasture streams, crayfish were able to take advantage of both allochthonous and autochthonous energy pathways. As omnivores, crayfish may have dual functional roles as both predators and processors of organic matter, and through production of FPOM they may make leaf matter available to a wider range of invertebrates (e.g. collectors) in stream ecosystems.

Juvenile crayfish had higher rates of assimilation for leaf detritus and higher ingestion rates of invertebrates and leaf detritus than adult crayfish, and most of the annual production of crayfish populations in both native forest and pasture streams was from juveniles. Age affected the role of crayfish in native forest streams where adult crayfish processed more leaf litter into FPOM, and juveniles were more carnivorous. However in pasture streams, the roles of juvenile and adult crayfish were similar, as large crayfish were able to utilise the abundant invertebrate resources. The role of crayfish as predators or processors of leaf detritus may change according to their growth requirements, but more importantly, according to environmental influences on local food resources. Flexible feeding habits have allowed *P. planifrons* to maintain their populations in pasture streams, despite considerable land use disturbance.

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A colourful bunch of people helped me on various nocturnal koura hunting trips, from accountants to marine ecologists, visiting Dutch and American students to computer modellers, and their ages ranged from 11 to 63 years old. My sister has not yet forgiven me for dragging her up and down steep slopes in the pitch dark and pouring rain to crawl around in a stream. The phrase "Trust me, it will be fun" was not strictly correct.

I am deeply grateful to NIWA for their funding and logistical support that made this study possible, and also to the NIWA Hamilton stream team (Ian Boothroyd, Kevin Collier, Glenys Croker, Jane Halliday, John Quinn, Mike Scarsbrook, and Brian Smith) and many others from NIWA, for their help, advice and encouragement throughout.

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Most of all I would like to thank my partner Paul Johnson for being interested and willing to hunt crayfish in the middle of the night, for kicking me out of bed on Saturday and Sunday mornings to finish writing my thesis, and for being a shoulder to lean on.

Thanks everyone, it's been fun.


THIS LOOKS LIKE A GREAT PLACE TO CATCH A CRAWDAD.
WHAT WILL WE DO WITH IT IF WE CATCH ONE?
© [illegible] Universal Press Syndicate
WELL THAT'S ONE THING WE DON'T NEED TO WORRY ABOUT.
WATERSON
7-27
YOU DON'T KNOW WHAT ONE IS EITHER, HUH?

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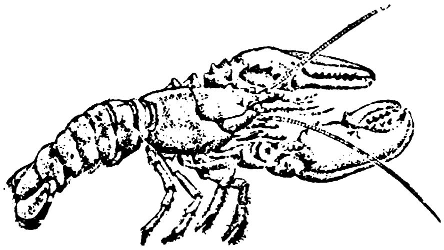


Chapter 1

General Introduction

The role of crayfish

The biology, dynamics, and trophic position of crayfish may be critical to understanding energy transformation in aquatic systems (Momot et al. 1978). Crayfish often dominate the invertebrate biomass of streams, are typically long-lived, and can have both direct and indirect effects on benthic food webs (Momot et al. 1978, Lodge et al. 1994, Rabeni et al. 1995, Nystrom et al. 1996, Parkyn et al. 1997). Rabeni et al. (1995) found that two species of crayfish (*Orconectes* spp.: Cambarinae) consumed as much or more animal matter, algae and detritus per year as all other benthic invertebrates in two Missouri streams. Crayfish can be significant detritivores (Webster & Patten 1979, Lugthart & Wallace 1992) and play an important role in processing leaf litter that is subsequently utilised by other stream invertebrates (Huryn & Wallace 1987).

In lakes, crayfish have been found to significantly reduce the abundance of macrophytes (Abrahamsson 1966; Coffey & Clayton 1988; Nyström & Strand 1996), however they may also enhance macrophyte growth by selectively feeding on herbivorous molluscs (Chambers et al. 1990, Hanson et al. 1990). Similarly, Matthews & Reynolds (1992) documented increases in new growth of dominant macrophytes as well as planorbid snails, most other snails (including *Potamopyrgus* sp.), Crustacea (predominantly *Gammarus* and *Asellus* spp.), and total invertebrate numbers in two Irish lakes after crayfish had been eliminated.

Crayfish are active foragers (Momot 1995) and their activity can cause significant bioturbation of benthic sediments (Parkyn et al. 1997, Whitmore 1997), as demonstrated for other stream invertebrates (e.g., shrimp, Pringle et al. 1993; stoneflies, Statzner et al. 1996 and Zanetell & Peckarsky 1996). In this way they may act as "ecosystem engineers", regulating the supply of resources to other species by causing physical changes to their environment (Jones et al. 1994).

Crayfish have been labelled as opportunistic omnivores, but their primary role was believed to be as herbivores or detritivores that convert detritus, periphyton, and macrophytes into a form that may be more readily available to higher trophic levels (Lorman & Magnuson 1978, Momot et al. 1978). However, Momot (1995) proposed that crayfish may act primarily as predators although their role as carnivores and modifiers of community structure has not been widely investigated.

In New Zealand there are two species of freshwater crayfish inhabiting lakes and streams, *Paranephrops zealandicus* and *P. planifrons* (Parastacidae) known locally by their Maori name “koura”. *P. planifrons* is found in the North Island and in Nelson, Marlborough and Westland of the South Island and is separated by the Southern Alps from *P. zealandicus*, which occurs in the south and east of the South Island and in Stewart Island (Chapman & Lewis 1976). Crayfish appear to be widespread in lakes and streams and have been found at depths of 185 m in Lake Taupo (Dr de Ronde, IGNS, pers. comm.) and altitudes of 1260 m a.s.l. in Tongariro National Park (Fordham et al. 1979). They occupy a diverse range of habitats (Devcich 1979) and appear to be polytrophic feeders with a gut microflora capable of digesting a wide variety of foods (Musgrove 1988b).

Major aquatic predators of crayfish include eels (Hicks 1997), perch (Scott & Duncan 1967) and trout (McDowall 1990) and terrestrial predators include kingfishers, shags (Scott & Duncan 1967), kiwi (Grzelewski 2000), rats and mustelids. Koura are also a culturally important food source for Maori and exploitation is restricted to iwi (tribes) in some Rotorua lakes. Although there has been considerable recent interest in aquaculture of both *P. planifrons* and *P. zealandicus* (Parkyn 1999), commercial exploitation of wild stocks of crayfish is prohibited by the Freshwater Fisheries Regulations 1983 (McDowall 1995).

Research on *Paranephrops* sp. has centred on aspects of their biology and population structure in lakes (Devcich 1974, 1979, Coffey & Clayton 1988, Musgrove 1988), growth and breeding of stream populations (Hopkins 1967a,b, Jones 1981a,b, Whitmore & Huryn 1999), and responses to introduced predators (Shave et al. 1994, Usio & Townsend in press). Few studies have investigated the ecological role of crayfish in New Zealand streams. *P. planifrons* was shown to have a significant effect on leaf litter processing and on invertebrate taxa richness in experimental artificial channels (Parkyn et al. 1997) and Whitmore (1997) investigated the role of *P. zealandicus* in a native forest stream in Otago. Based on gut content analysis and enclosure experiments he concluded that the primary role of *P. zealandicus* was unlikely to be as a predator and that effects on headwater stream invertebrate communities may occur as an indirect result of crayfish foraging behaviour and high biomass. However, Hicks (1997) used stable carbon and nitrogen isotope analyses of *P. planifrons* to demonstrate that crayfish were top invertebrate predators in Waikato streams.

The effect of land use change

The greatest threat to aquatic invertebrates in New Zealand has been habitat loss and degradation through catchment clearance, removal of riparian vegetation, channel engineering works, and changes to water quality and river flows (Collier 1993). Considerable land use change has occurred in New Zealand particularly over the past 150 years. Widespread deforestation and conversion to pasture has reduced the amount of forested land area to only 23% of the original size and over 50% of the land area has been converted to farmland (Pullar & McLeod 1992).

Land use change has effected the water quality, physical habitat, and biotic communities of New Zealand streams. Deforestation and conversion to pasture has led to increases in water temperature from decreased shade, and run-off or leaching of urine, dung, and fertiliser applications from paddocks has increased nitrogen and phosphorus concentrations in streams (Quinn et al. 1997, Harding et al. 1999). As a consequence of increased light levels and nutrients, periphyton biomass has increased, often to nuisance levels (Biggs 1985). Stream channel widths have narrowed and become incised (Davies-Colley 1997) and stream banks may be trampled by stock causing erosion and loss of habitat for fish (Williamson et al. 1992). Levels of suspended and benthic sediments have increased with pastoral land use (Quinn et al. 1997, Harding et al. 1999) and these sediments can fill interstitial spaces between gravels and reduce habitat quality for invertebrates (Jowett 1997).

The degree of catchment development to pastoral land use, water temperature and level of nutrient enrichment were identified as the most important factors affecting invertebrate community structure in a study of 88 New Zealand rivers (Quinn & Hickey 1990). Benthic invertebrate communities have increased in density and biomass in many pasture streams, but the community composition has changed to favour pollution tolerant species (Scott et al. 1994, Quinn et al. 1997). The lack of stream shade appeared to be the most important factor affecting invertebrate populations in Waikato hill-country streams (Quinn et al. 1997). Fish abundance and biomass has also increased in pasture streams due to increased temperature, nutrients and primary production (Hicks & McCaughan 1997), but the diversity of species has declined possibly due to a reduction in suitable habitats (e.g. woody debris) and increased siltation (Hanchet 1990).

Furthermore, agricultural practices may result in inputs of point source pollution through sheep and cattle access to streams, release of dairy shed effluents into streams (Hickey & Rutherford 1986), and from herbicide and pesticide inputs. Sheep dips and drenches were suggested to be partly responsible for the change to a benthic invertebrate community characteristic of polluted conditions in Southland pastoral streams (Scott et al. 1994).

Stream invertebrate communities can also be affected by the removal of riparian vegetation and loss of associated leaf litter inputs (Harding & Winterbourn 1995, Quinn et al. 1997) that are the carbon base of forested stream food webs (Kaushik & Hynes, Cummins 1974). Bird & Kaushik (1992) found that shredders and collectors were replaced by filter-feeders on leaf packs in an agricultural reach compared to a forested reach of the same stream. Stable isotope analyses have shown that invertebrates from forested streams depend almost entirely on allocthonous carbon (e.g. leaves and wood from terrestrial environment), whereas the invertebrate community in grassland streams use a mixture of autochthonous (e.g. periphyton or aquatic plants) and allochthonous carbon (Rounick et al. 1982, Winterbourn and Rounick 1985, Hicks 1997).

Crayfish have often been excluded in reviews characterising the effects of environmental factors on benthic invertebrate communities in New Zealand (e.g. Quinn & Hickey 1990, Collier 1993, Quinn et al. 1999) partly because they remain hidden during the day and are often missed by conventional stream invertebrate sampling techniques (Jones 1985, Collier et al. 1997). Consequently, little is known of the effect of deforestation and conversion to pasture on crayfish populations. Crayfish growth and survival may be affected by temperature (Devcich 1979, Jones 1981b, Lowery 1988) and declines in water quality can be deleterious to crayfish, particularly increases in turbidity, suspended solids and acidification, and decreases in dissolved oxygen content of the water (Westman 1985). Sediments may clog the gills of crayfish reducing oxygen uptake and sheep dip spills in British streams have caused dramatic declines in crayfish populations (Dr P. Bradley, Sheffield University, UK, pers. comm.). Furthermore, reduced inputs of riparian leaf litter may affect crayfish food sources as leaf detritus often dominates gut contents (Lorman & Magnuson 1978, Whitmore 1997, Whitledge & Rabeni 1997), and land use change may therefore influence their role as detritivores in pastoral streams.

In the only study that has looked at the distribution of crayfish, Jansma (1995) found anecdotal evidence of a decline in *P. zealandicus* numbers in Otago streams and that crayfish were negatively associated with agriculture, and positively with native riparian vegetation. Consequently, Hollows (1998) investigated the influence of land use change on growth and diet in *P. zealandicus* in Otago pastoral and native forest streams, but found little difference between the populations. However, no studies have compared crayfish population dynamics (i.e. abundance, life history, habitat, diet, growth and production) in native forest streams with populations in streams altered by pastoral land use.

Objectives of thesis

The effect of altered land use on *P. planifrons* populations in North Island streams is unknown. The main objective of this thesis was to determine how conversion to pasture and ongoing pastoral management has affected crayfish, by investigating their population dynamics, habitat, and diet in Waikato hill-country stream sites within native forest and pastoral catchments. Furthermore, the role of crayfish in aquatic systems appears to be uncertain with debate over the importance of detritus and invertebrate foods to crayfish nutrition (Momot 1995). Therefore, I also aimed to quantify the trophic role of crayfish in native forest and pasture streams and investigate whether the change in land use has affected their role in the stream community.

Outline of thesis

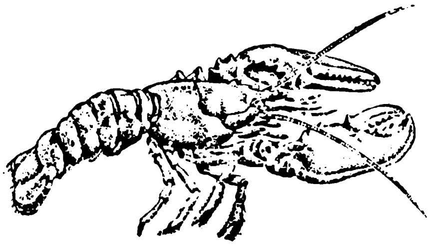
Of primary importance in understanding the role of crayfish within streams, and how environmental factors influence this role, is knowledge of crayfish population dynamics. To assess the resilience of crayfish populations to altered land use, Chapter 3 addresses differences in crayfish densities, biomass, life history, growth and production by comparing populations in native forest and pasture streams.

Freshwater crayfish populations may also be affected by habitat availability (Smith et al. 1996, Naura & Robinson 1998). Habitats for crayfish within streams are likely to have changed greatly with deforestation, through a decline in the amount of woody debris and leaf litter inputs (Hanchet 1990, Quinn et al. 1997) and an increase in levels of fine benthic sediments (Harding et al. 1999). The types of habitats utilised by crayfish are compared between native forest and pasture streams in Chapter 4. A major flood in the study streams during the course of this study enabled comparison of the relative stability of crayfish populations and their habitats to be made in native forest and pasture streams. No previous studies in New Zealand have investigated how crayfish respond to flood disturbance and whether or not their ability to survive disturbances has been altered with changes in land use.

Diet analyses are critical to understanding the role of crayfish in streams, and in Chapter 5 both gut content and stable carbon and nitrogen isotope analyses are used to assess the functional role and trophic position of crayfish in native forest and pasture streams. In addition, the role of crayfish may change with age, therefore the possibility of ontogenetic shifts in diet (Goddard 1988, France 1996c) are investigated.

Deforestation and conversion to pasture may affect the water temperature and the availability of crayfish food sources in streams, and therefore the influence of temperature and food source on growth rates of juvenile crayfish are assessed experimentally in Chapter 6. Crustacean growth is a function of both size increase at moult and the length of the intermoult period (Lowery 1988), so the influence of diet and temperature is assessed for both components of growth.

Production (Chapter 3) and diet (Chapter 5) analyses are combined with experimentally derived values of assimilation efficiency in Chapter 7, to quantify the trophic role of crayfish. The trophic basis of production, annual ingestion and egestion of juvenile and adult (reproductively mature) crayfish are assessed in both native forest and pasture streams to determine if the role of crayfish differs with age and environment. Major findings are synthesised in Chapter 8.



Chapter 2

Study sites

The study streams are located in the Hakarimata Ranges, west of Hamilton in the North Island of New Zealand (Fig. 2.1, Table 2.1). Three of the sites drain catchments entirely in pasture (PW2, PW3 and PW5) and three drain catchments in native forest (NW5, NF and NKL) (Plates 2.1 A-F). All are tributaries of the Waipa River; one site (NF) is a tributary of Firewood Creek that enters the Waipa River near Ngaruawahia and all others are in the Mangaotama Stream catchment in the AgReasearch Whatawhata Research Centre (Fig. 2.1). These sites are long-term monitoring sites for NIWA's River Ecosystems and Land Use Interactions research programme, and were chosen to complement previous and ongoing studies of land use impacts on water quality, benthic invertebrates and fish populations (Quinn & Cooper 1997, Hicks & McCaughan 1997). The native and pasture streams chosen were matched approximately by catchment size (0.5 to 3.2 km^2) and the site elevations and slopes did not differ significantly (Table 2.1).

Table 2.1. Site characteristics measured in November 1992 or 1994 as reported in Boulton et al. (1997), Quinn et al. (1997) and Davies-Colley & Quinn (1998). Land use differences are indicated by P values (Mann-Whitney U, Wilkinson 1997).

Site	Map Ref. (NZMS260 S14)	Site elevation (m a.s.l.)	Catchment area (km^2)	Channel slope ($m. m^{-1}$)	DIFN	Nov. low flows ($l s^{-1}$)
PW3	924763	100	0.49	0.035	0.450	7
PW2	923764	90	0.95	0.032	0.465	16
PW5	928777	60	2.59	0.018	0.323	36
NKL	919775	120	0.53	0.039	0.008	10
NF	976888	40	2.01	0.008	0.020	32
NW5	926785	70	3.20	0.010	0.056	48
P		ns	ns	ns	< 0.05	ns

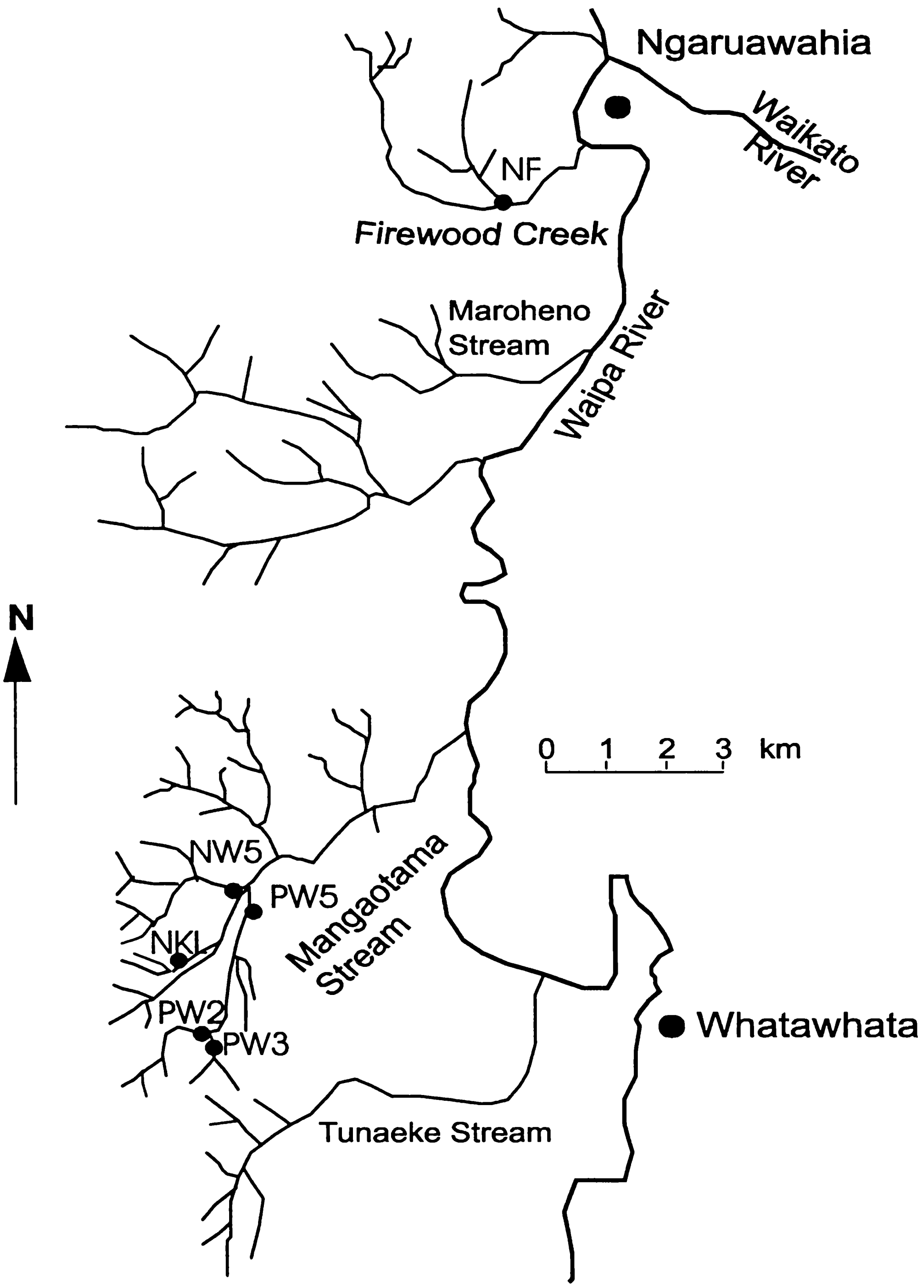


Figure 2.1. Location of sites on the Mangaotama Stream system at Whatawhata, and at Firewood Creek, Waikato, New Zealand (native forest sites = NKL, NW5, NF; pasture sites = PW3, PW2, PW5).

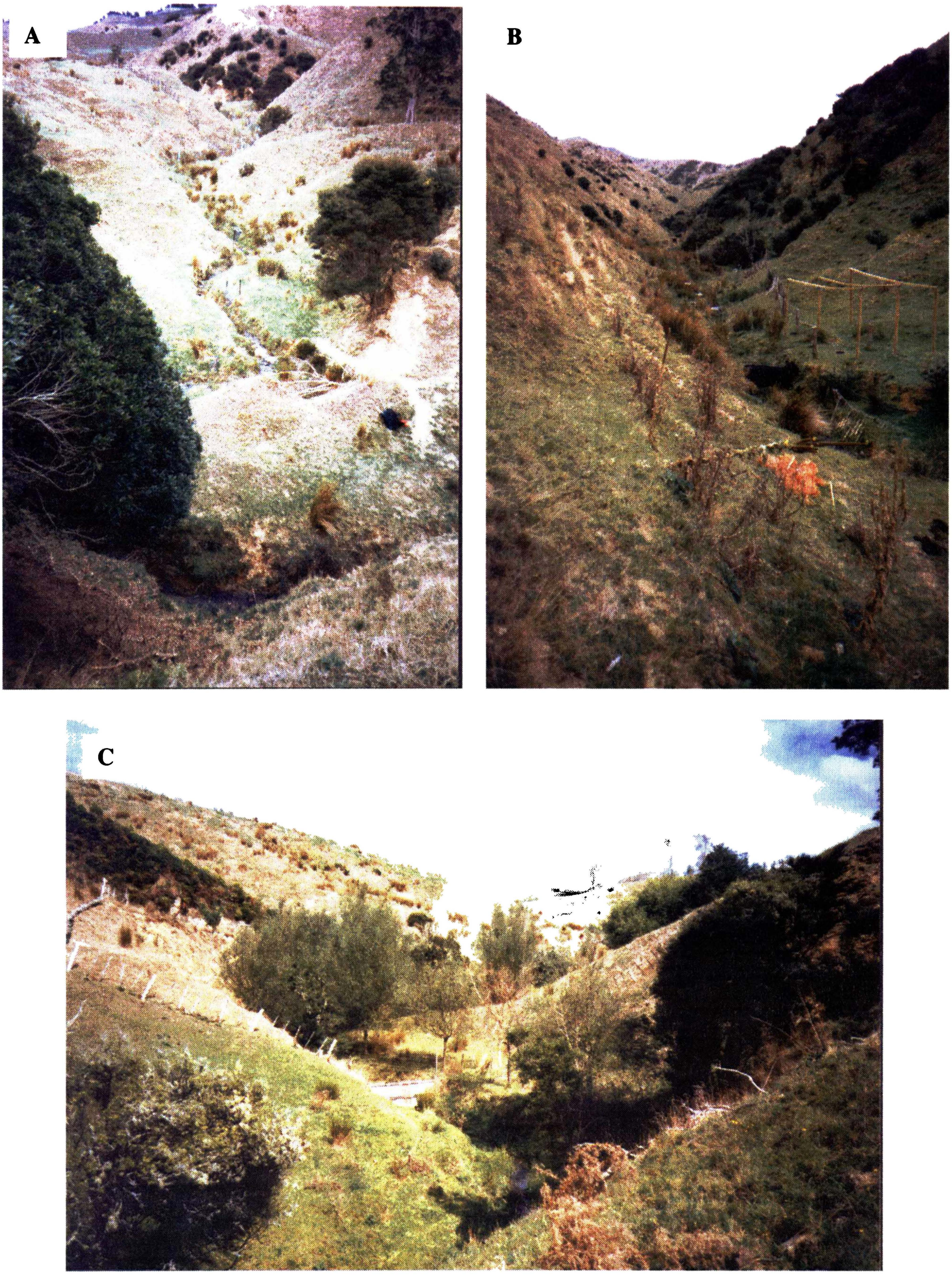


Plate 2.1. Study reaches of sites in pasture catchments; PW3 (A), PW2 (B), PW5 (C)

Plate 2.1 (cont.). Study reaches of sites in native forest catchments; NW5 (D) and NF (E).

Plate 2.1 (cont.). Study reach of the native forest site NKL (F).

Land development and vegetation

The pasture catchments were cleared of native bush c. 60 years ago and vegetated with clover and pasture grasses (Quinn et al. 1997). Small patches of the native trees mahoe (*Melicytus ramiflorus*), manuka (*Leptospermum scoparium*) and kanuka (*Kunzea ericoides*) were present in riparian areas of PW2 and PW3, but grasses and rushes (*Juncus effusus* and *J. gregiflorus*) were the most common vegetation along stream banks. The introduced crack willow (*Salix fragilis*) was the most common riparian tree at PW5, and occasional native manuka and kahikatea (*Dacrycarpus dacrydioides*) were also present. Within pasture streams, the emergent macrophyte *Rorippa nasturtium-aquaticum* was abundant during summer.

Sheep and beef cattle are carried at an average of 12 stock units per hectare and the largest paddock immediately surrounding the stream sites was 12.5 ha at site PW2 compared to 3.3 ha (PW3) and 1 ha (PW5). Current fertiliser use is 25 kg P ha^{-1} (reactive Phosphate rock) and 7 kg N ha^{-1} (Urea). Hormone sprays are used to control gorse and weed at average rates of 0.3 litre ha^{-1} (Grazon, MCPA/MCPB) and 0.06 litre ha^{-1} (2,4-D). Annual rainfall at Whatawhata Research Centre is 1608 mm (Quinn et al. 1999).

Tree ferns (*Cyathea* and *Dicksonia* spp.) and nikau palms (*Rhopalostylis sapida*) dominated the riparian areas of native forest stream sites. Other trees within the dense podocarp-hardwood forest included tawa (*Belschmiedia tawa*), rewarewa (*Knightia excelsa*), rimu (*Dacrydium cupressinum*), kahikatea, and mahoe. Selective logging occurred in the catchments of some stream sites once in the last 100 years (Quinn et al. 1999).

Water quality, temperature and stream flows

Water quality characteristics were measured monthly during 1996 for five of the study sites (Table 2.2, NIWA unpubl. data). Alkalinity and pH were similar at native and pasture stream sites, but levels of suspended solids, ammonia, and nitrates were all higher in the pasture streams. Although all pasture sites were within the same stream catchment, both the native forest and pasture catchments occurred in areas with similar geology of sandstone and siltstone (greywacke and argillite), so differences in water quality characteristics are likely to reflect the effect of land use rather than geology. The predominant soil type for all catchments was yellow brown earth soils (Smith et al. 1993).

Table 2.2. Annual means for water quality characteristics sampled monthly in 1996 at the stream sites in the Whatawhata Agresearch Station (NIWA, unpubl. data). EC = specific conductivity, TP = total phosphorus, SS = suspended solids.

Site	pH	EC (μs/cm) @ 25°C	Alkalinity (mg $CaCO_3$/L)	SS (mg/L)	Turbidity (NTU)	NH_4-N (μg/L)	TP (μg/L)	NO_3-N (μg/L)
PW3	7.35	93.7	17.3	18.2	15.3	20.4	67.6	940.4
PW2	7.49	92.1	16.5	19.2	17.6	14.1	46.0	523.9
PW5	7.31	94.3	16.9	16.8	17.5	15.9	40.1	496.5
NKL	7.27	105.6	17.8	7.9	12.4	7.9	35.3	244.0
NW5	7.45	111.7	22.2	4.8	9.1	6.2	47.6	103.7

Stream temperature was measured at each site at approximately 30 minute intervals with continuous data loggers (Onset Optical Stowaway) over 2 years beginning in September 1996. Mean monthly temperatures in pasture streams were on average c. 2°C higher than in native forest streams and there was a much greater range of temperatures, particularly during summer when maximum monthly temperatures were greater than 25°C but never reached 20°C in native forest streams (Fig. 2.2). Theft (NF only), logger malfunction, and loss, burial or lifting of the logger above the water column during floods (especially June 1998) caused interruptions to the data record at some point for most streams.

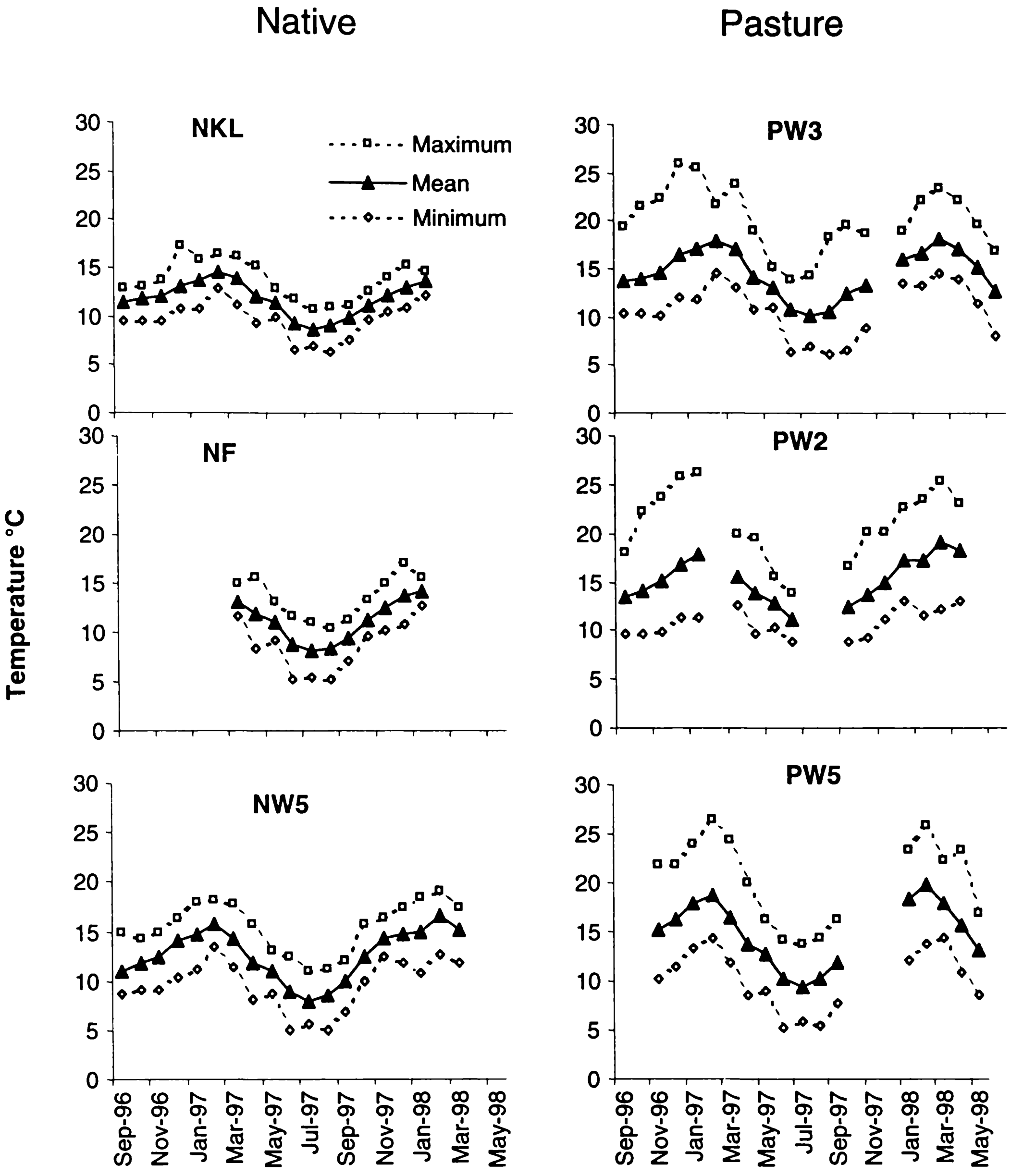


Figure 2.2. Mean monthly temperatures and monthly maximum and minimum temperatures from September 1996 to May 1998 for each stream site. See text for explanation of missing data.

Stream flows, measured at weirs situated on streams in a native forest (NW5) and pasture (PW5) catchment from September 1996 to March 1998, were highest from May to December (Fig. 2.3). Peak flows were generally greater in the pasture catchment (Mangaotama Stream) for equivalent storm events. Mean annual flows from six years of data were 80 L s^{-1} at the pasture stream weir and 50 L s^{-1} at the native stream weir (M. Bellingham, NIWA, pers. comm.). A one in 20 year flood in June 1998 (not shown in Fig. 2.3) caused peak flows of > 17 000 L s^{-1} at both the native forest and pasture streams.

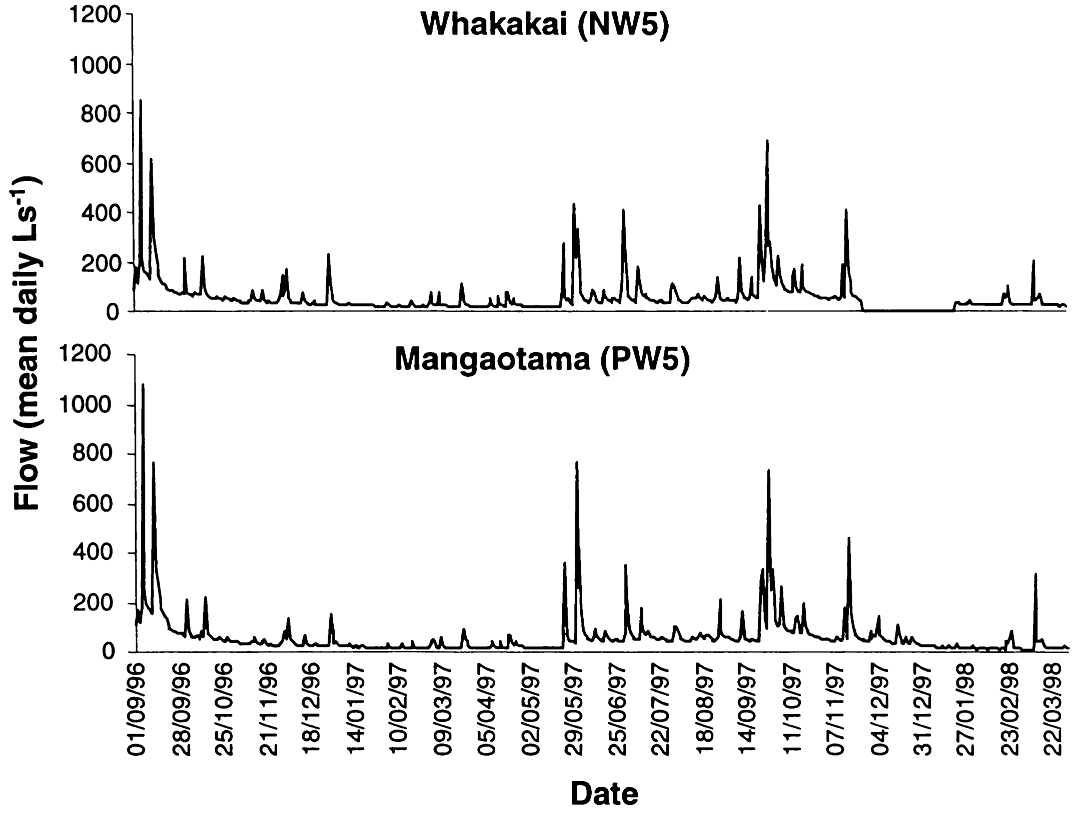


Figure 2.3. Stream flows measured between September 1996 and March 1998 by NIWA at weirs on the Whakakai Stream (native forest) and Mangaotama Stream (pasture) at the Whatawhata Research Station. Dr J. Quinn, unpubl. data (NIWA Hamilton).

Channel and water widths, water depths and velocities, and substrate size

Thalweg depth, current velocity (at 0.4 x depth, Montedoro-Whitney Model PVM2A meter), and channel and water widths were measured on five transects regularly spaced within each 6 – 8 m reach sampled for crayfish, in September 1996 and March 1997 (Table 2.3). All sites were shallow with occasional deep pools (> c. 50 cm), particularly in the larger native forest sites and PW5, and water velocity was about 0.2 m s^{-1} in both native forest and pasture sites. Channel and water widths were much greater at two native forest sites (NF and NW5) than in pasture streams, but the largest pasture site had the greatest average depth.

Particle size distribution was assessed using the "pebble count" method (Wolman 1954) at five cross-sections of each reach sampled for crayfish in March 1997, and included the occurrence of tree roots and wood (Fig. 2.4). The percentage of silt and sand was generally greater at pasture sites. Tree roots and wood occurred in the channel in native forest sites and also at PW5 where riparian trees occur sporadically alongside the study reach. The amount of large and small cobbles was greatest at the pasture site PW2 and the smallest native site NKL, whereas the widest native site (NF) had the largest amount of gravel substrate.

Table 2.3. Mean channel widths, water widths, velocity and depths measured in September 1996 and March 1997 at the time of crayfish sampling. Land use differences are indicated by P values (Mann-Whitney U, Wilkinson 1997).

Site	Channel widths (m)	Water widths (m)	Water velocity (m s^{-1})	Water depth (cm)
PW3	1.2	0.9	0.20	10
PW2	1.6	1.4	0.24	16
PW5	2.2	2.0	0.23	23
NKL	1.9	1.6	0.17	14
NF	4.1	2.9	0.17	17
NW5	3.9	3.2	0.16	17
P	ns	ns	< 0.05	ns

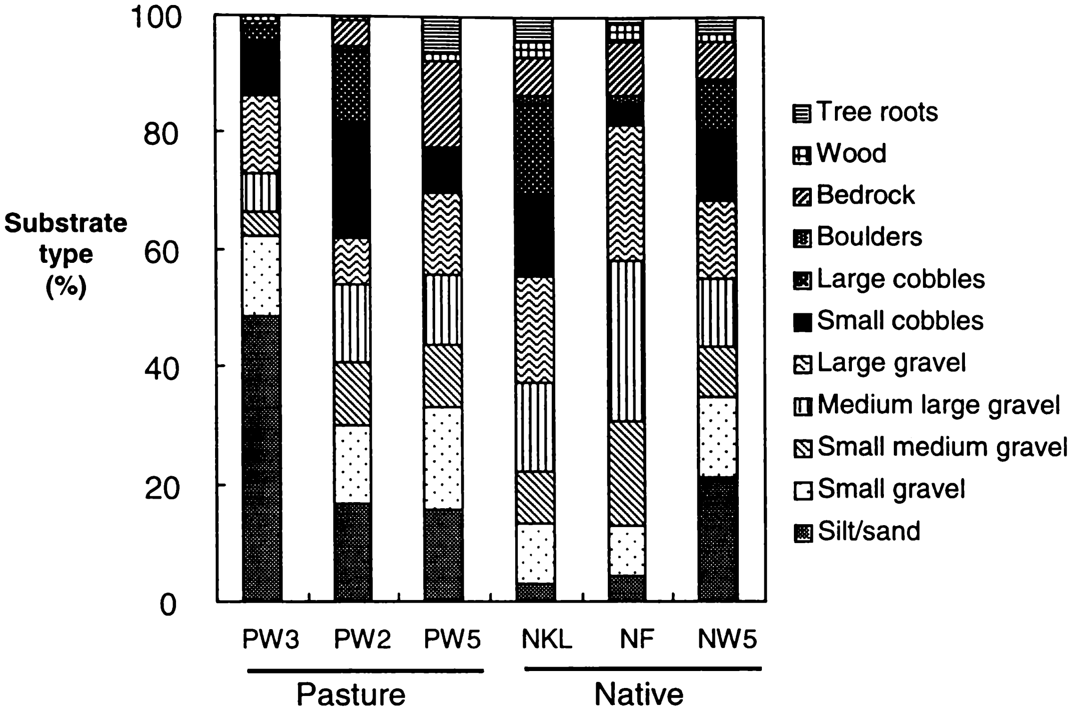


Figure 2.4. Mean percentage composition of different substrates (Wolman 1954) at each pasture and native forest stream site measured in four reaches in March 1997.

Potential food sources for crayfish

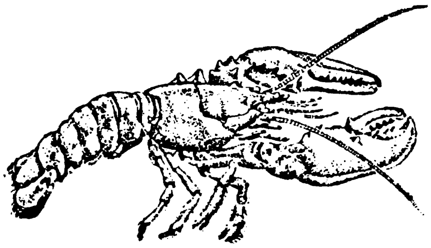
Leaf litter inputs in native forest streams were much greater than in the pastoral streams in this study (Dr M. Scarsbrook, NIWA, unpubl. data) but amounts of coarse particulate organic matter (CPOM, > 1 mm), were similar between native forest and pasture streams (Dr J. Quinn et al., NIWA, unpubl. data; Table 2.4). However, CPOM included measurements of macrophyte biomass, which can be seasonally abundant in pasture streams, as well as leaf litter. Periphyton was abundant in pasture streams where patches of filamentous green algae occur in summer. Invertebrate densities were much greater in pasture than in native forest streams, but the taxa richness of invertebrates was similar, although the composition had changed to species that utilise autochthonous energy sources (Quinn et al. 1997).

Potential crayfish predators

Hicks (1997) found crayfish remains in the stomachs of longfinned and shortfinned eels from native forest and pasture streams sampled in this study, but no other fish appeared to have consumed crayfish at the time of sampling (January and February). There are no introduced fish predators, e.g. trout, in these streams. Terrestrial predators that may consume crayfish include; kingfishers, rats, ferrets and humans who have access to site NF.

Table 2.4. Mean amounts of coarse particulate organic matter (CPOM, > 1 mm), medium particulate organic matter (MPOM, 250 µm < x < 1 mm), periphyton biomass, chlorophyll a (CHLa) content and invertebrate densities and taxa richness taken in four seasonal samples by Dr J. Quinn, unpubl. data (NIWA, Hamilton) between December 1995 and September 1996 (n = 4). Land use differences are indicated by P values (Mann-Whitney U, Wilkinson 1997).

Site	CPOM g dw m^{-2}	MPOM g dw m^{-2}	Periphyton mg AFDW m^{-2}	CHLa mg m^{-2}	Invertebrate density (0.4 m^{-2})	Invertebrate taxonomic richness (in a 0.4m^2 sample)
PW3	6.17	2.55	4036.0	35.5	1113.0	34.9
PW2	4.50	3.17	14772.6	94.7	1476.4	30.7
PW5	5.06	1.20	3597.6	21.9	1446.7	36.6
NKL	6.46	1.73	1596.0	1.1	318.1	30.9
NF	14.02	1.23	884.8	1.3	438.2	33.3
NW5	3.54	0.83	1092.9	3.7	816.3	35.4
P	ns	ns	< 0.05	< 0.05	< 0.05	ns



Chapter 3

Population dynamics of the New Zealand crayfish (*Paranephrops planifrons*) in streams within native forest and pastoral land uses.

Abstract

The population dynamics of crayfish in Waikato streams in native forest and pastoral land uses were sampled seasonally from September 1996 – July 1998. Crayfish densities were generally greater in native forest streams due to high recruitment over summer, but varied greatly between streams in both native forest and pasture land uses. Peak densities in summer were 9 crayfish m^{-2} in native forest and 6 crayfish m^{-2} in pasture streams, and mortality of young-of-the-year was greatest during winter in both land uses. However, peak biomass in summer was much greater in pasture streams than in native forest streams. Mark-recapture data showed that crayfish, particularly juveniles, in pasture streams grew faster than in native forest streams, through both greater moult frequency and larger moult increments. Females in pasture streams reached reproductive maturity after their first year at c. 20 mm OCL, but in native forest streams, females took two years to reach reproductive maturity at about the same size. There was no difference between growth rates of male and female crayfish, although crayfish > 2 years old in pasture streams and > 3 years old in native forest streams were not compared due to low numbers. Estimates of annual crayfish production (range = 0.8 – 3.4 g dw m^{-2} y^{-1}) were similar in streams of native forest and pasture land use, and P/B ratios were between 0.95 and 1.2. Juvenile production was greater than that of adult (reproductively mature) crayfish, due to high growth rates (P/B = 2.7 and 0.4, respectively), particularly in pasture streams. Despite deforestation and conversion to pasture, crayfish in these Waikato hill-country streams have maintained similar levels of annual production to those in native forest streams, although juvenile growth rates have increased and longevity has decreased.

Introduction

In New Zealand there are two species of freshwater crayfish, *Paranephrops planifrons* and *P. zealandicus* (Parastacidae), known locally by the Maori name "koura". *P. planifrons* is found in the North Island and in the north and west of the South Island and *P. zealandicus* in the south and east of the South Island. Considerable land use change has occurred in New Zealand particularly over the past 150 years. Widespread deforestation and conversion to pasture have affected the water quality, physical habitat and biotic communities of New Zealand streams through increases in water temperature, nitrogen and phosphorus concentrations, periphyton biomass, and levels of suspended and benthic sediments (Collier 1993, Quinn et al. 1997, Harding et al. 1999). Benthic invertebrate communities have increased in density and biomass in pasture streams, but community composition has changed to favour pollution tolerant species (Scott et al. 1994, Quinn et al. 1997). Fish abundance and biomass have also increased in pasture streams, but the diversity of species has declined (Hanchet 1990, Hicks & McCaughan 1997). Jansma (1995) found a negative relationship between the distribution of *P. zealandicus* and agricultural land use in Otago streams, but the effect of deforestation and conversion to pastoral land use on the population dynamics of *P. planifrons* is unknown.

In order to determine how the change in land use has affected crayfish within streams, it is necessary to consider their life history, growth, and secondary production. Secondary production is a measure of population success over time, as it combines both individual growth and population survivorship (Benke 1984). Environmental factors can affect growth rates and also the losses to the population from predation, non-predatory mortality or emigration through changes in habitat or predator populations.

Temperature has been described as the primary determinant of crayfish growth (Lowery 1988, Musgrove & Geddes 1995, Whitmore 1997) and stream temperatures have increased in response to deforestation (Quinn et al. 1999). Growth can also be influenced by the quality (Ackefors et al. 1992, McClain et al. 1992) and availability (Abrahamsson 1966, Jones & Momot 1983) of food, water chemistry (particularly calcium content, which is required during the moult process; Lowery 1988), shelter availability (Figler et al. 1999), environmental stress from water currents (Flint 1975) and density-dependent factors (Hopkins 1966, Morrissy et al. 1995). These factors may differentially affect the separate components of crustacean growth, i.e. the size of moult increment and length of intermoult period.

The aims of this study were to (1) provide a detailed description of the life history, abundance, biomass and longevity of *P. planifrons* in native forest and pastoral streams, (2) measure the growth rates of crayfish in terms of both moult increment and moult frequency, and (3) compare the annual production of crayfish from native forest and pastoral streams, as a comparative measure of population success in streams that have experienced significant land use change.

Methods

Crayfish density and weight

Crayfish populations of three streams draining native forest catchments (NKL, NW5, NF) and three streams draining pastoral catchments (PW2, PW3, PW5) in the Whatawhata AgResearch Station and Hakarimata Ranges west of Hamilton (Chapter 2) were monitored on four seasonal sampling dates per year from September 1996 to July 1998. Estimates of crayfish abundance were determined by electrofishing four 6 – 8 m long reaches at each site. Electrofishing was used as a collection tool as it was considered to be most effective at removing crayfish from beneath heavy cover (Rabeni et al. 1997). Reaches were chosen using a stratified random method where 10 reaches consisting of a pool and a run or riffle flow habitat were identified within a 100 - 200 m stretch of stream, and four were randomly chosen from these. A pool was included in each to standardise comparisons between the reaches. Each reach was fished by three people, using a push net (2.5 mm mesh), dip nets, and an EFM 300 electrofishing machine (Kainga Instrument Systems) powered by a 12 V battery, in an upstream direction using two to four consecutive passes to achieve > 75 %

reduction in numbers. The decline in the number of crayfish caught in each pass was used to estimate the population number in the reach (Armour et al. 1983).

Wetted channel widths (mean of five equi-distant cross-sections in each reach) and reach lengths were measured on each seasonal sampling date to estimate wetted area (m^2) and length sampled. Population numbers were expressed by area (m^2) and by length (lineal metre) of each reach, and density estimates for each stream were the mean of the four reaches. Where the population estimate failed because there was no reduction in numbers, the estimate for that reach was not included in the mean for each site. Biomass on each sampling date was calculated by multiplying the density estimate per reach at each site with the mean weight of all crayfish captured at that site on each date.

Orbit-carapace length (OCL) was measured with electronic Vernier calipers (0.1 mm) from the back of the eye socket to the mid-dorsal posterior border of the carapace (Hopkins 1967b, Jones 1981b). Crayfish > c. 7 mm OCL were sexed, and for all crayfish the number of chelae, and the presence of a soft carapace (indicating a recent moult), eggs, spermatophores or young were recorded as necessary. OCL lengths were converted to dry weights (g) for each crayfish and used to determine biomass, mean cohort weight and production at each site. Relationships between carapace length (OCL) and dry weight (0.0001 g W) were developed prior to sampling, for crayfish that had two, one or no chelae (n = 74, 7.8 – 25.5 mm OCL) and were described by the power regression equations: $W = 0.0001\ OCL^{3.264}$; $W = 0.0001\ OCL^{3.240}$; $W = 0.0001\ OCL^{3.125}$, respectively; $R^2 = 0.96$ for all equations. There appeared to be no difference between regression equations for female and male crayfish, although numbers of large crayfish (> 20 mm OCL) were low. Some crayfish species show allometric differences in growth whereby males develop larger chelae and females develop wider abdomens when they become reproductively mature (Lowery 1988). However, sexual dimorphism in *P. planifrons* was not obvious and any difference in the relationship between length-weight of males and females was assumed to be negligible.

Temperature

Stream temperature was monitored continuously using Onset temperature loggers in each stream from September 1996 to March 1998 (Chapter 2). Mean, maximum, and minimum temperatures for each month were averaged over the three sites in each land use type (Fig. 3.1).

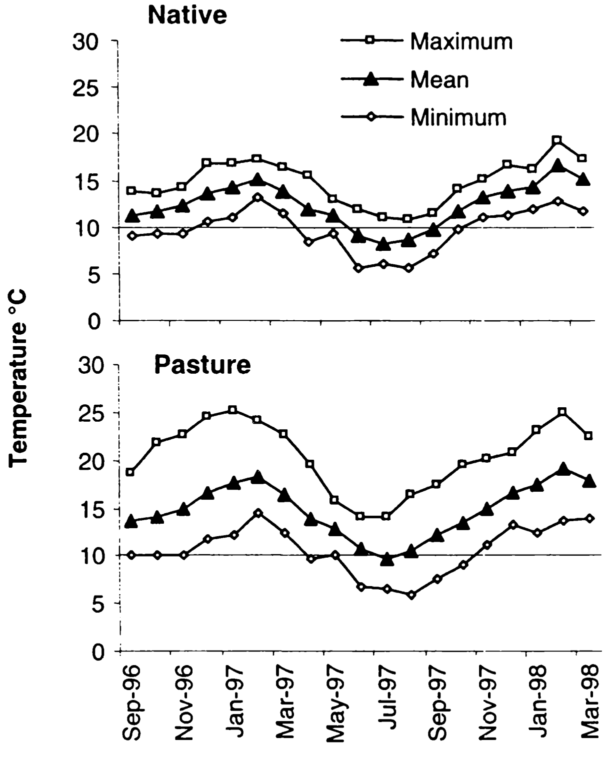


Figure 3.1. Mean monthly maximum, minimum, and mean temperatures for three native forest and three pasture stream sites in the Waikato region from September 1996 to March 1998. The line at 10°C represents the threshold for mean temperatures below which growth may not occur (see text).

Growth of mark-recapture crayfish

Mark-recapture was used to follow the growth of crayfish in each stream over two years. Crayfish > c. 7 mm OCL were marked with visible implant fluorescent elastomer tags (Northwest Marine Technology Inc.) injected into abdominal tissue. The elastomer is a biocompatible material, which upon mixing with a curing agent will set into a pliable solid within hours. This tagging system has been successfully used with salmonids (Morgan & Paveley 1996) and the crayfish *Paranephrops zealandicus* (Hollows 1998). The elastomer was injected into crayfish tail muscle with a 0.3 ml hypodermic syringe, and excess elastomer was wiped from the needle exit point to minimise the chance of tag loss. An initial experiment was conducted to test the effectiveness of elastomer tags by marking 10 crayfish (12.9 - 24.3 mm OCL) and holding these in an aquarium at 17°C for 7 weeks. During this time all crayfish retained their tags although some tags had shifted slightly within the muscle. One crayfish had moulted over this time and also retained its tag.

Crayfish were individually identifiable once tagged by using the method of Hollows (1998). The ventral surfaces of abdominal segments 1 – 4 were assigned a number on either side of the central nerve according to the geometric series 1+2+4+8+16+32+64+128. Elastomer could be injected into these positions giving a total of 255 tag combinations; for example, a crayfish marked in all the possible positions identifies it as number 255. Over the course of the two year study three colours of elastomer were used giving a total of 765 possible tags at each site. After marking, crayfish were returned to the location from which they were captured. At each successive sampling, recaptured crayfish were measured as above.

Additional marking of crayfish between study reaches was conducted at least once in all streams and up to 6 times at one pasture site (PW2) that had low crayfish densities, to add to the numbers of marked individuals in each stream. Initial sampling between reaches began in February 1997. A 100 m tape was laid along the thalweg of each stream beginning above the furthest downstream reach. Crayfish were sampled by electrofishing in an upstream direction and were measured and marked as above. The habitat, and position (in metres above the furthest downstream reach), of each crayfish was recorded and crayfish were released near their original habitat. Subsequent sampling between reaches was performed at the time of the seasonal sampling described above.

Success of tagging. Crayfish appeared to retain their tag marks successfully through many moults. However in some cases tags had shifted within the muscle or only "flecks" of elastomer remained at the entry point indicating that the tag had been lost. This made identification more difficult, but only 4% of recaptured crayfish could not be identified. Movement of the elastomer within the tail muscle appeared to be caused by the flicking action of the tail during escape swimming and was most likely to occur in the time before the elastomer had cured. Movement and loss of tags was most common with smaller crayfish (< c. 15 mm OCL), and was consistent with the observation that, on release to the water, small crayfish were more likely than large crayfish to use "tail-flicking" as a means of escape.

Production

Crayfish annual production was estimated from quarterly samples taken between December 1996 and December 1997 at each site. Three cohort year classes were identified in pasture streams and four in native forest streams from size frequency distributions and growth of mark-recapture crayfish (see results). Actual numbers of crayfish caught in each reach within each cohort size class were expressed as number m^{-2} and averaged over the four reaches. The annual density and weight (W) of each cohort was taken as the mean of the five sampling dates. Biomass was the product of density and mean weight of each cohort. The instantaneous growth method (Benke 1984) was used to calculate the production of the interval between year classes using the equation:

$$P = \mathrm{G}\, B$$

where production (P) was the product of the mean biomass (B) and instantaneous growth rate (G; $G = \ln (W_{final}/W_{initial})$ of the interval. Annual production (P) was the sum over all age classes (Rabeni et al. 1995). Annual turnover rates (P/B ratios) were generated from annual production and the sum of biomass estimates used to calculate production.

Production was calculated separately for crayfish identified as juveniles (i.e. those that had not reached reproductive maturity; c. < 20 mm OCL) and for adults (c. ≥ 20 mm OCL). Juveniles become reproductively mature after 1 year in pasture streams and after 2 years in native forest streams. Juvenile production was calculated for the interval between first and second year classes in pasture streams, but in native forest streams, production was the sum of the intervals between the first to second and second to third year classes.

Statistical analysis

Log transformed densities and biomass per m^2 and per lineal metre of crayfish from native forest and pasture land uses were compared using two-way nested ANOVAs of sites within land use, over all sampling dates. Growth of crayfish recaptured three or more times was followed through time and the growth rates of male and female crayfish (slopes of linear regression lines) were compared with a t-test. Differences between native forest and pasture streams in the regression lines of annual growth increments against initial carapace length, were compared with analysis of covariance (ANCOVA) after homogeneity of slopes analysis showed there was no significant difference between slopes. Moult increments were determined from quarterly growth increments and observations of recorded moults from field data, and differences in the regressions of moult increment with size between native forest and pasture land uses was tested with ANCOVA as above. Annual production estimates expressed on an areal and a lineal basis were compared for differences between land use with a t-test.

Results

Population density and biomass

Crayfish abundance varied greatly between seasons and between stream sites from September 1996 to July 1998 (Figure 3.2 A). Mean densities ranged from < 1 - 6 m^{-2} in pasture streams and from < 1 - 9 m^{-2} in native forest streams. Population numbers peaked in March when the majority of juveniles had entered the sampled population in both native forest and pasture streams. Variation between reaches (as indicated by error bars) was also high, due to variable availability of habitats that crayfish occupy within and between sample reaches.

Despite high variation between sites, log transformed densities of crayfish from native forest streams were higher than from pasture streams ($P < 0.05$), with sites nested into land use and over all sampling dates combined, and there was no significant interaction between land use and sampling date. The pasture site PW2 had consistently low numbers throughout the study period. Some study reaches sampled in September 1996 differed from those used in the rest of the study, possibly contributing to the low numbers recorded on that sampling date.

The smallest streams, NKL and PW3 appeared to support the highest densities (m^{-2}) of crayfish. However, crayfish were most often found associated with the banks of streams, and expressing density per m^2 may underestimate population density in wider streams. Native forest streams were generally wider than the pasture streams (see Chapter 2), and therefore the area sampled was greater, although crayfish were not usually present in the middle of these streams due to the lack of cover habitats. When densities were expressed per lineal metre to account for this difference (Fig. 3.2 B), peak densities in pasture streams were highest at the largest stream, PW5 (9 m^{-1} in March 1998) and the variation between sites was less. Numbers of crayfish per lineal meter of native forest stream were higher than in pasture streams ($P < 0.001$) and there was no interaction between land use and date. Densites per lineal metre remained high at the smallest site NKL (11 m^{-1} in March) and this site supported the highest densities regardless of the manner in which data were expressed.

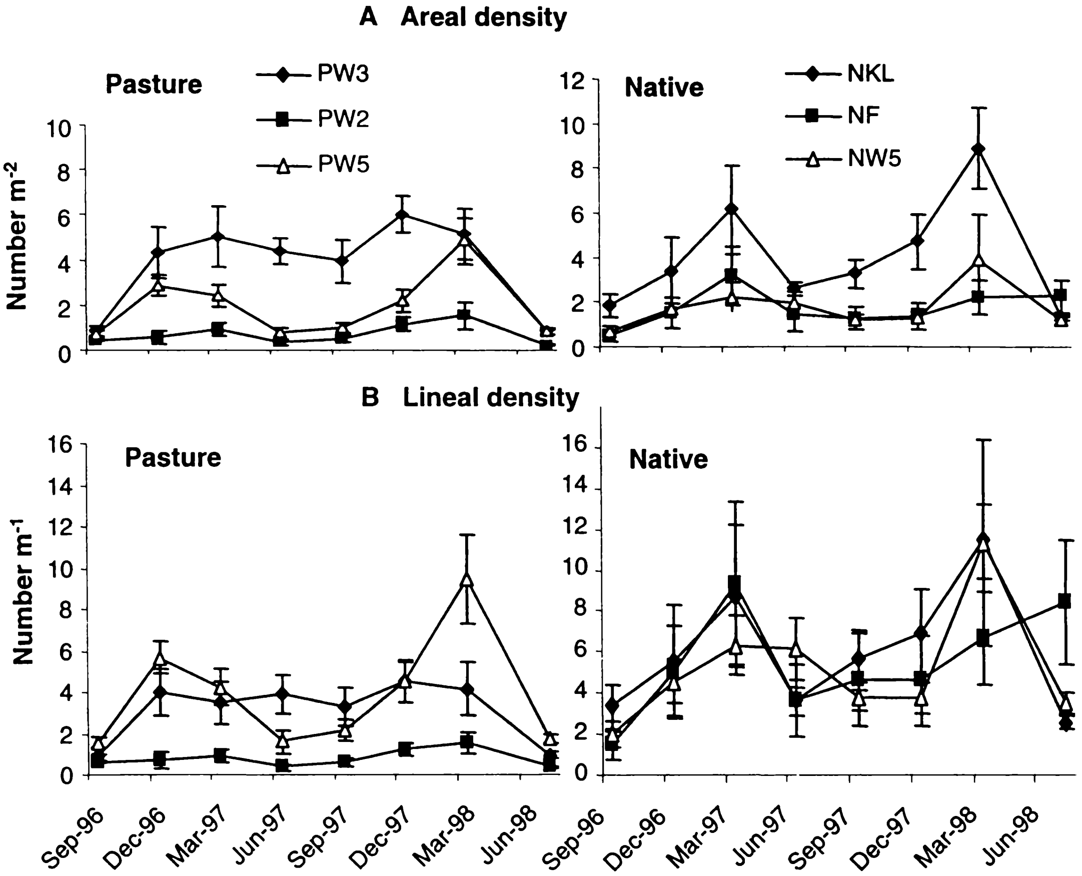


Figure 3.2. Mean (± 1 SE; n = 4) density of crayfish from three pasture and three native forest sites in the Waikato region between September 1996 and July 1998. A. Number m^{-2}; B. Number per lineal metre.

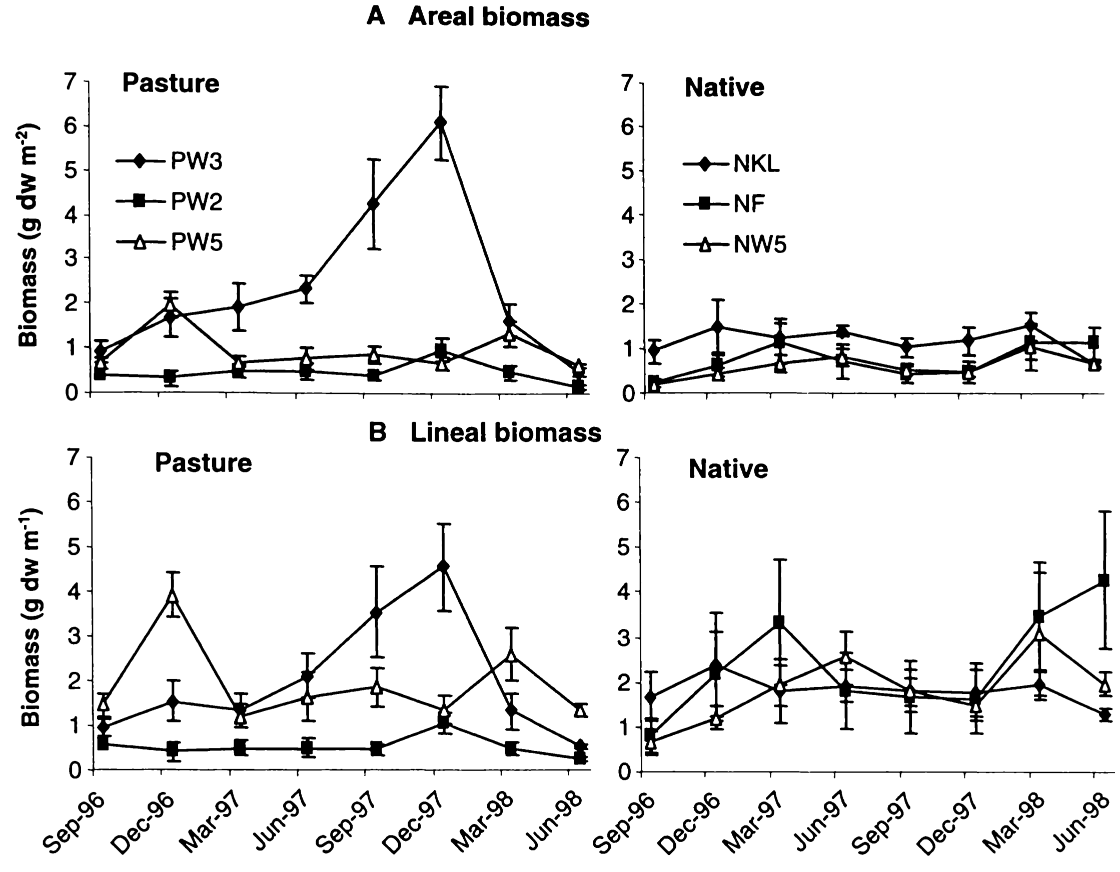


Figure 3.3. Mean (± 1 SE; n = 4) biomass (g dry weight) of crayfish from three pasture and three native forest sites between September 1996 and July 1998. A. Biomass m^{-2}; B. Biomass per lineal metre.

Biomass (g dry weight) of crayfish populations in pasture streams was significantly higher than native forest streams when expressed on an areal basis ($P < 0.001$; Fig 3.3 A) due largely to the extremely high biomass at site PW3, particularly in December 1997 (6 g dw m^{-2}). However, when biomass was expressed per lineal metre, crayfish in native forest streams had significantly higher biomass than pasture streams ($P < 0.001$) over all dates and with sites nested into land use. Expressing biomass per lineal metre in native forest streams distinguished the summer peaks in juvenile numbers that were not evident when biomass was expressed on an areal basis. Peaks in biomass m^{-1} were lower than for pasture streams, as the slow growth of juveniles in native forest streams resulted in very low mean individual weights, but greater densities (m^{-1}) contributed to the higher biomass over all dates when expressed per lineal metre. In pasture streams a combination of high numbers and high growth (see below) over summer dramatically increased peak biomass estimates. Mean (± 1 SE) individual weights of the populations were similar between sites within each land use and were greater in pasture (0.7 g dw ± 0.03) than native forest (0.4 g dw ± 0.02) streams (t-test, $P < 0.01$). However, despite higher growth rates in pasture streams, overall population biomass and variation between land uses were influenced primarily by differences in density.

Size frequency

Three size classes were identified as cohorts in pasture streams and four in native forest streams (Fig. 3.4; Table 3.1). Crayfish > 26 mm OCL were identified as > 4 years old in native forest streams and crayfish > 30 mm OCL were > 3 years in pasture streams, but numbers were too low to reliably identify year classes. The largest crayfish found in pasture streams was 37 mm and was estimated to be 4 years old, whereas the largest crayfish from a native forest stream was a 41 mm OCL female (in January 1998; not included in size-frequency analysis) estimated to be 7 years old based on reproduction and growth data. The young-of-the-year (YOY) cohort (Fig 3.4; open bars) in pasture streams entered the population between September and December 1996, earlier than in native forest streams, and their growth was much faster, although the variability was also high. In their first year of growth, juveniles grew to between 7 and 22.9 mm OCL in pasture streams and between 5 and 10 mm OCL in native forest streams (Table 3.1). Mortality was high for the first year cohort in pasture streams (39% mortality between March 1997 and September 1997), whereas in native forest streams mortality was 18% between the same time period. In December 1997, juveniles of the new YOY cohort once again entered the population in pasture streams, earlier than in the native forest streams.

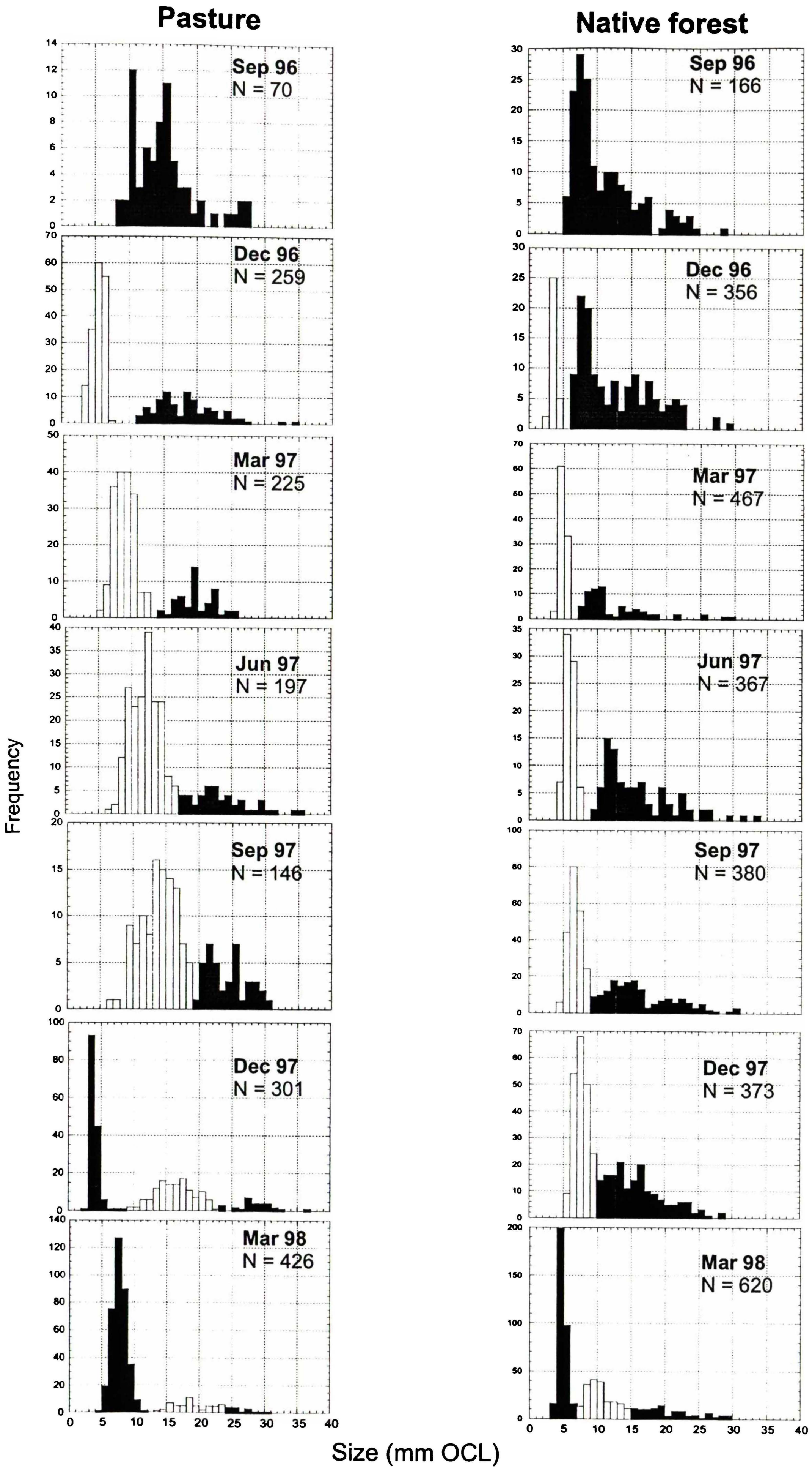

Pasture
Native forest
Sep 96
N = 70
Sep 96
N = 166
Dec 96
N = 259
Dec 96
N = 356
Mar 97
N = 225
Mar 97
N = 467
Jun 97
N = 197
Jun 97
N = 367
Sep 97
N = 146
Sep 97
N = 380
Dec 97
N = 301
Dec 97
N = 373
Mar 98
N = 426
Mar 98
N = 620
Frequency
0 5 10 15 20 25 30 35 40
Size (mm OCL)

Table 3.1. Changes in size classes (mm orbit-carapace length; OCL) for each cohort in native forest and pasture streams over one year, identified from size frequency graphs (Fig. 3.4) and analysis of mark-recapture growth data (Fig. 3.8).

Cohort	Land use	Size class (mm OCL)				
		Dec 96	Mar 97	Jun 97	Sep 97	Dec 97
0 – 1 year	Native	<4.9	<7.9	<8.9	<8.9	<10
	Pasture	<7.9	<12.9	<16.9	6-18.9	7-22.9
1 – 2 years	Native	5-12.9	8-14.9	9-17.9	9-17.9	10-19.9
	Pasture	11-21.9	14-23.9	17-24.9	19-26.9	23-29.9
2 – 3 years	Native	13-18.9	15-23.9	18-23.9	18-23.9	20-24.9
	Pasture	22-28.9	24-26.9	25-31.9	27-32.9	30-32.9
3 – 4 years	Native	19-23	24-26	25-26	25-26	>25
> 3 years	Pasture	>30	>30	>34	>34	>34
> 4 years	Native	>26	>26	>26	>26	

Reproduction

The sex ratio of males:females was close to 1:1 in both native and pasture land uses (0.95:1 and 0.91:1, respectively). Females carrying eggs (berried) were found from March to September in native forest streams and those carrying young were only found in December. In pasture streams, females with eggs or young were found in June or September. Two males with sperm evident (a toothpaste-like extrusion from the genital openings) were found in March 1998 in a native forest and a pasture stream. Females that were carrying eggs (khaki brown in colour) had also been found in March (1997 and 1998) with a triangular shaped spermatophore placed centrally under the thorax, beneath the genital openings on the second pair of walking legs. Mating appeared to occur in autumn (March – June) and females carried their eggs through winter, and released the juveniles generally between September and December in pasture streams and between December and March in native forest streams. The colour of the eggs changed from light brown to light red to dark red during development, but no attempt was made to record egg numbers systematically.

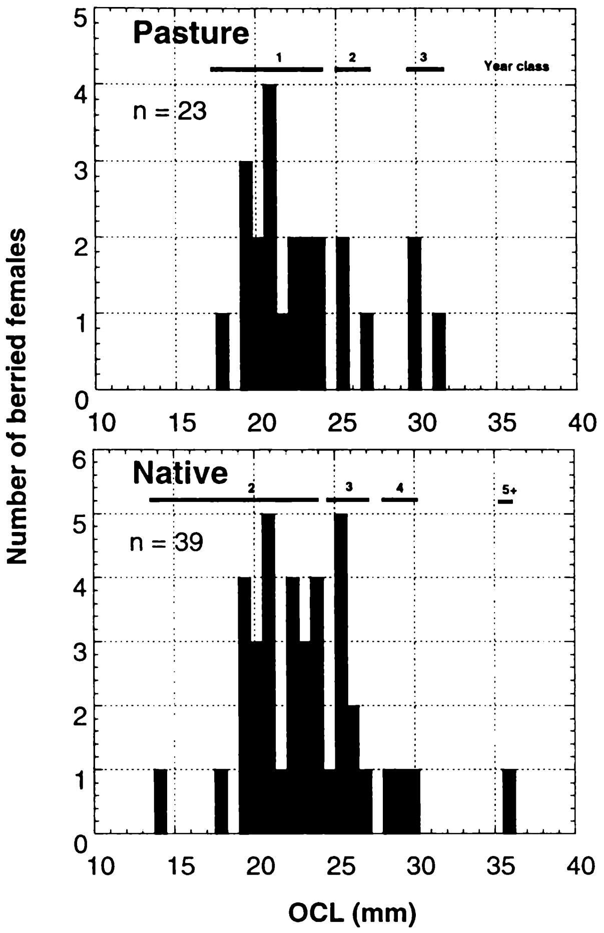


Figure 3.5. Size frequency plots of berried females in native forest and pasture streams (three streams pooled) from March to September. Year classes were identified from the size that each cohort reached in March when mating occurs. OCL = orbit-carapace length.

In pasture streams, the total number of berried females caught was 23 compared to 39 in native forest streams (Fig. 3.5). Females up to three years old were identified in pasture streams but females five years or older were evident only in native forest streams, based on the size range of each cohort in March (Table 3.1). Females may be capable of reproduction after the first year in pasture streams at c. 20 mm OCL (range = 17 – 24 mm OCL) in March, but in native forest streams they appear to reach reproductive maturity after two years, generally at the same size. The smallest berried female (14 mm OCL) was found in a native forest stream, but carried only 11 eggs. Although females take longer to achieve reproductive maturity in native streams, they may also live longer and survive to reproduce several times. Only six berried females > 25 mm OCL were found in the study reaches of pasture streams, compared to 12 in native forest streams. Large females are also known to have more eggs than smaller females (Hopkins 1967a), so the combination of longevity and greater fecundity of large females could contribute to the higher number of crayfish observed in native forest streams.

Movement

Approximately 350 crayfish were marked in each pasture stream and 420 in each native forest stream by July 1998 (Fig. 3.6). The number of recaptured crayfish in the stream populations increased as more crayfish were marked until September 1997. However, between December 1997 and March 1998 the number of recaptured crayfish declined greatly, despite a high number of marked crayfish in the population. The pattern is the same in both native and pasture streams suggesting greater movement during summer. The number of new marked crayfish increases in December and March of both years, more than in any other period, indicating that crayfish from other areas may be entering the study reaches during summer and that mortality is not the cause of the decline in the number of recaptured crayfish. Summer was also the time of most activity where crayfish have been seen moving during the day (SMP pers. obs.). The juvenile cohort is too small to be marked at that time in native streams so would not affect the numbers of new marked crayfish, although fast growing juveniles in pasture streams may be entering the marked population in March. A flood in June 1998 affected the number of recaptures in July (Chapter 4).

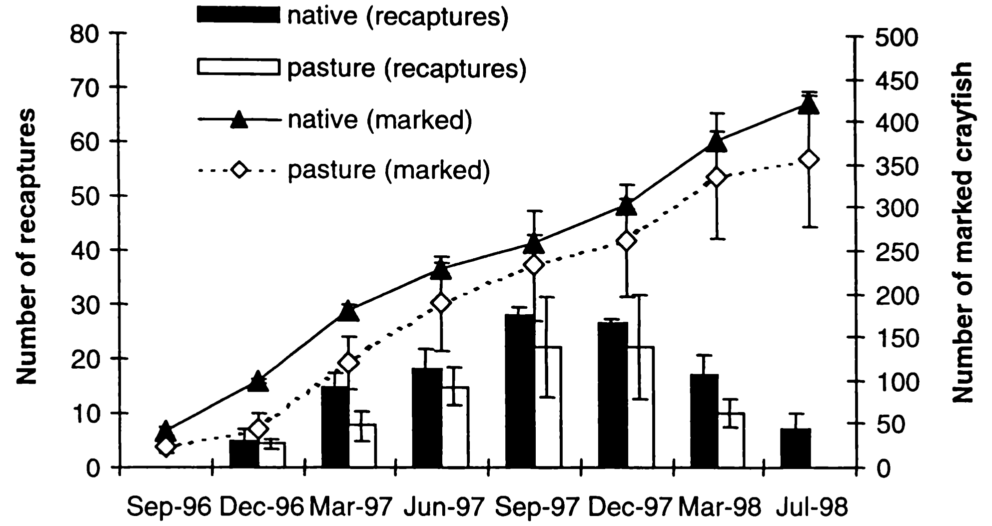


Figure 3.6. Mean (± 1 SE) cumulative number of marked crayfish (lines) and number of recaptured crayfish (bars) on each sampling date for three streams within each land use type.

Growth of mark-recapture crayfish

Growth occurred all year round in both native forest and pasture streams, but the percentage of crayfish that had grown during each quarterly monitoring period decreased during winter (Fig. 3.7). Only 50% of crayfish in native forest streams had moulted between June and September and this period coincided with a drop in mean temperatures below the 10°C threshold believed to limit crayfish growth (Fig. 3.1; Whitmore 1997, Hollows 1998). However, moulting did not cease entirely and only declined by 20% in pasture streams suggesting that the length of time that mean temperatures remained below 10°C was probably an important factor. Mean temperatures in pasture streams were below 10°C only in July 1998, compared to all three winter months in native forest streams. Crayfish that were old enough to moult only once or twice a year were excluded from this analysis as factors controlling their growth may be more strongly related to physiological age rather than environmental factors that could be influenced by land use change.

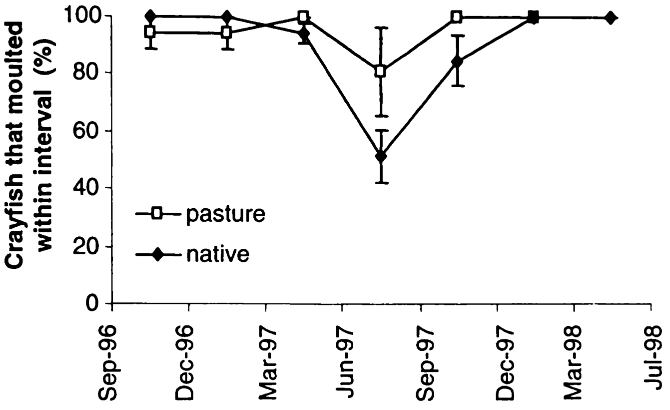


Figure 3.7. Mean (± 1 SE) percentage of recaptured crayfish that had moulted during each three month interval from September 1996 to July 1998 from three native forest and three pasture streams.

Three year classes in pasture streams and five year classes in native forest streams were identified from following the growth of individually marked crayfish that were recaptured more than three times during September 1996 to July 1998 (Fig. 3.8). Variation in individual growth rates was high within the year classes. In pasture streams, YOY were large enough to mark (c. > 7 mm OCL) in March, and grew to between 14 and 22 mm OCL by December of that year. In native forest streams, YOY grew to a mean of 11 mm by December. Crayfish appeared to moult only once or twice per year after 2 - 3 years in pasture streams and > 4 years in native forest streams. Numbers of large crayfish caught were low and variation in growth was high, which caused the declines in mean size between some sampling periods, but should not be interpreted as a decline in growth rates (Fig. 3.8).

Growth rates of female and male crayfish determined from recapture of marked individuals, were compared in the first and second year classes in pasture streams and the second and third year classes in native forest streams (Fig. 3.8). Linear regression equations were generated for each male and female crayfish and the growth rates (slopes of the lines) were compared using a t-test to examine differences between sexes within the year classes. In pasture streams, YOY males grew faster in their first year than females ($P < 0.05$), however numbers of females were low and there were no other significant differences between sexes for other age classes within land use. Difference in growth rates between males and females is most likely to occur when females reach reproductive maturity as they are unable to moult while carrying eggs or young, but there were too few crayfish with long term growth records in this age group to enable comparison.

Annual growth increments, determined from OCL measurements of crayfish marked and recaptured after a 12 month period between September 1996 and July 1998, showed that crayfish achieved significantly greater lengths in one year in pasture streams than in native forest streams (ANCOVA $F = 15.1$, $P < 0.001$, Fig 3.9). Variation in growth was high, particularly in small sized crayfish. Annual growth declined with the size of crayfish due to a reduction in the frequency of moulting with age (Fig. 3.8), as moult increment increased with crayfish age (see below, Fig. 3.10).

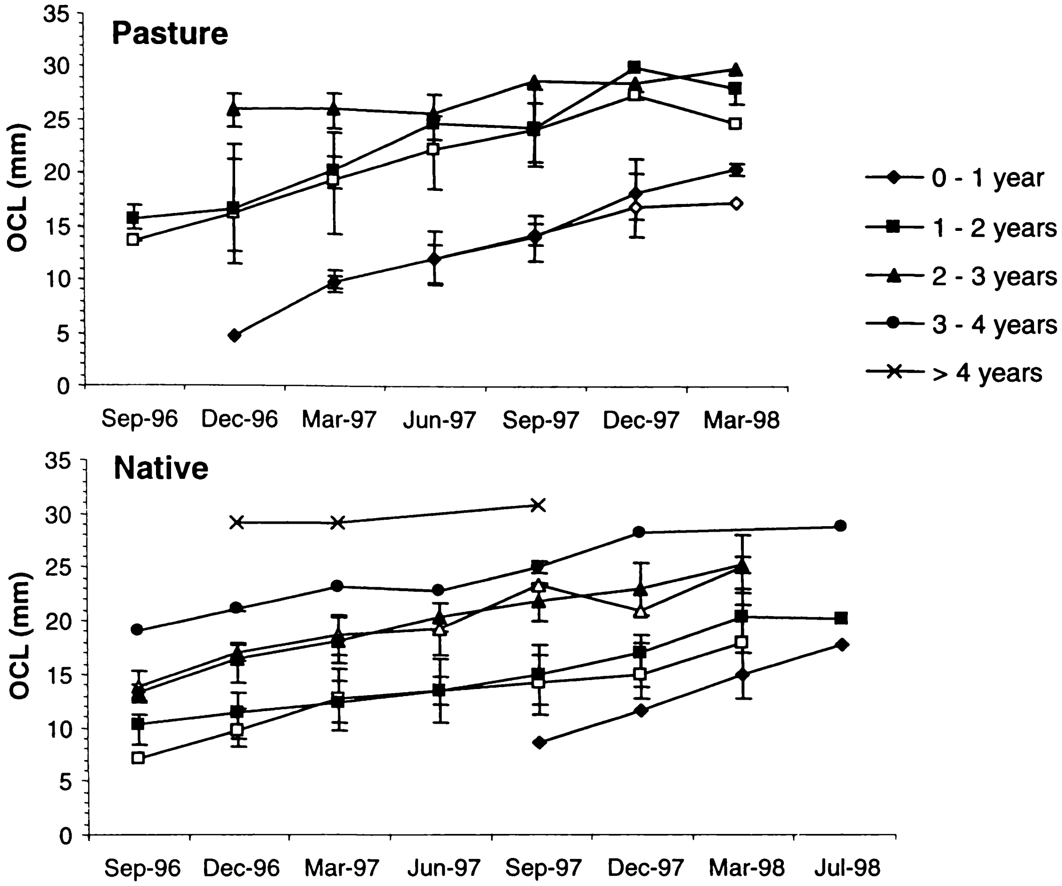


Figure 3.8. Mean growth in length of year classes identified from individually marked crayfish that were captured three or more times from September 1996 to July 1998 in native forest and pasture streams. Error bars = range of sizes. Open symbols = females, closed symbols = males, for the two year classes with sufficient numbers to enable comparisons, otherwise both sexes combined. OCL = orbit-carapace length.

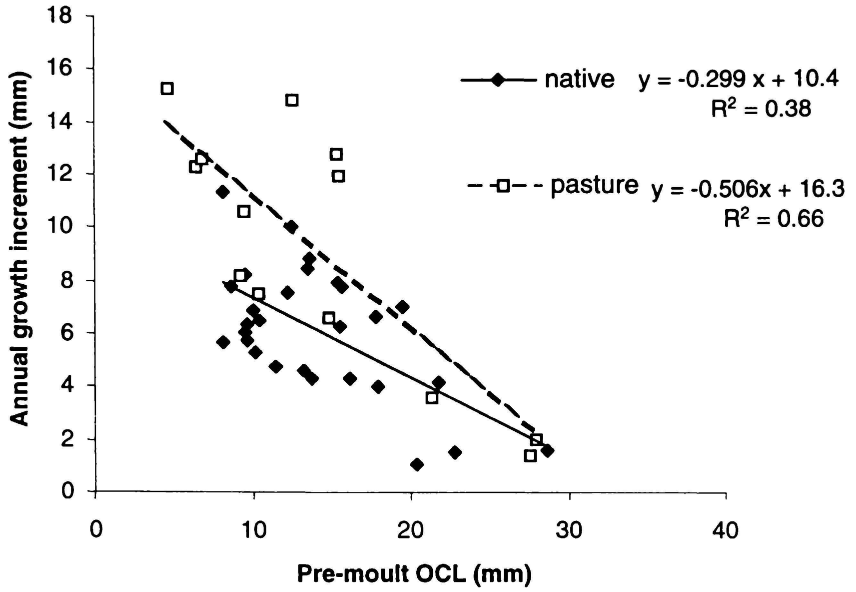


Figure 3.9. Annual growth increment plotted against pre-moult length (mm OCL) for crayfish recaptured after a 12 month period between September 1996 and July 1998 from three native forest and three pasture streams.

Crustacean growth is a function of both size increase at moult (moult increment) and the moult frequency. In order to separate these components of growth from field mark-recapture data, the growth increments for crayfish that had moulted between each quarterly sampling date (the smallest time interval measured) were plotted against pre-moult OCL (mm) (Fig 3.10). To identify the size of an individual moult increment, I compared Figure 3.10 to the regression of moult increments (observed in the field) with crayfish size (Table 3.2). In addition, moults that occurred in the summer periods (December – March in both years) were highlighted (open symbols) as multiple moults may be more likely to occur in summer when temperatures are higher (Chapter 6).

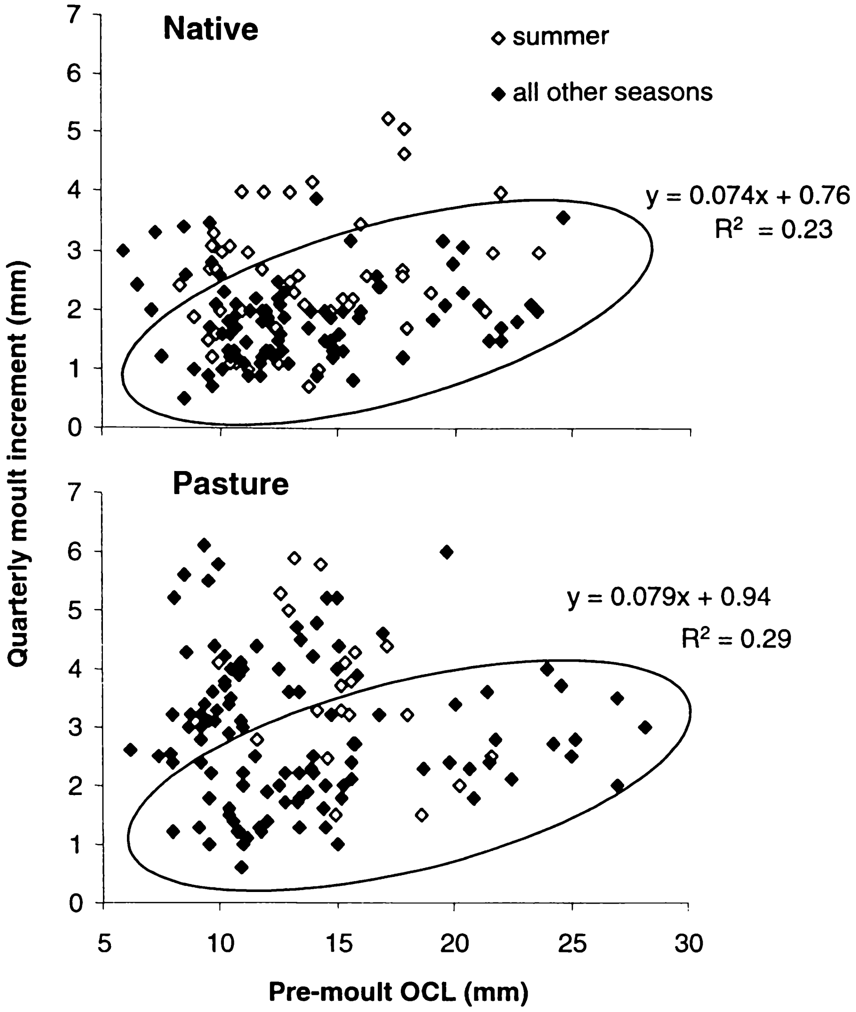


Fig. 3.10. Growth increments of recaptured crayfish that had moulted between each quarterly sampling date from September 1996 to July 1998 plotted against pre-moult length (mm OCL) in native forest and pasture streams. Moults that occurred in the summer periods (December – March) are shown separately (open symbols) to help identify multiple moults, as moult frequency may increase at warmer temperatures. Ellipses contain single moult increments determined from these data and observed moult increments (Table 3.2). Equations represent linear regressions of moult increment from data within the ellipses against pre-moult length (mm OCL). OCL = orbit-carapace length.

Table 3.2. Moult increments recorded from observed moults during field sampling at native forest (NKL and NF) and pasture (PW3 and PW2) streams and the regression equation derived from the relationship between pre-moult OCL and moult increment for all sites and sexes combined.

Site	Date	Sex	Pre-moult OCL (mm) x	Post-moult OCL (mm)	Moult increment (mm) y
NKL	June 97	-	5.0	6	1
NF	Sept 97	m	15.1	16.7	1.6
NF	Mar 98	f	23.6	26.6	3
NF	July 98	m	28.0	31.2	3.2
PW3	June 97	f	9.8	12	2.2
PW3	June 97	f	10.6	13.2	2.6
PW2	Sept 97	m	14.8	16.3	1.5
Regression equation			$y = 0.078x + 0.968$		$R^2 = 0.58$

There was considerable variation in the size of single moult increments (indicated by ellipses in Fig. 3.10), although increments increased with crayfish size, and at a constant rate between land uses. Comparisons between land use regressions of identified moult increments to pre-moult size showed that crayfish in pasture streams had a greater size increase at moult than crayfish in native forest streams (ANCOVA $F = 8.84$, $P < 0.01$). Thus for crayfish sized 10, 15, 20, and 25 mm OCL the moult increments were identified from the equations in Figure 3.10 as 1.5, 1.9, 2.2, and 2.6 mm in native forest streams, and as 1.7, 2.1, 2.5, and 2.9 mm in pasture streams.

Moult frequency also appeared to be greater in pasture streams, particularly with small crayfish (< 15 mm OCL) that may have moulted up to two times in native forest streams and up to three times in pasture streams within any three month period. Crayfish in native forest streams were more likely to have moulted twice in summer (Fig 3.10) whereas crayfish in pasture streams exhibited multiple moults in all seasons (particularly spring and autumn). However, crayfish between 5 and 10 mm OCL were found to have moulted three times only in summer in pasture streams.

The difference in annual growth increments between native forest and pasture stream crayfish (Fig. 3.9) may therefore be due to both the greater size of moult increment in pasture streams and the higher moult frequency of small-sized crayfish.

Cohort growth and production

Size classes for each year cohort present in the populations of native forest and pasture streams (Table 3.1) were determined from size frequency graphs (Fig. 3.4) as well as analysis of long-term growth data from mark-recapture crayfish (Fig. 3.8) and moult increments (Fig 3.10). The mean weights of each cohort present from December 1996 to December 1997 were plotted in chronological order to show the growth of crayfish over time. Variation was low between sites for each land use (indicated by error bars; Fig. 3.11). Growth in crayfish from both native forest streams and pasture streams was exponential for the first two years and became linear in the third year corresponding to an OCL length of 13 - 19 mm and 22 - 29 mm, respectively. Growth per year became linear when crayfish moulted only once or twice per year, usually in spring and autumn (stepwise growth). Individual weights for each year cohort were lower in native streams primarily due to greater initial growth rates in the first year of growth for pasture stream crayfish (Table 3.3). Annual growth rate was much higher for pasture stream crayfish in the first year allowing them to attain weights 13 times greater than native stream crayfish (0.9 and 0.07 g dry weight, respectively) at the end of the first year. Growth rates declined for both native and pasture crayfish in subsequent years as the number of moults decreased.

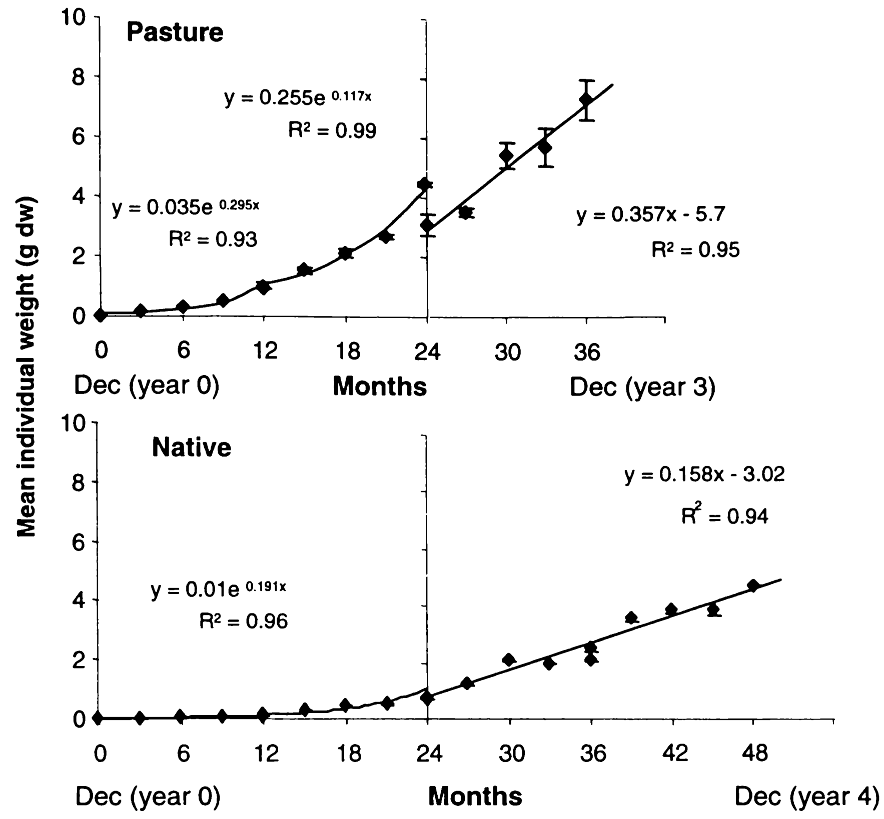


Figure 3.11. Average individual dry weight (g) for each cohort identified from one year (December 1996 to December 1997; Table 3.2) plotted consecutively to show the growth of crayfish over time. Means (± 1 SE) are for three native forest and three pasture streams. Equations represent exponential growth for crayfish up to two years of age and linear growth for crayfish > 2 years in both native forest and pasture streams. Growth equations are presented for each year class in pasture streams, as year-to-year variation between cohort weights was greater than for native forest streams, precluding use of a general growth equation.

Table 3.3. Growth rates for each of the cohorts present in the populations of native forest and pasture streams from December 1996 to December 1997. Growth rates (G) were determined using mean weights (W) by the equation $G = \ln(W_{final}/W_{initial})$ for each year class.

Cohort	Natural log of relative growth rate (G) Native	Pasture
0-1 year	2.43	3.71
1-2 years	1.52	1.49
2-3 years	1.16	0.86
3-4 years	0.82	

Crayfish annual production ranged from 0.8 – 3.4 g dw m^{-2} y^{-1} in pasture streams and from 0.8 – 1.6 g dw m^{-2} y^{-1} in native forest streams, but was not significantly different between land uses (Table 3.4). Site PW2 had very low production because of consistently low density throughout the study. The smallest streams in both native forest (NKL) and pasture (PW3) had the highest production values although this may be an artefact of the way that N m^{-2} may overestimate densities in small streams relative to wider streams (see Population density and biomass). When expressed per lineal metre of stream bed sampled, crayfish production at all native sites was similar (3.0 – 3.2 g dw m^{-1} y^{-1}), but production remained high in the smallest pasture stream (4.0 g dw m^{-1} y^{-1}). However, there was no significant difference in mean annual production per lineal metre between land uses. Crayfish biomass (g dw m^{-2}) in native forest streams was half that in pasture streams, although when expressed per lineal metre, the biomass estimates were almost equal. P/B ratios were near one for crayfish in both native forest and pasture streams, which is within the range found for most crayfish species (0.5 – 1.5; Momot 1995), but were lower for crayfish in most pasture stream sites due to high biomass.

Table 3.4. Annual production, biomass and production/biomass (P/B) ratios for crayfish populations at three native forest and three pasture streams and the mean for each land use, determined using the instantaneous growth method (see text for calculation details). Production and biomass are expressed per areal and per lineal metre of stream bed sampled.

Site	Biomass (g dw)		Production (g dw yr^{-1})		P/B
	m^{-2}	m^{-1}	m^{-2}	m^{-1}	
Native forest					
NKL	1.35	2.67	1.59	3.14	1.18
NF	0.69	2.77	0.80	3.20	1.16
NW5	0.70	2.54	0.83	3.00	1.20
Mean	**0.91**	**2.66**	**1.07**	**3.10**	**1.18**
Pasture					
PW3	3.60	4.20	3.41	4.01	0.95
PW2	0.67	1.04	0.80	1.24	1.19
PW5	1.31	2.84	1.27	2.76	0.97
Mean	**1.86**	**2.69**	**1.83**	**2.70**	**1.04**

Most of the total annual production per m^2 of streambed was due to juvenile crayfish (c. < 20 mm OCL) in both native forest (72%) and pasture (77%) streams (Table 3.5). Biomass (g dw m^{-2}) of the adult crayfish population was greater than juvenile biomass in each stream, but production of juvenile crayfish was three times that of adult crayfish and more than double that of their own biomass, due to the high growth rate of juvenile crayfish. The mean turnover (P/B) ratios for juvenile crayfish (2.7) were almost 7 times that of adult crayfish (0.4) in both native forest and pasture streams.

Table 3.5. Biomass and annual production estimates for juvenile and adult crayfish at each stream site. Production was calculated for juvenile crayfish corresponding to the age that they become reproductively mature (after one year in pasture and 2 years in native forest streams).

Site	Biomass (g dw m^{-2})		Production (g dw m^{-2} y^{-1})	
	Juvenile	Adult	Juvenile	Adult
Native forest				
NKL	0.44	0.90	1.22	0.37
NF	0.23	0.46	0.57	0.23
NW5	0.25	0.44	0.67	0.16
Mean	**0.31**	**0.60**	**0.82**	**0.25**
Pasture				
PW3	1.20	2.40	2.60	0.80
PW2	0.13	0.55	0.55	0.25
PW5	0.39	0.92	0.81	0.45
Mean	**0.57**	**1.30**	**1.32**	**0.50**

Discussion

Life history

Recruitment of juvenile (0 – 1 year class) crayfish in pasture streams (monthly average water temperature from June to September = 14 – 16°C) occurred approximately two months earlier than in cooler native forest streams (10 – 12°C). Egg development time was shorter in pasture streams than in native forest streams and appeared to be related to the stream temperature. Jones (1981a) increased development of *P. planifrons* eggs from 7 months at 10 – 15°C to 6 months at 20°C in laboratory conditions. Hopkins (1967a) found that *P. planifrons* in a pasture stream near Wellington mated in autumn and the females carried eggs over the winter for a period of 16 – 17 weeks. During spring and early summer, depending on temperature, eggs hatched into juveniles that were carried by the mother for several weeks and underwent two moults before they became independent. In a cool native forest stream in Otago, *P. zealandicus*, appeared to have a much longer incubation period with a mating season between December and January and egg hatching in December of the following year (Whitmore 1997). The development time of hatchlings is highly variable with some leaving the mother weeks before others. The total incubation time from eggs to independent juveniles for *P. planifrons* has been estimated as 6 months (Hopkins 1967a) compared to 15 months for *P. zealandicus* (Whitmore 1997).

Juveniles that enter the population in spring or early summer are also likely to grow larger in their first year than those that leave the female in late summer as they have the advantage of growth through the early summer months. *P. planifrons* is thought to reach reproductive maturity in 18 months to 2 years (Jones 1981a), depending on temperature. Crayfish in the pasture streams of my study reached reproductive maturity after 1 year, much earlier than in native forest streams, and earlier than many other crayfish species (c.f. 3 years for *Pacifastacus leniusculus*, Lewis 1997, Guan & Wiles 1999; 6 – 7 years for *P. zealandicus*, Whitmore & Huryn 1999). Free-living juveniles that entered the population between September and December in warm pasture streams grew to 7 – 22 mm OCL in one year and those c. 20 mm OCL

(17 – 24 mm OCL) were reproductively mature in the following autumn. In cooler native forest streams, most juveniles became independent between December and March and after 2 years reached a similar size to those in pasture streams before becoming reproductively mature. As the greatest mortality for juvenile cohorts occurred during winter, crayfish in pasture streams did not have to experience two winter periods before reproducing, possibly enabling them to achieve similar production estimates to crayfish in native forest streams.

The life cycle of crayfish in pasture streams was accelerated due to faster growth and they appeared to attain maximum ages after 3 – 4 years (c. 35 mm OCL), whereas the largest crayfish found in native forest streams was estimated to be 7 years old (41 mm OCL). Devcich (1979) showed that populations of *P. planifrons* in lakes grew to much larger sizes (c. 50 mm OCL; 9 - 10 years old) than those in streams and concluded that stream crayfish reached senescence at a much earlier age. Populations of *Austropotamobius pallipes* in large lakes in Britain grew more slowly than those found in rivers because the larger water body took longer to reach maximum summer temperatures and never attained temperatures equivalent to the river (Lowery 1988). The largest *P. zealandicus* found by Whitmore (1997) was estimated to be 25+ years old (85 mm carapace length) in a stream with cool annual temperatures (1.8 – 11.9°C).

The sex ratio of males to females was 1:1 in both native forest and pasture streams and females did not appear to breed every year. Fecundity is dependent on the size of the female, and Hopkins (1967a) found about 20 – 30 eggs on 17 mm carapace length females of *P. planifrons*, compared to up to 150 eggs on 30 mm carapace length females. The longer life of crayfish in native forest streams combined with the greater fecundity of large females suggests that the recruitment of juveniles may be greater in native forest streams and lead to higher population density, particularly during the peak recruitment period in summer.

Compared to the number of juveniles that entered the population, few crayfish survived beyond their first year. Greatest mortality occurred during winter (March - September) but was higher for crayfish in pasture (39%) than native forest (18%)

streams. Eels are the main predators of crayfish in these streams. The abundance and biomass of eels is greater in pasture streams than in native forest streams (Hicks & McCaughan 1997), and crayfish are likely to be most susceptible to predation when small. The greater moult frequency of juveniles in pasture streams than in native forest streams may also leave them more vulnerable to predation due to the higher number that will be soft (from moulting) in pasture streams. Floods or high flows in winter may also contribute to the decline in numbers, and floods are likely to affect crayfish in pasture streams more than in native forest streams as the habitat is less stable (Chapter 4).

Growth

Growth in *P. planifrons* occurred all year round in both types of stream, but declined in winter, especially in native forest streams (50% of marked crayfish did not moult) where mean water temperatures were below 10°C from June to August. Growth halts completely for *P. zealandicus* in Otago streams where the mean temperatures are below 10°C for 9 – 10 months of the year (Whitmore 1997, Hollows 1998). Temperature has been shown to be the primary determinant of growth for many crayfish species and growth often ceases over the winter months (Lowery 1988, Kawai et al. 1997, Turvey & Merrick 1997c, Whitmore & Huryn 1999). Jones (1981b) followed the growth of *P. planifrons* in heated (18 – 21°C) and unheated (10 – 21°C) aquaria for two years. He found that in unheated aquaria crayfish grew to 20 mm OCL after 12 – 18 months but this was increased to 35 mm OCL in 18 months in the heated aquaria. Diet can also affect growth rates of many species of crayfish (Ackefors et al. 1992, McClain et al. 1992) and best growth and survival has been achieved with animal protein (Oliviera & Fabião 1998) and zooplankton diets (Brown et al. 1992, Verhoef et al. 1998b).

Growth in crayfish is a function of size increase at moult (moult increment) and the length of time between moults (intermoult period). Crayfish in the warmer pasture streams of this study exhibited greater annual growth than in native forest streams, largely due to the higher moult frequency (i.e. shorter intermoult period) for YOY crayfish in pasture streams. The highest annual increase recorded for crayfish from pasture streams was 16 mm OCL compared to 12 mm OCL for crayfish in native forest streams. Only juvenile crayfish (< 20 mm OCL) moulted more than once in a quarterly sampling period and small crayfish (< 15 mm OCL) were able to moult up to three times in pasture streams, but only twice in native forest streams. Variation in moult frequency was particularly high for juvenile crayfish, contributing to the variation in annual growth increment. Growth in adult crayfish will be less affected by temperature than juvenile crayfish, as they moult only once or twice per year regardless of environment. Therefore, moult increment is more important for growth than moult frequency and this can be influenced by diet, particularly invertebrate food sources (Chapter 6).

The effect of temperature appears to have decreased the egg development time resulting in early summer recruitment of YOY and increased moult frequency. These factors have enabled YOY crayfish in pasture streams to attain much greater sizes and mean cohort weight by the end of their first year. Growth rates of older crayfish in pasture streams matched those of crayfish in native forest streams, but the size range and mean weight of the cohort was considerably greater in each consecutive year than in native forest streams. Moult frequency of YOY crayfish may also be influenced by diet (Chapter 6), therefore the higher consumption of invertebrates by crayfish from pasture streams (Chapter 5) may contribute to increased growth rates, in conjunction with warmer temperatures. Hopkins (1966) measured growth of *P. planifrons* in pasture streams near Wellington and found the slowest growth rates in streams with the highest densities of crayfish, although he did not compare growth rates with stream temperature. The densities of crayfish in his streams (up to 27 m^{-2}) were much higher than in this study and therefore density-dependent factors (e.g. cannibalism, resource (food or habitat) limitation) were unlikely to have been the primary factors affecting growth rates of crayfish in these hill-country streams.

Warm temperatures increase moult frequency, but may decrease (Verhoef et al. 1998a) or have no effect (Chapter 6) on the size of moult increment. Moult increments increased with crayfish size and were higher for all sizes of crayfish in pasture streams than in native forest streams. A diet of invertebrates produced higher moult increments in juvenile *P. planifrons* than did a diet of leaf litter (Chapter 6), and *P. planifrons* consumed more invertebrates in pasture streams than in native forest streams (Chapter 5). Therefore, diet may be a significant factor affecting the moult increments of crayfish between streams with different adjacent land uses.

Variation in the size of moult increments was high for crayfish in both native forest and pasture streams. Similar variation in moult increment by the Australian parastacid crayfish *Euastacus spinifer* was attributed to food availability or population density (Turvey & Merrick 1997c). Temperature is unlikely to cause variation in moult increments, as it would not vary greatly within the stream sections that crayfish were sampled from. Therefore, diet, genetic variability between individuals, and differential uses of flow habitats that require energetic expenditure (Flint 1975) may affect individual growth.

Density, biomass and production

Crayfish densities were greater in native forest streams than in pasture streams, although there was high variation between the stream sites. Expressing densities per lineal metre of stream, as crayfish were most likely to be found along stream banks, provided a more accurate representation of the summer peaks of YOY crayfish in native forest streams. Densities over all dates combined were significantly higher when expressed either per m^2 or per metre in native forest streams than in pasture streams and this was probably largely due to higher recruitment over summer. However, greater mortality during winter reduced the population densities to similar levels as in pasture streams. All native forest streams and the pasture site with riparian trees (PW5) appeared to have a slightly higher recruitment of YOY in the second summer season sampled, possibly indicative of a stable winter period, although differences in the proportion of females breeding from year to year may be a factor.

One pasture site (PW2) had consistently low crayfish densities throughout the study. The reasons for this are unlikely to be due to water quality or pollution as this stream does not appear to differ in water chemistry from the other pasture streams in this study and stream invertebrates (other than crayfish) are present at high densities (Chapter 2). However, this site is within the largest paddock of any stream site in this study and may therefore be subject to higher numbers of stock accessing the stream (Plate 2.1 B). Furthermore, the channel of this stream was affected by erosion from floods in June 1998 more than any other stream (Chapter 4). Therefore, instability of habitat either through stock trampling of banks or flood events may be the greatest influence on crayfish density in this stream.

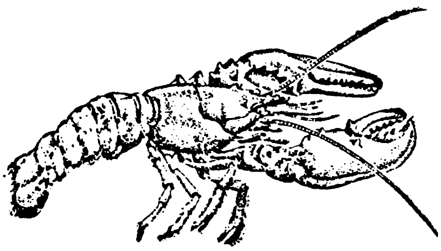
Peaks of crayfish biomass during summer were much greater in pasture streams than in native forest streams, due to the faster growth rate of YOY crayfish. Mean weights of individual crayfish in pasture streams were higher than in native forest streams, as YOY became free-living earlier and gained substantial weight in the first few months, either through warmer stream temperatures, from consuming more invertebrate food or a combination of these factors. Once again expressing biomass per lineal metre provided a better representation of the peaks of recruitment in native forest streams, as the middle area of streams that are largely under-utilised by crayfish, were not included in this analysis.

Crayfish annual production did not differ between native forest and pasture streams. The lack of an effect of deforestation is somewhat surprising given that Hopkins (1976) found that the total invertebrate production was lower in shaded sections of two North Island streams. Similarly, the production of fish was higher in pasture than native forest streams (Hicks & McCaughan 1997). Higher densities of crayfish in these native forest streams were balanced by the greater growth and mean weight of crayfish cohorts in pasture streams, resulting in similar values of annual production. Two species of crayfish (*Orconectes* sp.) in Missouri streams had equal estimates of annual production (4.9 g dw m^{-2} y^{-1}) despite production of *O. luteus* being due to high densities, while production of *O. punctimanus* was the result of high growth rates (Rabeni et al. 1995). The variation in annual production estimates between the streams in my study was largely due to the variation in density rather than mean cohort weights, which were remarkably similar within streams of the same land use type despite high variation in individual growth.

Roell & Orth (1992) found that production of three crayfish species (*Orconectes* sp.) in a river appeared to be lower than that of the same species in small streams, but concluded that production of crayfish per stream length was greater in the river. When annual production for *P. planifrons* was expressed per lineal metre, the estimates of production more than doubled in native forest streams and the variation was greatly reduced. However, in pasture streams the smallest site (PW3) supported the highest estimate of crayfish annual production, when expressed on either an areal or a lineal basis. Crayfish production appears to be most accurately represented in native forest streams on the basis of stream length rather than bed area, due to the lack of cover habitats across most of the wetted channel width. However, crayfish utilisation of the full width of streams may increase at night while they are foraging, and expressing production on a lineal basis is of limited value for comparisons between studies of crayfish annual production.

Production of *P. planifrons* (0.8 – 3.4 g dw m^{-2} y^{-1}) in these streams was lower than that of the other New Zealand crayfish species *P. zealandicus* (2 – 11 g AFDM m^{-2} y^{-1}, approximately equivalent to 3 – 16.5 g dw m^{-2} y^{-1}) in a cool temperate Otago stream (Whitmore & Huryn 1999). The high annual production of *P. zealandicus* was due to high biomass and longevity rather than high growth rates, as turnover rates (P/B) were very low (0.33-0.43). P/B ratios were considerably higher for *P. planifrons* (0.95 – 1.2) due to higher growth rates, and within the range found for most other crayfish species (0.5 - 1.5; Momot 1995). Annual production of juvenile crayfish was three times greater, and turnover ratios (P/B) seven times greater, than for adult (reproductively mature) crayfish, due to the higher growth rate (moult frequency) of juveniles.

Crayfish in pasture streams have maintained similar levels of production to those in native forest streams, despite the considerable change that deforestation and conversion to pastoral land use has caused to stream systems. However, crayfish densities are lower in pasture streams due to higher recruitment of YOY in native forest streams, which may be influenced by the greater longevity of crayfish there. Water temperature seems to be a major factor contributing to the higher growth rates and consequently shorter life cycle of crayfish in pasture streams.



Chapter 4

Habitat use and the effect of a flood on populations of the New Zealand crayfish *Paranephrops planifrons* in native forest and pasture streams

Abstract

A major flood (1 in 20 year return period, peak flows 18 - 22 $m^3 s^{-1}$) in June 1998 significantly affected crayfish (*Paranephrops planifrons*) populations in hill-country pasture streams, Waikato, New Zealand. Population densities (m^{-2}) and habitats of crayfish in three native forest and three pasture streams had been measured seasonally for two years prior to the flood and many crayfish had been marked with individually identifiable tags. In July 1998 (post-flood), pasture streams had significantly lower densities of crayfish than native forest streams and no previously marked crayfish were identified in any pasture stream. Banks of pasture streams were scoured during the flood and channels widened significantly at one stream. In native forest streams, banks in the study reaches remained stable during the flood due to established riparian forest, and pools, tree roots and undercut banks provided refugia for crayfish. Macrophytes and cobbles were the dominant habitats of crayfish in pasture streams, but they did not provide stable refugia during the flood. Crayfish density in one pasture stream was monitored 2, 5, 9 and 12 months following the flood. Recovery of the population was very slow and one year after the flood (June 1999) density was only 16% of that in June 1997 indicating that *P. planifrons* does not exhibit resilience traits and requires stable refugia to enable population re-establishment after large floods. Therefore, the extent of stable habitat is of fundamental importance to the persistence of crayfish populations through disturbances, and the absence of stable patches of headwater forest coupled with the slow reproductive rate of crayfish affect their recovery from disturbance. Deforestation and conversion to pasture has reduced the amount of stable habitat available to crayfish in these Waikato hill-country streams.

Introduction

Over the past 150 years, widespread deforestation and conversion to pastoral land use has effected the water quality, physical habitat and biotic communities of New Zealand streams. Removal of riparian vegetation has caused increases in water temperature (Quinn et al. 1997), and sheep and cattle farming has increased inputs of diffuse and point source pollutants (Collier 1993). This has lead to increases in nitrogen and phosphorus concentrations, periphyton biomass, and levels of suspended and benthic sediments (Quinn et al. 1997, Harding et al. 1999). Cattle grazing on the banks of small streams can cause degradation of bank habitat (Williamson et al. 1992) and the loss of riparian vegetation reduces the amount of in-stream cover for fish through decreasing the amount of woody debris entering streams and de-stabilising undercut banks that were bound by tree roots (Hanchet 1990). The impact of habitat degradation from agricultural activities has been demonstrated for benthic invertebrate (Scott et al. 1994, Quinn et al. 1997) and fish (Hanchet 1990, Hicks & McCaughan 1997) communities, but the effect of deforestation and conversion to pastoral land use on the habitat use of the native crayfish (*Paranephrops planifrons*) is unknown.

Cover is a very important habitat feature for crayfish species. Darkness (i.e. shadow provided by cover) was the primary factor influencing the cover seeking behaviour of juvenile and adult *Orconectes rusticus* and *Procambarus clarkii* in laboratory experiments (Alberstadt et al. 1996, Steele et al. 1997). Deforestation of Waikato hill-country streams has resulted in a change from heavily-shaded, forest streams where associated leaf litter inputs, coarse woody debris and tree roots can potentially provide cover for crayfish, to incised, open channels that receive 1000 times more light (%DIFN; Quinn et al. 1997) and are often grazed to the stream edge by sheep and cattle. The abundance and biomass of eel predators has also increased in pastoral compared to native forest streams in the Waikato region (Hanchet 1990, Hicks & McCaughan 1997). Jansma (1995) found anecdotal evidence that the distribution and abundance of crayfish (*Paranephrops zealandicus*) appeared to be declining in Otago streams and that agriculture negatively impacted on crayfish distribution, although the mechanisms of impact were not apparent at the spatial scale of that study.

The most important reason, apart from disease, for the disappearance of crayfish from inland waters in Europe has been the destruction of habitat by canalising, dredging, embanking and damming waterways (Westman 1985). Catchment clearance, channel modification and regulation of flow regimes are also threats to aquatic invertebrates in New Zealand streams (Collier 1993). In British streams, the presence of the crayfish *Austropotamobius pallipes* has been strongly linked to habitat characteristics associated with the riparian environment, particularly the extension of tree roots into the water (Smith et al. 1996) and tree shading, whereas eroding cliffs and reinforced banks have been associated with the absence of this crayfish species (Naura and Robinson 1998).

Deforestation not only alters the physical habitat available to crayfish, but it can also increase peak flows and water volumes during flood events (Rowe et al. 1997). In general, flood discharges in New Zealand streams are high on a world scale, due to high rainfall and steep terrain, and floods may be frequent but of short duration (Winterbourn 1995). Disturbance through flooding is a major determinant of community structure in streams and an important selective force in the evolution of life history characteristics (Resh et al. 1988, Townsend 1989). To persist in streams that experience disturbance, populations may exhibit resilience (the capacity to rapidly increase in density following disturbance) or resistance through refugia within spatially heterogeneous stream systems (Townsend et al. 1997). Invertebrate populations recover quickly from the effects of floods through recolonisation by drift, oviposition by adult insects or by finding refugia within the substrate or hyporheic zone (Scarsbrook 1995, Jowett 1997). However, fish recolonise streams by migration and may take several years to re-establish after severe floods (Jowett 1997). No studies in New Zealand have investigated how crayfish respond to flood disturbance and whether or not their ability to survive disturbances has been altered with the changes in land use.

On 9 June 1998 a significant rainfall event (maximum intensity 34.2 mm h^{-1}) occurred in the Waikato region producing stream flows at the AgResearch Whatawhata Research Station with a calculated return period of 21 years. Peak flows of 17.7 m^3s^{-1} were measured at the Mangaotama stream weir (2.6 ha pasture catchment) and 21.8 m^3s^{-1} at the Whakakai weir (3.2 ha native forest catchment) where mean flows had been recorded for 6 years as 0.08 and 0.05 m^3s^{-1}, respectively (M. Bellingham, NIWA, pers. comm). Population densities and the habitats of crayfish in three native forest and three pasture streams in this region had been monitored seasonally from September 1996 to March 1998 prior to the flood and were re-sampled three weeks after the flood in July 1998 to assess whether crayfish populations had been affected.

Although predation has been shown to influence the habitat choice and distribution of many crayfish species (Stein 1977, Kershner & Lodge 1995, Jordan et al. 1996a, Usio & Townsend in press), few studies have addressed the importance of hydrological factors in determining the habitat and distribution of crayfish in streams. The aim of this study was to investigate whether deforestation altered crayfish habitat and whether a large flood disturbance had a greater impact on crayfish populations in pasture streams than in native forest streams. To achieve this aim, I determined: (1) the types of crayfish habitats in native forest and pasture streams, (2) crayfish densities before and after the one in 20 year flood, and (3) the rate of recovery of a crayfish population in one small pasture stream without native forest headwaters to determine whether crayfish exhibited resistance or resilience traits to disturbance.

Methods

Measurement of crayfish density, habitat and movement

Crayfish populations of three streams draining native forest catchments (NKL, NW5, NF) and three draining pastoral catchments (PW2, PW3, PW5) in the Whatawhata Agresearch Station and Hakarimata Ranges west of Hamilton (Chapter 2) were monitored on four seasonal sampling dates per year from September 1996 to March 1998 prior to the flood, and in July 1998, three weeks after the flood. Estimates of crayfish abundance were determined from the removal method by electrofishing four 6 – 8 m long reaches at each site. Electrofishing was used as a collection tool as it was considered to be most effective at removing crayfish from heavy cover (Rabeni et al. 1997). Potential sampling reaches were chosen using a stratified random method where 10 reaches comprising a pool and a run or riffle were identified within a 100 - 200 m stretch of stream, and four of these were randomly chosen for sampling. A pool was included in each reach to standardise comparisons between reaches. Each reach was fished by three people, using a push net (2.5 mm mesh), dip nets, and an EFM 300 electrofishing machine powered by a 12 V battery, in an upstream direction using two - four consecutive passes (Rabeni et al. 1997). The decline in the number of crayfish caught in each pass was used to estimate the population number of the reach (Armour et al. 1983). In March 1997, eel density in the study reaches was estimated from depletion electrofishing as above. Eels are significant predators of crayfish in these streams (Hicks 1997) and crayfish distribution may be affected by differences in the densities of eel populations.

Wetted channel widths (mean of five equidistant cross-sections in each reach) and reach lengths were measured on each seasonal sampling date to estimate wetted area (m^2) and length sampled. Population numbers were expressed by the area (m^2) of each reach and density estimates for each stream were the mean of the four reaches. Where the population estimate failed because there was no reduction in numbers, the estimate for that reach was not included in the mean for each site.

Crayfish were measured with electronic Vernier calipers (0.1 mm) from the back of the eye socket to the mid-dorsal posterior border of the carapace to give the orbit-carapace length (OCL; Hopkins 1967b, Jones 1981b). Crayfish (> c. 7 mm OCL) were marked with visible implant fluorescent elastomer tags (Northwest Marine Technology Inc.) injected into their abdominal tissue so that they were individually identifiable (Chapter 3) and crayfish were returned to the stream in approximately the same location. Crayfish movement patterns could be followed by recapture of individually marked crayfish from within the sampling reaches. Occasionally the stream was sampled between the reaches to mark additional crayfish for growth analyses (Chapter 3) and their positions were recorded as a distance (m) from the furthest downstream reach. Crayfish were recorded as being in the same position if they were in the same sampling reach or within 7 m of initial capture position. Crayfish that were found in different locations were recorded as "upstream" or "downstream" of initial capture. The total length of time between recaptures (residence time within reaches) was recorded for each crayfish and grouped as three, six, 9 - 12, and >12 months for each stream.

The physical locations of each crayfish caught between December 1996 and December 1997 were recorded in terms of the flow characteristic (run, riffle, pool) and the immediate cover (e.g. undercuts, tree roots, cobbles). The areas of each cover type were determined in March and September 1997 and expressed as a percentage of the total wetted stream bed area sampled. Substrate composition was measured by particle size analysis (Wolman 1954) at five cross-sections of each reach in March and September 1997. The proportion of the larger substrate items with interstitial space utilisable as cover for crayfish (large gravels, cobbles and boulders) were combined as a measure of cover and termed "cobbles".

Recovery of a crayfish population

One pasture site (PW3) was monitored two, five, nine and 12 months after the flood to assess the recovery of the crayfish population. The same four reaches at that site were sampled using depletion electrofishing to estimate population numbers. Each crayfish was measured (mm OCL), marked with individually identifiable tags, its habitat type was recorded, and it was then returned to the stream in approximately the same locality as capture. The channel and water widths, the area of cover and the substrate size distribution were measured as described above on each sampling occasion.

Statistical Analysis

Numbers of crayfish found in each flow habitat type (run, riffle, pool), position (same, upstream, downstream) and residence time interval (3, 6, 9 - 12, > 12 months) were expressed as proportions of the total numbers. After inspection of probablility plots to approximate the normal distribution, all proportions were arcsine square root transformed and tested for differences with one-way ANOVAs. Pearson Correlation analysis was used to explore the relationship between (i) total cover (m^2 per m^2 of wetted streambed) and the densities of crayfish or eels, and (ii) densities of crayfish and eels, measured at each reach in March 1997. Differences between native and pasture densities on each sampling date before and after the flood, and differences between densities in July 1998 and June 1997 at both native and pasture sites were assessed using a nested ANOVA where sites were nested into land use. Densities measured in September 1996 (Chapter 3) were excluded from this analysis as the electrofishing operator, and some sample reaches, differed from those sampled from December 1996 onwards. All crayfish density estimates were log transformed after inspection of probability plots. Stream channel widths (log transformed) from before and after the floods were also tested with one-way ANOVAs. The differences in crayfish densities on each sampling date at PW3 after the flood were tested with a repeated measures ANOVA. All analyses were performed in SYSTAT 7.0.

Results

Crayfish habitat

In native forest streams, tree roots, undercut banks and "cobble" substrates were the most important habitats used by crayfish (Fig. 4.1). In unshaded pasture streams "cobble" substrates, macrophytes and grass growing in the stream were the most common and widely used habitats. However, in the one pasture stream (PW5) with riparian trees, tree roots became available as cover and were the most commonly used habitats (40%). Leaf litter and wood were generally abundant in native forest streams but relatively low percentages of crayfish were found in these habitats. Cobble substrate was particularly important at site PW2.

Crayfish densities within the sampling reaches were positively correlated with the amount of total cover (predominantly macrophytes; $r = 0.66$, $n = 11$, $P < 0.05$) of pasture streams, but not in native forest streams ($r = 0.57$, $n = 12$, $P = 0.055$). Surprisingly, crayfish in pasture streams were abundant in reaches where eel densities were also high ($r = 0.65$, $n = 10$, $P < 0.05$) as eel densities were also significantly correlated with total cover ($r = 0.70$, $n = 11$, $P < 0.001$).

Crayfish in native forest streams were more likely to be found in pools than in runs or riffle habitats ($P < 0.001$, Fig. 4.2), but there was no significant difference between crayfish preference for flow habitats in pasture streams. The proportion of crayfish in riffle habitats was significantly higher in pasture than in native forest streams ($P < 0.05$).

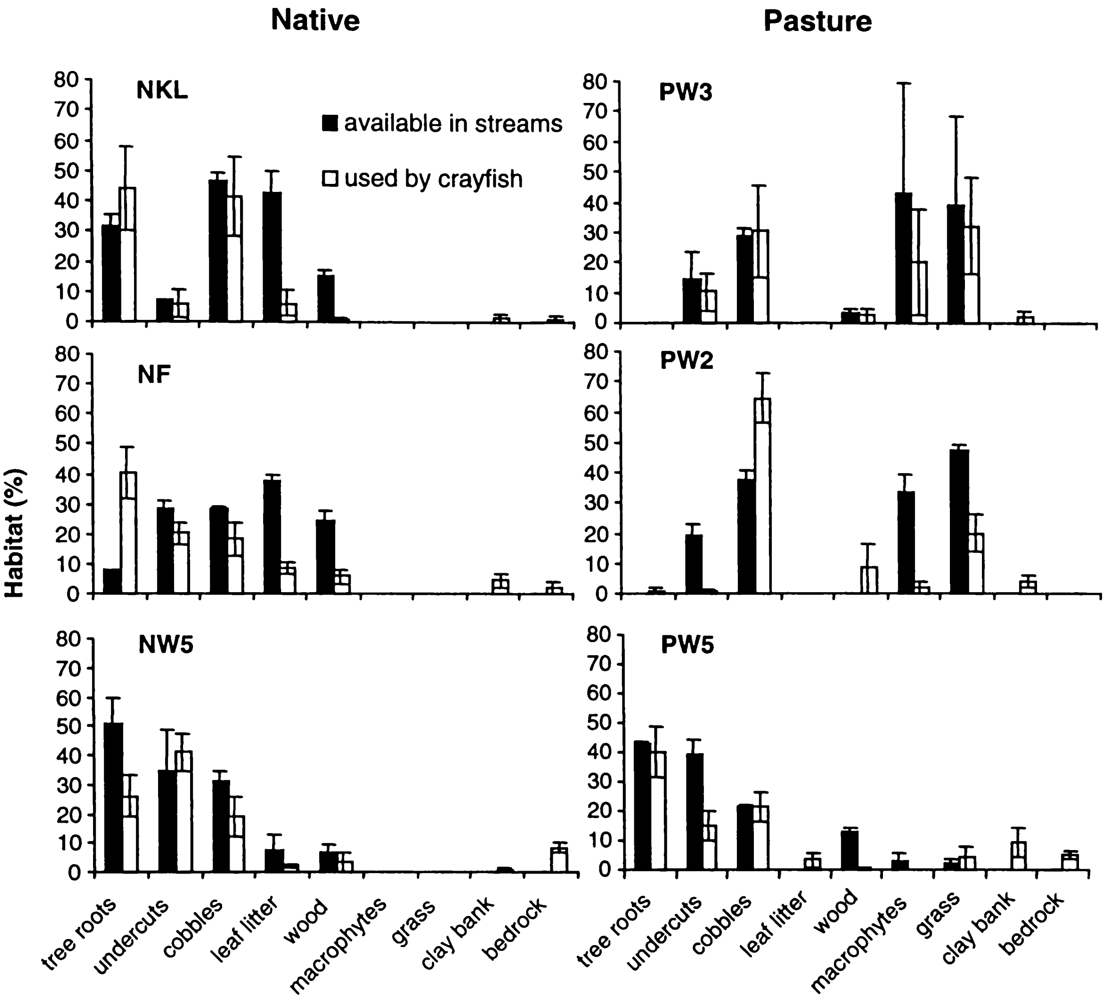


Figure 4.1. Mean (± 1 SE) percentage of habitat types used by crayfish on five sampling occasions from December 1996 – December 1997 and the percentage of habitat potentially available to crayfish in March 1997 and September 1997 at three native forest and three pasture stream sites. The percentage of available habitat labelled "cobbles" is an estimate of the percentage of the stream bed that can be used by crayfish as habitat and includes large gravels, cobbles and boulders from particle size analysis (Wolman 1954). For all other habitat types, area measurements were converted to a percentage of the total area of habitat measured to assess availability.

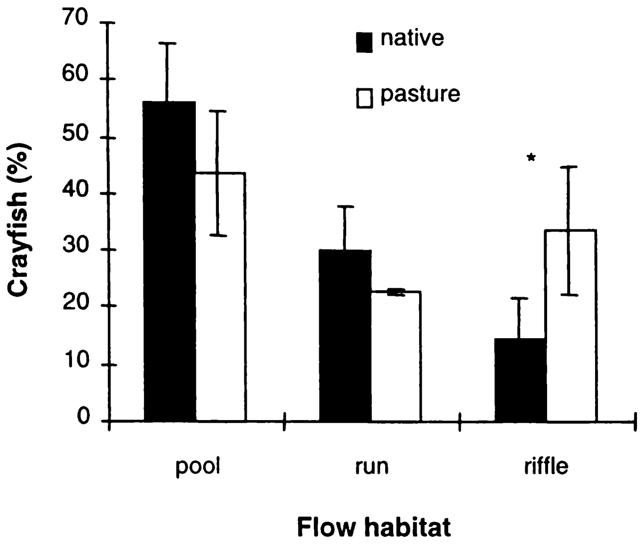


Figure 4.2. Mean (± 1 SE) percentage of crayfish found in pools, runs or riffles in pasture and native forest stream sites (n = 3) over five sampling occasions from December 1996 - December 1997. * indicates significant differences between land uses ($P < 0.05$).

Many crayfish were recaptured several times in both native forest and pasture streams in the same reach or position of initial capture. This finding indicates that the residence time of crayfish within a location can be long (e.g. > 12 months), although many of the crayfish that were marked in the study streams were never recaptured. Crayfish recaptured in native forest streams were equally likely to have stayed in the same place over three, six or 9 - 12 months ($P < 0.01$, Table 4.1). In contrast, the residence time for the majority of crayfish in pasture streams was only three months ($P < 0.001$), indicating that many crayfish move in and out of the study reaches and are not using the habitat long-term. In addition, there was significantly more movement upstream ($P < 0.05$) and downstream ($P < 0.001$) of the initial capture site in pasture streams than for crayfish in native forest streams, and fewer crayfish in pasture streams were consequently recaptured from the location of initial capture (P <

0.01, Table 4.1). The shorter residence time and greater movement away from the location of initial capture in pasture streams, suggests that the available habitat for crayfish may be less suitable than in native forest streams.

Table 4.1. Mean (± 1 SE) percentages of crayfish from three native forest and three pasture streams that were recaptured upstream, downstream or in the same location of initial capture, and the length of time between recapture, from quarterly sampling occasions between December 1996 to July 1998. P values refer to the difference between native and pasture land uses (across columns). Within each land use, values with different superscript letters are significantly different (P < 0.001, down columns).

	Crayfish (%)		
	Native	Pasture	P <
Residence Time (months)			
3	37.5 ± 3.9^a	52.0 ± 1.8^a	0.05
6	25.1 ± 3.6^a	23.8 ± 0.4^b	ns
9 - 12	28.5 ± 0.2^a	21.5 ± 1.8^b	0.05
> 12	8.8 ± 3.8^b	2.7 ± 0.3^c	ns
Direction of movement			
No change	87.3 ± 0.5^a	65.1 ± 4.6^a	0.01
Downstream	4.6 ± 0.5^b	15.8 ± 0.6^b	0.01
Upstream	8.2 ± 1.0^c	19.1 ± 4.0^b	0.05

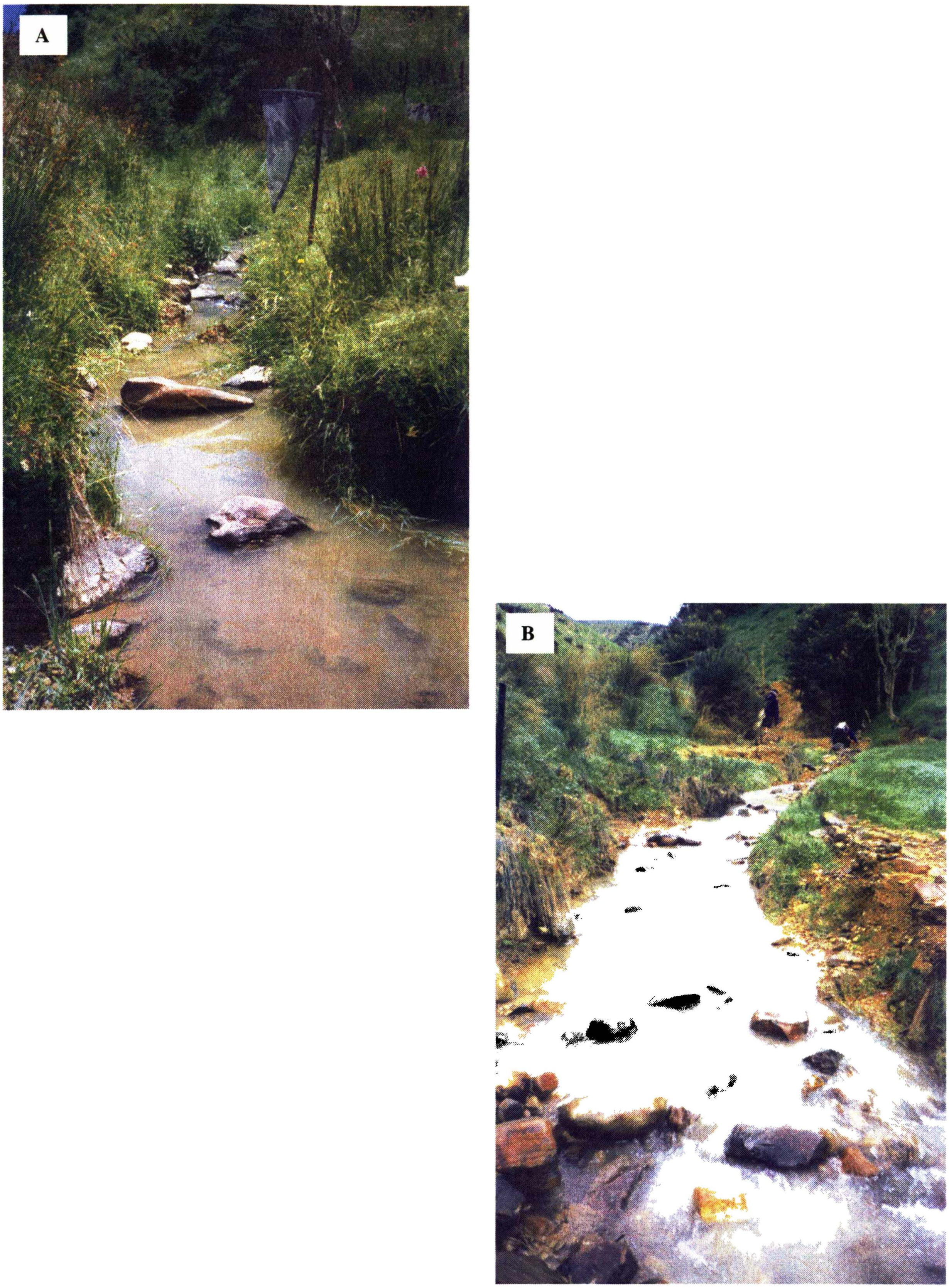


Plate 4.1. A pasture stream reach at site PW2 before (A) and after (B) the flood.

Plate 4.1 (cont.) A stream reach in native forest at site NKL before (C) and after (D) the flood.

Effects of the flood

Physical habitat. The intense rainstorm and flash flood of 9 June 1998 affected pastoral catchments more than native forest through scouring of wetlands and eroding banks, resulting in stream channel widening (Table 4.2). The small pasture stream PW2 had a significantly wider channel after the flood than in March 1998 ($P < 0.01$). The effect of eroding stream banks on the small pasture streams tended to straighten the channel, and pools were filled in with deposited cobbles, gravels and silt (Plate 4.1 A & B). Loose sediment was also deposited on the banks from the many landslides in the pastoral catchments and the suspended sediment loads during the flood were 62% of the annual average loads measured during 1995 – 1997 from the Mangaotama catchment (Quinn et al. 1998). The larger pasture stream site, PW5, had some well established riparian trees, a lower gradient and a wider floodplain, which may have alleviated the effects of the flood on stream banks. All native forest sites had dense undergrowth along stream banks and tree ferns and nikau palms could be found at the stream edge. Native stream banks were not eroded by the flood, although logs and objects across the streams had been dislodged (Plate 4.1 C and D). This storm caused many slips and bank collapses throughout the Whatawhata station area, which was further affected by more storms during June and July producing a wetter than average winter (Quinn et al. 1998).

Table 4.2. Mean (± 1 SE) channel widths of four reaches per stream where five measurements were taken at equidistant cross-sections within each reach in March 1998 (pre-flood) and in July 1998 (post-flood). P values compare the difference in widths before and after the flood for each stream.

	Channel width (m)		
	Pre-flood	Post-flood	P <
Pasture			
PW3	1.4 ± 0.2	1.7 ± 0.1	ns
PW2	1.4 ± 0.1	2.7 ± 0.3	0.01
PW5	2.1 ± 0.1	2.2 ± 0.1	ns
Native			
NKL	1.9 ± 0.1	2.1 ± 0.1	ns
NF	4.2 ± 0.4	4.1 ± 0.2	ns
NW5	3.1 ± 0.3	3.8 ± 0.5	ns

Crayfish density and habitat. Crayfish population density (expressed as number per m^2 of stream bed) did not differ significantly between native or pasture land uses on any sampling date from December 1996 to March 1998, except after the major flood when densities measured in pasture streams in July 1998 were much lower ($P < 0.001$, Fig. 4.3). The estimates of crayfish abundance before the flood have a wide variance associated with them due to the variability of crayfish numbers between stream reaches and between stream sites. However, variability in density estimates decreased after the flood, as numbers were low at all sites. Higher numbers than before the flood were found at two reaches in the native site NF that were bordered by upstream waterfalls. Presumably, crayfish had been swept down during the storm and may have been deposited in the pools at the base of these waterfalls or they may have migrated back upstream but were unable to pass the waterfalls.

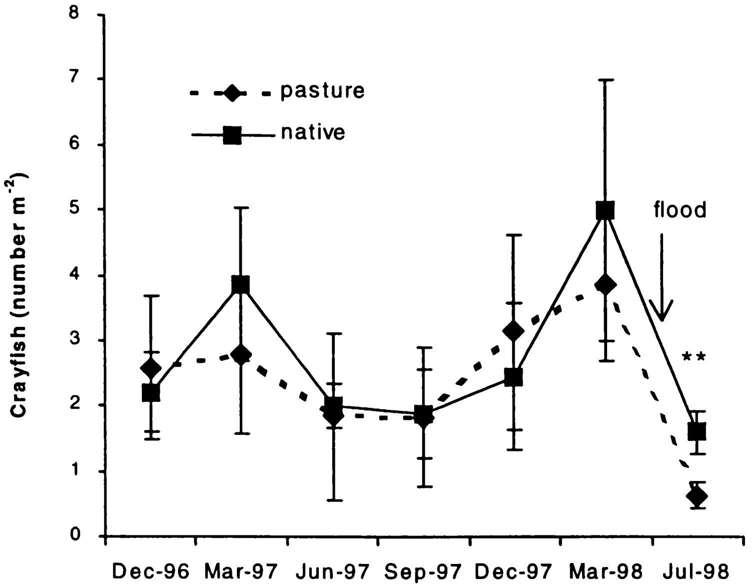


Figure 4.3. Mean (± 1 SE) crayfish abundance estimates (m^{-2}) for three sites within each land use. ** indicates significant differences between land uses on that date ($P < 0.01$).

Because of the cyclical nature of population numbers (peaks occurred in summer when juveniles entered the population), the most valid comparison of density following the June 1998 flood was with the same period in the previous year. Pasture streams had significantly fewer crayfish in July 1998 than in June 1997 ($P < 0.05$) whereas native streams were not significantly different (Fig. 4.3).

The large number of marked crayfish within the populations in each stream could be used to show whether crayfish were able to persist in the streams during the flood. There were fewer recaptured crayfish in native forest streams immediately after the flood than on sampling dates before the flood, however, in all pasture streams there were no marked crayfish recaptured in the study reaches. This finding indicates that crayfish in native forest streams were able to persist during the flood, whereas the ability of crayfish in pasture streams to remain in the study reaches was greatly reduced.

As an indication of the types of habitat that may provide long-term cover for crayfish in native forest streams, the flow and cover habitats of recaptured crayfish (i.e. those that had remained within the sampling reaches for three or more months) were compared to the averages for all crayfish sampled. In addition, the habitats of crayfish that were recaptured after the flood provided an indication of which habitats may have been refugia (Fig. 4.4 A and B). There was an increasing trend for pools and undercut banks to be used as long-term habitats, but "cobbles" appeared to provide temporary habitats and few recaptured crayfish remained in "cobble" habitat, particularly after the flood. No crayfish were recaptured after the floods in pasture streams, suggesting that the available habitats provided unsuitable refugia from severe floods.

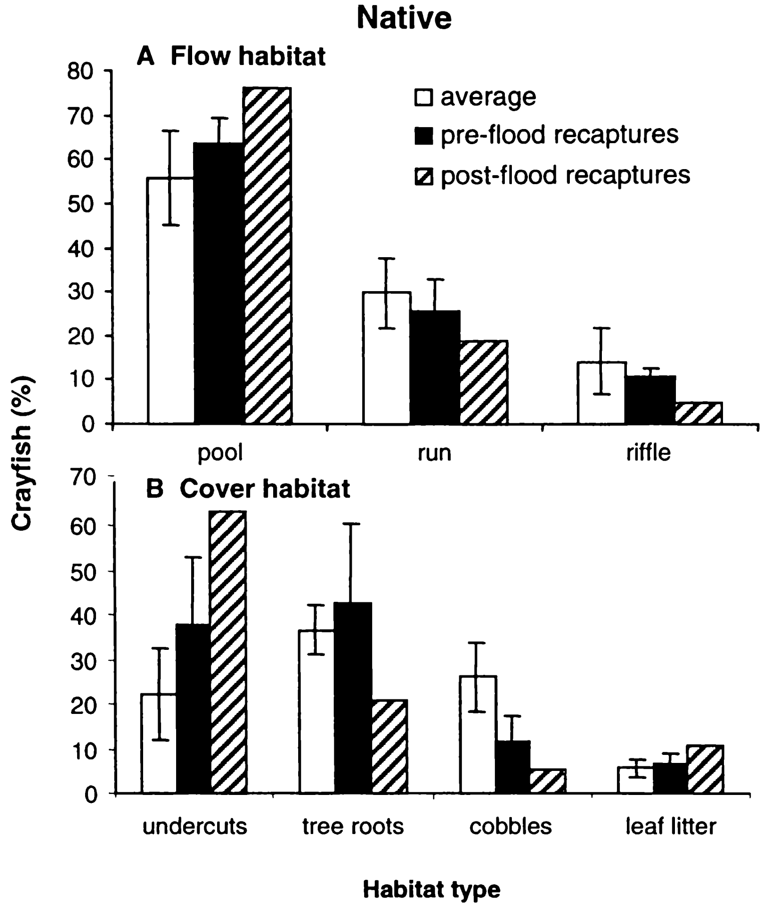


Figure 4.4. Mean (± 1 SE where appropriate) percentage of crayfish from the three native forest streams found in flow (A) and cover (B) habitats. "Average" refers to all crayfish sampled in the three streams (mean of five sampling occasions from December 1996 – December 1997). "Pre-flood recaptures" refers to crayfish from the three stream sites that were marked and then recaptured in the same reaches during quarterly sampling from December 1996 to March 1998. "Post-flood recaptures" were those crayfish that had been marked prior to the flood and were recaptured in the study reaches in July 1998 (pooled over three sites due to low numbers).

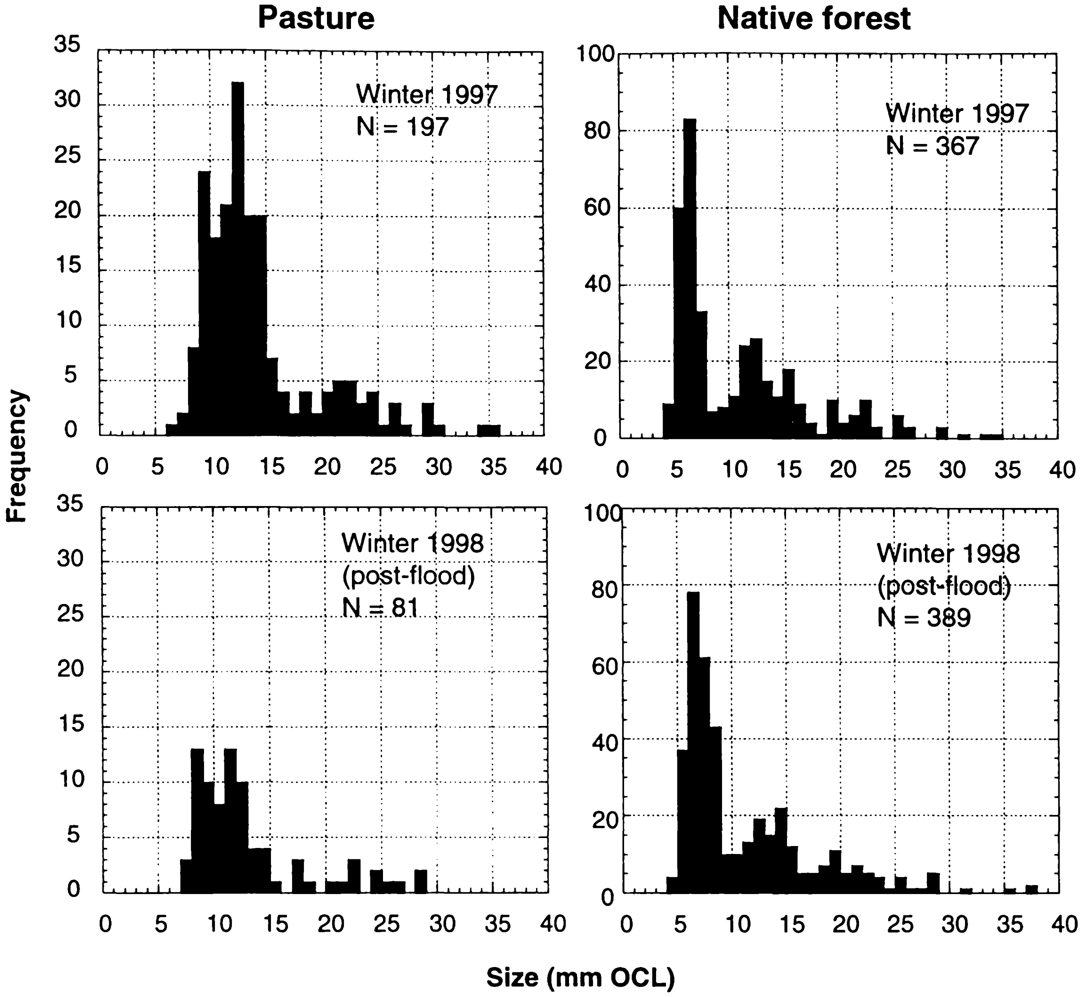


Figure 4.5. Size frequency of crayfish found in four sample reaches at three land use sites (pooled) in June 1997 and in July 1998 after the flood.

The size structure and numbers of the crayfish population caught in native forest streams following the flood in July 1998 was similar to that in June 1997 (Fig. 4.5). In contrast, numbers of the fastest growing juveniles of the 0 – 1 year cohort (10 – 15 mm OCL) in pasture streams were greatly reduced after the flood and very few crayfish of the second and third year classes remained.

Recovery of a crayfish population

Crayfish abundance at site PW3 was > 4 m^2 from December 1996 to March 1998, but densities declined dramatically after the flood (Fig. 4.6). The population numbers declined further in September after above average rainfall during winter and the recovery was very slow, possibly hampered by stock access to the stream and trampling of the banks that was evident in March. Crayfish density increased slightly in the year after the flood, but a repeated measures ANOVA showed no significant increases on any sampling date. Densities in June 1999 were 16% of the population density in June 1997 prior to the flood.

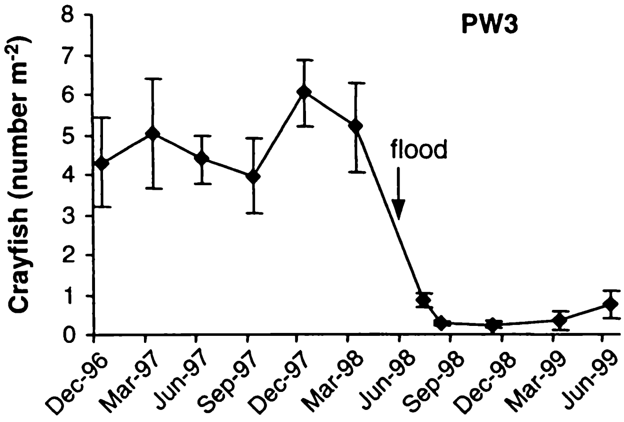


Figure 4.6. Mean (± 1 SE) crayfish abundance estimates of the four reaches at site PW3 sampled before the flood (December 1996 - March 1998) and post-flood (July 1998 - June 1999).

Crayfish numbers first began to increase in a reach with a relatively deep pool formed by large woody debris that was not dislodged during the flood. "Cobbles" and then macrophytes (watercress *Rorippa nasturtium-aquaticum*) were important cover habitats for crayfish recolonising the sampling reaches (Fig 4.7 A). Macrophytes increasingly dominated the available cover over summer (Fig 4.7 B) as flows reduced and silt and sand accumulated to provide substrate for macrophyte growth (Fig. 4.7 C). By June 1999, 100% of the crayfish collected were associated with macrophytes.

The recovery of the population at PW3 was hampered by the loss of most of the 1998 0 – 1 year cohort which would have been able to breed in the following March (Chapter 3). No females with eggs or young were found in the study reaches in August or November 1998, although juveniles of the new young-of-the-year cohort (< 11 mm OCL) were present in the study reaches in March 1999. By June 1999 a greater number of the juvenile cohort (10 – 15 mm OCL) had moved into the study reaches (18 juveniles as opposed to six in March 1998) and one female (21 mm OCL) was found with eggs.

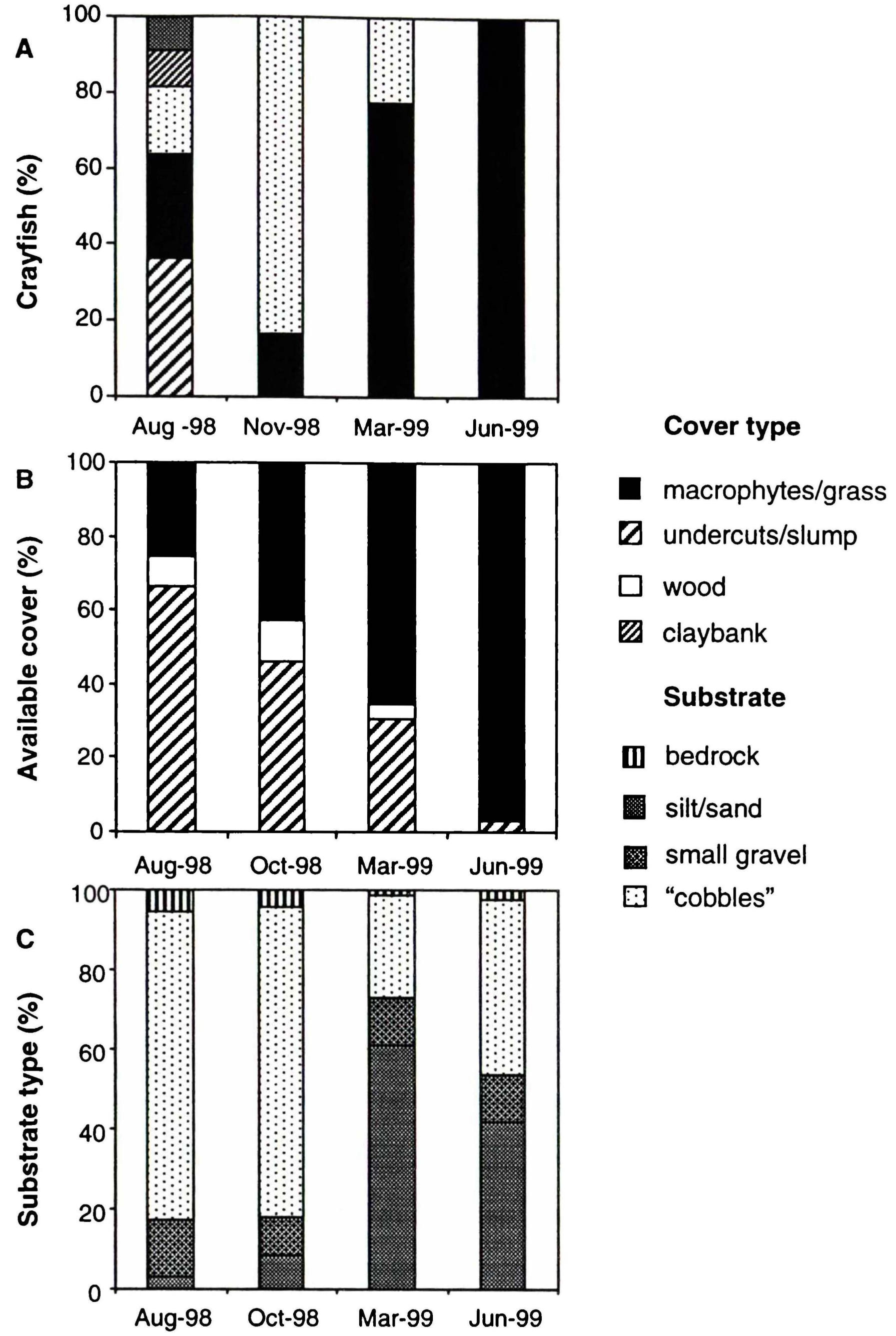


Figure 4.7. Percentage of crayfish found in each habitat type (A), percentage of available cover (% of wetted stream bed area) other than stream bed substrate (B) and percentage of stream bed substrate types estimated using the Wolman (1954) particle size method (C). "Cobbles" also includes large gravels and boulders. Data were measured at four reaches at site PW3 following the flood from August 1998 to June 1999. Note that cover and substrate were measured at the same time as crayfish sampling except in November 1998 where cover and substrate were measured two weeks before crayfish sampling (flows remained low during this period).

Discussion

Crayfish habitats in native forest and pasture streams

Removal of riparian trees and conversion to pastoral land use has changed the types of habitats available to crayfish, but under normal flow conditions the habitats in pasture streams supported similar crayfish densities as native forest streams. In streams with riparian trees, tree roots, undercut banks, and large substrate ("cobbles") were the most commonly used habitat, whereas in unshaded pastoral streams, "cobbles" and in-stream vegetation such as macrophytes and grass were the most important habitats.

Habitat choice may be an evolutionary response to predation, such that complex low-risk habitats are chosen because predation rates are lower in these environments (Jordan et al. 1996b). Hill & Lodge (1994) found that crayfish (*Orconectes* spp.) chose habitat on the basis of food availability when predation risk was low and on the basis of shelter availability when risk was high. *P. planifrons* in both pasture and native forest streams in the Waikato region are susceptible to predation by eels (Hicks 1997). Large eels commonly occur in pools with adequate cover such as macrophytes, undercut or overhanging banks and woody debris (Burnet 1952, Glova et al. 1998) and therefore share similar habitats to crayfish. In the pasture streams of my study, macrophytes provided structurally complex habitats that allowed crayfish and eels to co-occur. Structural complexity from strands of simulated vegetation has been shown to decrease crayfish (*Procambarus alleni*) susceptibility to predation by largemouth bass (Jordan et al. 1996b).

Macrophytes are seasonally abundant in summer and autumn in the pasture streams in this study, but generally decline over winter, and they may also be damaged by stock if allowed access to the streams. Cobble substrates may therefore be the most stable habitat available to crayfish in pasture streams, and are also the habitats least preferred by eels (Glova 1999). Several species of crayfish have been shown to prefer cobble habitats because of the low predation risk demonstrated for cobble substrate (Hill & Lodge 1994, Kershner & Lodge 1995).

In addition to cover, water velocity and depth have been shown to be important factors determining the abundance and habitat preferences of crayfish (Peterson et al. 1996, Englund 1999). Usio and Townsend (in press) found that *P. zealandicus* in a forested Otago stream was negatively associated with the presence of trout predators and current velocity, and positively associated with water depth, leaf litter cover and wood. In my study, *P. planifrons* was most commonly found in pools in native forest streams, particularly after the flood. Pools may be preferred habitats because (1) the low velocities may mean that crayfish need not expend energy to maintain their position in the current, (2) additional depth provides protection from terrestrial or avian predators, or (3) pools are important refugia for crayfish during floods in native forest streams. In native forest streams in the Waikato region, pools were more often formed by coarse woody debris (Quinn et al. 1997) and had seven times more woody debris cover than pools in pasture streams (Hanchet 1990). Pools formed by tree roots and woody debris supported the highest densities of crayfish in these streams suggesting that these features provide cover from predation, and potentially stabilise the pool structure during high flows.

In contrast, crayfish were equally likely to be found in pools, runs or riffles in pasture streams. The pools in the pasture streams of my study lacked pool-forming cover elements in general, were often sandy bottomed, and tended to support high crayfish densities only when macrophytes were present. Kutka et al. (1996) also found lower densities of *Orconectes propinquus* in pool habitats with fine substrate. Crayfish may make greater use of riffle habitats in pasture streams to utilise the cobble substrate and avoid eel predators that tend to inhabit pools (Glova et al. 1998). Furthermore, pool structure in pasture streams may be less stable than in native forest streams, influencing the habitat use of crayfish. Englund (1999) found that, although shallow pools provided refuge from fish predators for the crayfish *Cambarus bartoni*, these habitats supported low densities of crayfish, either from higher predation pressure by terrestrial predators or a greater impact of floods, in shallow pools.

Flood impacts on crayfish populations

The flood had a greater impact on crayfish populations in pasture streams than in native forest streams primarily due to the stability of the bank habitat provided by tree roots in the riparian zone of native forest streams. Undercut banks in particular appeared to provide refugia during the flood in native forest streams. In pasture streams without riparian trees, undercuts were not commonly used habitats, perhaps because during flood events these can be washed away without the stabilising effect of associated tree roots.

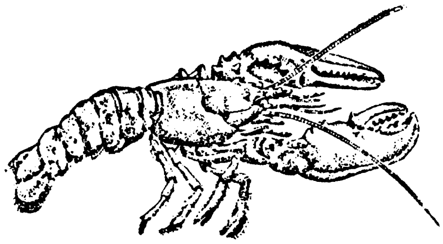
Similarly, pools did not appear to be refugia for crayfish in pasture streams during the flood, which may be related to the absence of stable pool forming elements. In severe floods, pools may be the areas of greatest disturbance, whereas riffles are less disturbed (Jowett 1997). Furthermore, peak flows and volumes during floods have increased with the change in land use from forest to grassland (Rowe et al. 1997). Therefore, the greater relative increase in velocity during floods in pools than in riffles, coupled with the reduction in stable pool forming elements and the higher flood volumes in pasture streams may contribute to the higher number of crayfish in riffles in pasture streams compared to native forest streams.

Habitat can be an important factor determining the distribution and abundance of many crayfish species (Peterson et al. 1996, Smith et al. 1996, Arrignon 1997). The influence of the riparian environment, in particular the presence of riparian shrubs and trees and the extension of their roots into the water, was related to the abundance of *Austropotamobius pallipes* populations in a survey of 62 streams in Britain (Smith et al. 1996). Naura & Robinson (1998) also surveyed *A. pallipes* in British rivers and identified the presence of overhanging boughs and tree shading as positive variables, and eroding cliffs and reinforced banks as negative variables predicting the presence or absence of crayfish.

Although macrophytes and cobbles may offer protection from predation in pasture streams, these habitats appear to offer little protection from large flood events. Tree roots and undercut banks in native forest streams seemed to provide stable, long-term habitats. Residence time within reaches was greater in native forest streams than in pasture streams and crayfish were able to persist in native forest streams during the flood.

The slow recovery of crayfish in a pasture stream with no native forest headwaters to provide a source of recolonists indicates that *P. planifrons* are not resilient to catchment-wide perturbations. The impact of the flood on fast growing juveniles of the 0 – 1 year cohort, which would have been reproductively mature in March of the following year, would also have contributed to the slow recovery rate. Loss of the first year size class may affect the reproductive success of the population in the years to come as the natural mortality of the first year cohort can be extremely high (Chapter 3). In addition, crayfish have a slow reproductive cycle where one cohort is produced per year and females appear to mate biannually (Chapter 3).

This study has demonstrated one possible mechanism for the decline of crayfish observed in Otago pasture streams by Jansma (1995). The intensity of floods has increased with the conversion of forest to pasture and the types of habitat available to crayfish have changed. Macrophytes and cobbles are dominant habitats in pasture streams and, while they may provide good protection from predation, they do not provide stable refugia for crayfish in major flood events. In native forest streams, riparian tree roots appeared to provide stability to undercut banks that were refuges for crayfish during the flood. *P. planifrons* abundance within streams appeared to be linked to the amount of cover habitat available and crayfish were reliant on stable habitat to be able to persist through disturbance. Therefore, the extent of stable habitat, largely provided by riparian trees, is of fundamental importance to the persistence of crayfish populations through catchment-scale disturbance events, such as one in 20 year floods. The absence of stable patches of headwater forest and the slow reproductive rate of crayfish are likely to be significant factors retarding their rate of recovery from disturbance. Deforestation and conversion to pastoral land use seem to have reduced the amount of stable habitat available to crayfish in these Waikato hill-country streams.



Chapter 5

Energy sources and the functional role of the crayfish *Paranephrops planifrons* in New Zealand native forest and pastoral streams: gut content and stable isotope analyses

Abstract

The food sources of crayfish in streams draining catchments in native forest and pastoral land were investigated using analyses of both stomach contents and stable isotopes of carbon and nitrogen. In native forest streams, crayfish stomach contents were dominated volumetrically by leaf detritus (> 60 %), but in pasture streams, aquatic invertebrates constituted > 40% of stomach volumes and leaf detritus < 30%. Stable isotope analyses revealed that crayfish from both native forest and pasture streams obtained most of their energy from aquatic invertebrates. Native forest stream food webs were based on inputs of allochthonous leaf litter, whereas crayfish from pasture streams appeared to utilise both allochthonous and autochthonous sources of energy. The main pathway for incorporation of these energy sources into crayfish body tissue was through predation of the invertebrate community. In native forest streams, adult crayfish (≥ 20 mm OCL) consumed greater amounts of leaf detritus than juvenile crayfish, but ontogenetic shifts in diet were not consistent between land use, and a corresponding change in stable isotope signatures was not detected. Therefore, it is suggested that changes in local habitat and food resources as a result of land use change affect crayfish food choice more than age and size. As omnivores, *P. planifrons* may have dual functional roles as both predators and processors of organic matter, with direct and indirect effects on other invertebrates in stream ecosystems. However, their relative importance as predators or detritivores seems to vary with land use, largely in response to changes in the abundance of local food resources.

Introduction

New Zealand has experienced a dramatic change in land use since human habitation, particularly over the past 150 years. Over 50% of the land area has been converted to farmland and only 23% of the original forested area remains (Pullar & McLeod 1992). Streams have been strongly affected by the change in land use from forest to pasture, including effects on water quality and temperature, sedimentation, periphyton biomass, benthic invertebrate community composition (Scott et al. 1994, Quinn et al. 1997) and fish (Hanchet 1990, Hicks & McCaughan 1997). However, the effect of land use change on crayfish populations in New Zealand streams has been largely overlooked, partly because of the poor understanding of their functional role in streams and partly because they are not commonly encountered using conventional benthic sampling methods.

Crayfish may occupy several trophic levels in aquatic food webs and have been variously classified as scavengers (Huxley 1880), herbivores or detritivores (Lorman & Magnuson 1978), opportunistic omnivores (Whitmore 1997, Hollows 1998) and predators (Momot 1995). Reported modes of feeding by crayfish are also varied. Most crayfish seem to probe the substrate for food with the first two pairs of walking legs, but certain species may also "bulldoze" sediments to sieve food (Turvey & Merrick 1997b), filter-feed (Budd et al. 1979), and hunt and capture small fish and tadpoles using the chelae (Turvey & Merrick 1997b). In addition, the mandibles of many crayfish species are specialised to either cut, grind, or scrape food (Holdich & Reeve 1988). Traditionally, however, detritus and vegetation have been assumed to be the major food sources of many crayfish species (Goddard 1988).

An increasing recognition of the importance of animal food to crayfish nutrition (McLain et al. 1992) has led to debate over the role of crayfish in streams (Momot 1995, Huner 1998). Crayfish often dominate the biomass of invertebrate communities in stream systems (Huryn & Wallace 1987, Rabeni et al. 1995, Whitmore 1997). However, Momot (1995) argues that crayfish could not achieve dominance of the invertebrate biomass without a substantial contribution of invertebrates to their diet. It has long been recognised that juvenile crayfish of many species feed predominantly on invertebrate prey, whereas adult crayfish are believed to shift their food requirements to vegetation and detritus (Goddard 1988). Therefore, the effects of crayfish on the benthic community and resource partitioning may differ with age, although the factors that cause this ontogenetic shift have not been fully investigated.

Paranephrops planifrons (Parastacidae) is commonly found in streams and lakes of the North Island, New Zealand and is geographically and morphologically distinct from the other species, *P. zealandicus*. Gut content analyses of *P. zealandicus* from lakes and streams indicated that macrophyte detritus (Musgrove 1988a) and leaf detritus (Whitmore 1997) were the main food sources, however, studies of their digestive capabilities reveal them to be unspecialised generalists (Musgrove 1988b). Little is known about the diet of *P. planifrons*, although it is also assumed to be a detritivore (Devcich 1974, Chapman & Lewis 1976).

If crayfish are largely detritivores, a potentially major impact of deforestation on New Zealand crayfish populations is the decline in leaf litter inputs to streams. To investigate the feeding ecology of *P. planifrons* in streams draining native forest and pastoral hill-country, I asked three central questions: 1) what are the main energy sources for crayfish; 2) how has crayfish diet changed with the conversion of catchments from native forest to pasture; and 3) what insights do diet analyses provide about the functional role of crayfish in these hill-country streams? Most direct evidence of the role of crayfish as detritivores originates from gut content analysis, which may be biased towards foods that breakdown slowly and does not account for the bioenergetic value of food items (Momot 1995). A combination of gut content and stable isotope analyses was used in this study to assess the origin of carbon and nitrogen that was actually assimilated into crayfish tissue. Relative amounts of the stable isotopes ^{13}C and ^{15}N can discriminate between food sources as animals remain relatively unchanged or slightly enriched in the heavier isotope relative to their food sources. The $\delta^{13}C$ value of the animal is ≈ 1 ‰ greater than their food source (Deniro & Epstein 1978, Rounick & Hicks 1985), and the $\delta^{15}N$ value is ≈ 2-3 ‰ greater (Minagawa & Wada 1984).

Stable isotope analysis may be used to assess changes in the food base of stream communites in response to environmental change (Rounick et al. 1982, Doucett et al. 1996b). However, there is some debate over the utility of stable isotope analysis in discerning allocthonous and autochthonous sources of carbon, without accompanying nitrogen isotopes (Peterson & Fry 1987), based largely on the variability of algal $\delta^{13}C$ (France 1995, 1996a, Bunn & Boon 1993). In addition, France (1996a) suggests that more extensive sampling of freshwater biota may reveal large differences in $\delta^{13}C$ signatures, within the same species and at a particular site, as a result of ontogenetic diet shifts, variable foraging locations or feeding idiosyncrasies, thus limiting the use of stable isotope analysis in detecting changes in carbon pathways. In this study *P. planifrons* was intensively sampled from within and between stream sites, and over four seasons, using both carbon and nitrogen isotopes to resolve potential individual variability and ontogenetic shifts in diet.

Methods

Crayfish gut content analysis

Twenty crayfish (*P. planifrons*) ranging in size from 5 - 32 mm orbit-carapace length (OCL, measured from the eye socket to the mid-dorsal posterior edge of the carapace; after Hopkins 1967b) were sampled from each of six study streams in December 1996 and March, June and September 1997. The sites were all hill-country streams in the Waikato region and are described in Chapter 2. The crayfish were captured from a mixture of pool, riffle or run sections of the streams soon after dark using electrofishing and handnetting, and were immediately put on ice and frozen on their return to the laboratory. Later, the OCL of each thawed crayfish was measured to the nearest 0.1 mm, sexed, and carapace hardness was determined as an indication of a recent moult. The stomachs were dissected out and placed into vials of 70% isopropyl alcohol (IPA). A section of abdominal muscle was also removed for stable isotope analysis as described below. Crayfish that had moulted recently before capture were excluded from analysis of stomach contents as they generally had empty stomachs (due either to the cessation of feeding before moulting or to the inability to feed with softened mouthparts), but their muscle tissue was included in stable isotope analysis.

Percent volume of each food type was assessed visually through a binocular microscope by spreading the stomach contents evenly in the bottom of a small glass dish placed over a sheet of graph paper (1 mm grid). Particulate organic matter (c. > 0.5 mm CPOM) was identified as leaf detritus, grass, woody detritus, fern detritus, macrophytes and moss, filamentous green algae, terrestrial invertebrates, or aquatic invertebrates. Invertebrates were identified to the lowest practicable level using the keys of Winterbourn and Gregson (1989), Winterbourn (1973), and descriptions of CSIRO (1970) and Walker (1984). To distinguish invertebrates that were consumed directly rather than co-incidentally when feeding on other food sources (e.g. leaves), invertebrates were recorded as present only if they were largely whole, their cases were accompanied with corresponding chitinous material, or gastropod opercula were accompanied by pieces of shell or flesh. The fine particulate organic matter (< 250 μm FPOM) portion of the diet was searched under a binocular microscope in several samples to check for the presence of a significant diatom food source. Diatoms were not found in large numbers and those present may have been ingested with other food sources. The FPOM fraction of the gut contents was not dealt with further as microscopic examination suggested that this fraction was largely the by-product of digestion of the larger particles found in the gut.

Percent frequency of occurrence and percent volume of food items in the diet, and proportions of aquatic invertebrates, were tested for differences between land uses using ANOVA in SYSTAT 7.0 after arcsine square root transformation using Tukey's post-hoc test for differences between means (Wilkinson 1997). The volumes of the three main food sources (leaf detritus, aquatic invertebrates, and seeds) in native and pasture stream crayfish were tested for differences between seasonal sampling dates with ANOVA as above. Differences in $\delta^{13}C$ and $\delta^{15}N$ of crayfish between seasons at each site were tested with ANOVA and Tukey's post-hoc test for differences between means.

Abundance of stream invertebrates

Stream invertebrates were sampled at each of the six streams in each season, two - four days prior to the crayfish sampling, to compare the proportions of taxa found in the environment with those found in crayfish stomachs. Ten 0.025 m^2 Surber samples were taken from random points at equidistant cross-sections of a 100 m long reach at each stream, and combined into one sample. Invertebrates were sorted live from the organic matter and preserved in 70% IPA for later identification using the key of Winterbourn and Gregson (1989). Differences in the proportions of taxa from native and pasture streams were tested with ANOVA using SYSTAT 7.0 after arcsine square root transformation.

The proportions of taxa in crayfish diets relative to their availability in the environment in each season were tested for evidence of selective predation using the electivity index E^* of Vanderploeg and Scavia (1979) as recommended by Lechowicz (1982). This is expressed as:

$$E_i^* = [W_i - (1/n]/[W_i + (1/n)]$$

where $$W_i = [r_i/p_i]/[\Sigma r_i/p_i]$$

and n = the number of kinds of food items, p_i = the relative availability of food types in the environment, and r_i = their relative utilisation in the diet.

Values near –1 indicate that the taxon was not preferred above its availability in the environment, values near 0 indicate random selection and values near +1 indicate positive selection relative to availability.

Stable isotope analysis

Crayfish. Crayfish abdomen muscle, dissected from each of the 495 previously frozen crayfish collected seasonally from the six streams, was dried at 50°C for 24 hours, then ground in a mortar and pestle. Any visible parasites were removed from the flesh prior to drying to avoid contamination. A small subsample (0.1-0.3 mg) was analysed for stable carbon and nitrogen isotopes using a Finnigan MAT Delta Plus continuous flow, isotope ratio mass spectrometer (NIWA, Wellington). The precision was ± 0.17 ‰ for $\delta^{13}C$ and ± 0.09 ‰ for $\delta^{15}N$.

Ratios of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ were expressed as the relative per mille (‰) difference between the sample and the standards:

$$\delta X = [R(\text{sample})/R(\text{standard}) - 1] \times 1000 \ (‰)$$

where $X = {}^{13}C$ or ^{15}N and $R = {}^{13}C/^{12}C$ or $^{15}N/^{14}N$.

Potential food sources. Samples of aquatic invertebrates were collected using a kick net at each site at the time of crayfish sampling. Filamentous green algae (FGA) and epilithon were collected by brushing streambed stones with a scrubbing brush in pasture sites and scraping stone surfaces with a knife in native sites. Samples were frozen on return to the laboratory and kept in storage until the results of crayfish gut and stable isotope analyses were known.

The two dominant invertebrates found in crayfish gut contents, snails and mayflies, were chosen for stable isotope analysis in both native and pasture streams. Specimens collected in December 1996 were used to supplement isotope data for conditioned leaf litter, eels, and other invertebrates collected from streams in the same region by Hicks (1997) who sampled in January 1993 and 1994. Epilithon and FGA, were also collected from the streams in December 1996, if present The mayfly *Deleatidium* sp. and the snail *Potamopyrgus antipodarum* had their gut contents removed and the snails were extracted from their shells to avoid contamination from non-dietary carbon (Hicks 1997). Because of the small size of the invertebrates compared to the amount of material required for analysis, each sample consisted of several individuals, and only one or two samples per stream were possible. Samples were then dried at 50°C for 24 hours and ground in preparation for stable isotope analysis.

To characterise the autochthonous energy base of these streams further, five additional epilthon samples were collected in early September 1999 from run habitats at each site. Stone surfaces of three – six large gravel or small cobble-sized stones (Wolman 1954) were rubbed free of sediment and invertebrates by hand and brushed with a stiff-bristled scrubbing brush to remove epilithon, which was collected in a small amount of water. Samples were transferred on ice to the laboratory where they were filtered into containers through a 250 μm-mesh sieve to remove silt and small invertebrates, and left to settle and evaporate and in a drying oven at 70°C for 48 hours.

Small subsamples (3 - 6 mg) of the dried and ground material were analysed with the Europa Scientific Tracermass mass spectrometer with a precision of c. 0.1‰ for ^{13}C and 0.3‰ for ^{15}N (University of Waikato, Hamilton). Ratios of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ were expressed in the same way as for crayfish using the equation above.

Results

Occurrence of food items in gut contents

The most frequently occurring food items in stomach contents of *P. planifrons* from both native and pasture sites were aquatic invertebrates and detritus derived from terrestrial plants (Fig. 5.1). The mean frequency of occurrence of total aquatic invertebrates ingested by crayfish in both native and pasture streams, 68% and 82% respectively, was not significantly different ($P = 0.085$, ANOVA). Leaf detritus occurred in more crayfish stomachs from native than pasture streams ($P < 0.05$, ANOVA). Fern leaves were identified in over 20% of crayfish gut contents in native forest streams. No green leaf matter was found in the guts of crayfish suggesting that leaf matter required some degree of conditioning before becoming palatable. Seeds and spores, woody detritus, terrestrial invertebrates, and flesh also featured frequently in the diet (> c. 10%), but filamentous green algae, macrophytes and moss were only occasionally found (< 5 %). Seeds were more often found in the diet of pasture than native forest stream crayfish ($P < 0.001$), whereas terrestrial invertebrates were more frequently found in gut contents of native forest stream crayfish ($P < 0.01$).

There was no difference in the frequency of aquatic invertebrates and leaf detritus in the diets of native stream crayfish. However, for pasture stream crayfish, aquatic invertebrates featured more often in their diets than the two other frequently occurring (> 30 %) food items, leaf detritus ($P < 0.05$) and seeds ($P < 0.0001$).

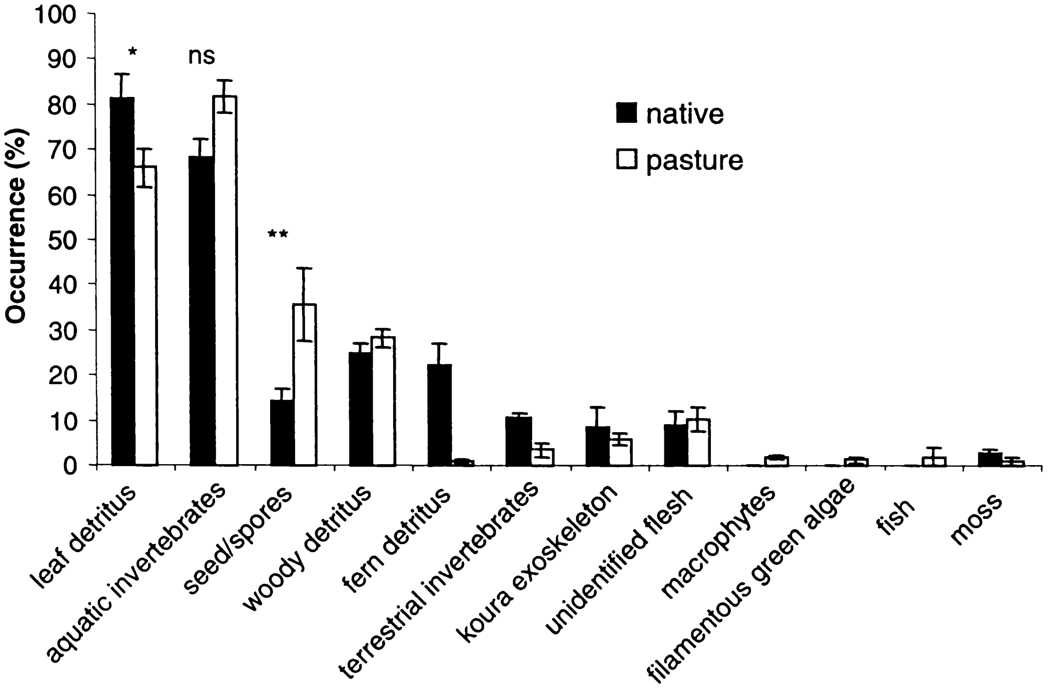


Figure 5.1. Mean % occurrence (± 1SE) of all items found in *P. planifrons* stomach contents from three native forest and three pasture sites pooled over four seasonal sampling dates between December 1996 and September 1997. Significant differences for the three main food groups (> 30% frequency of occurrence; aquatic invertebrates, leaf detritus, and seeds/spores) are displayed. Asterisks refer to significant differences between native and pasture crayfish for each item (* = P < 0.05, ** = P < 0.01, ns = not significant).

Scales and vertebrae of fish (bullies; *Gobiomorphus* sp.) were found in the guts of several crayfish from one pasture stream, but only in summer. Crayfish exoskeleton was found in many stomachs over all seasons and was considered to represent consumption of exoskeleton after moulting rather than cannibalism, as it was not accompanied by flesh. Gastroliths, which are normally attached to the outside of the stomach wall, were also frequently found inside the stomach. These stores of calcium form after the resorption of calcium from the old exoskeleton, and at ecdysis the lining of the gut and the gastroliths are shed into the foregut lumen where they are gradually broken down to release calcium (Lowery 1988). Moulting appeared to occur in all of the seasons sampled and the number of stomachs in which exoskeleton was present was not significantly different between native and pasture stream crayfish. Sand or gravel were not found in any crayfish stomachs indicating that the feeding method "bulldozing" observed in other species of crayfish (Turvey & Merrick 1997b), where the substrate is consumed and sieved for organic matter, is not utilised by *P. planifrons* in these hill-country streams.

Volume of food items in gut contents

The mean volumes of food items found in the guts of native forest and pasture stream crayfish (Fig. 5.2), also showed that aquatic invertebrates and detritus were the dominant food items. The volume of terrestrial plant detritus (all types combined but largely "leaf detritus") was significantly greater in native forest than that in pasture stream crayfish guts ($P < 0.01$). Conversely, the volume of aquatic invertebrates in pasture stream crayfish guts was significantly higher than that for native forest stream crayfish ($P < 0.01$). For native forest stream crayfish, the amount of total detritus consumed was significantly higher than the amount of aquatic invertebrates ($P < 0.0001$). However, there was no difference between the volume of invertebrates and detritus in the stomachs of pasture stream crayfish.

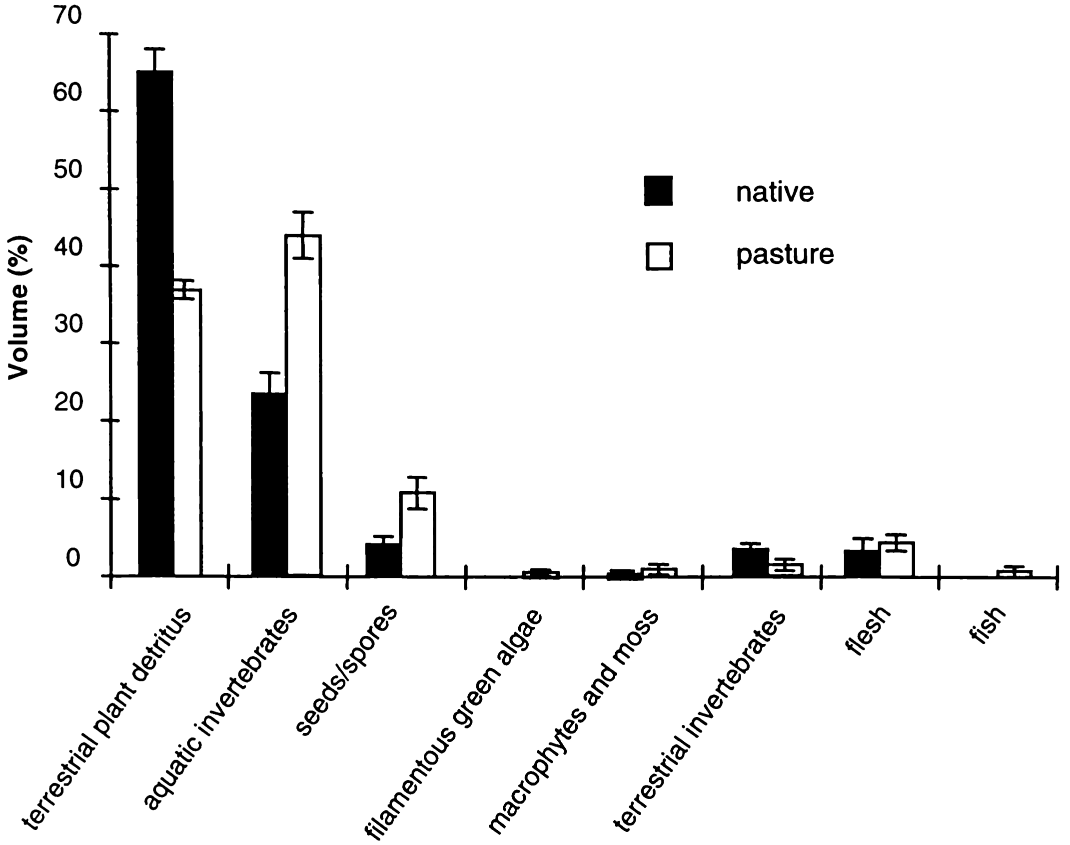


Figure 5.2. Mean % volume (± 1SE) of food items found in *P. planifrons* stomach contents from three native forest and three pasture sites averaged over four seasonal sampling dates.

Effect of season. Volumes of the three main food groups (aquatic invertebrates, leaf detritus and seeds and spores) in the diets of both pasture and native forest stream crayfish varied little with season, except for leaf detritus (Fig. 5.3). Volumes of aquatic invertebrates remained relatively constant throughout the year in both native forest and pasture streams, but in pasture streams, detritus consumption increased from March to September ($P < 0.05$). Greater consumption of leaf detritus in winter may correspond to a greater availability of leaves in the streams after autumn leaf fall, as the dominant riparian trees in this pasture catchment are deciduous. Consumption of seeds (mainly grass seeds) was higher after summer (March) than in September ($P < 0.01$). In native forest streams, varied types of leaf litter and seeds are plentiful year round, although there was a significant increase in the consumption of seeds in March compared to June ($P < 0.05$), and a significant increase in detritus consumption in June compared to September ($P < 0.01$).

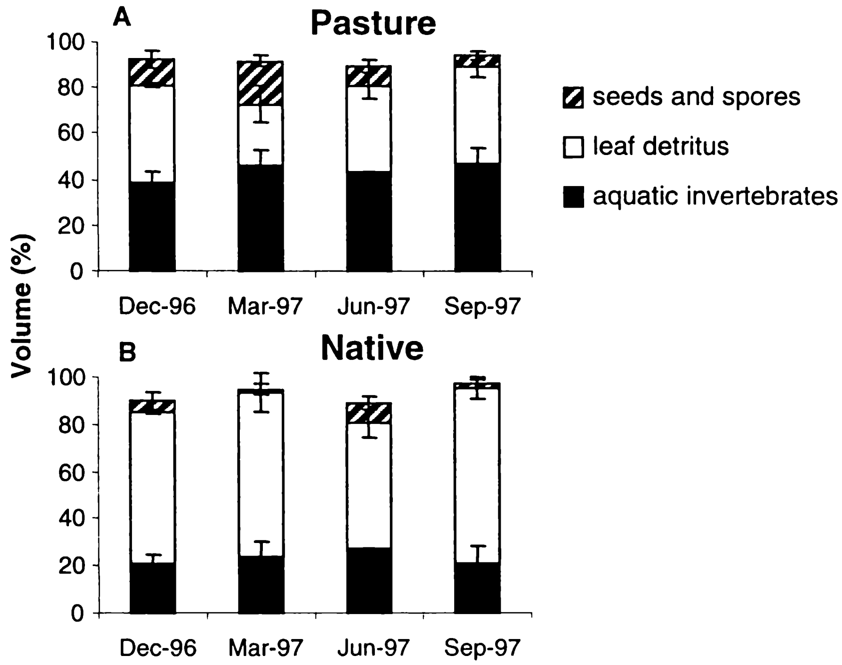


Figure 5.3. Mean % volume of the three main food groups (totalling > 90 % of stomach volumes) for crayfish from pasture (A) and native forest (B) streams (mean (± 1 SE) of three land use sites) on each of the sample dates.

Effect of size. A marked difference in consumption of leaf detritus or aquatic invertebrates was detected in crayfish larger than 20 mm OCL on examination of scatterplots of crayfish size against volume of food sources. The two size classes were similar to those identified as juvenile (< 20 mm OCL) and adult (reproductively mature; ≥ 20 mm OCL) crayfish (Chapter 3). Adult crayfish ate significantly more detritus than small crayfish in native forest streams ($P < 0.05$, Fig. 5.4A), while juvenile crayfish ate significantly more aquatic invertebrates ($P < 0.01$). However, in pasture streams there was no significant difference between the amounts of aquatic invertebrates eaten by both size classes, and there was significantly less detritus found in adult crayfish guts than in juvenile crayfish ($P < 0.05$, Fig. 5.4B).

Composition of invertebrate diet

The numbers of aquatic and terrestrial invertebrate taxa found in crayfish guts from each site and sampling season are listed in Appendix 5.1. Crayfish consumed a broad range of aquatic invertebrate groups and a total of 70 taxa were found. The highest number of individual invertebrates found in any crayfish stomach (55) was from a pasture site and consisted largely of chironomids (*Cricotopus* sp.) and the snail *Potamopyrgus antipodarum*. The highest number of individuals found in a crayfish stomach from a native site (20) consisted mainly of chironomids.

The invertebrate taxa most frequently found in crayfish guts were Ephemeroptera, Chironomidae, gastropod molluscs and Trichoptera, in particular cased caddisflies (Table 5.1). The relative importance of these taxa differed for crayfish from native forest and pasture streams. In native streams, 55% of crayfish had Ephemeroptera (mainly leptophlebiid mayflies such as *Zephlebia* sp. and *Deleatidium* sp.) in their guts whereas in pasture streams 48% of crayfish contained gastropod molluscs (almost exclusively *Potamopyrgus antipodarum*). Nevertheless, although their relative importance differed, the top four most frequently occurring taxa were the same in both land uses.

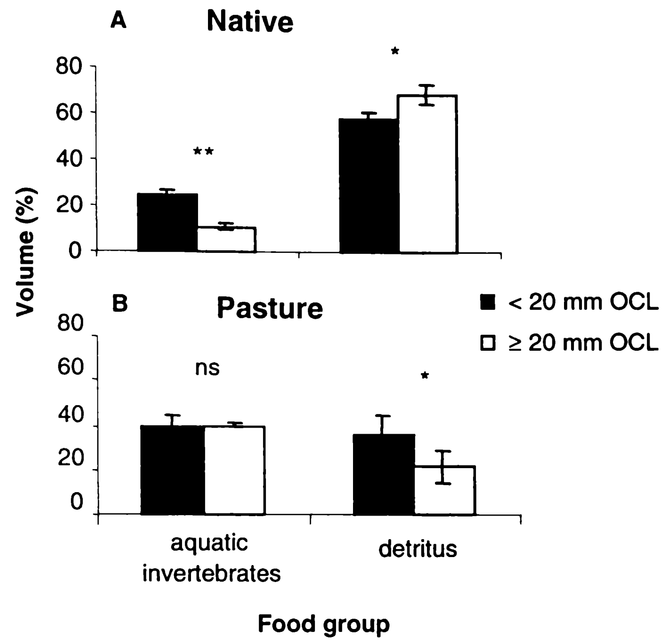


Figure 5.4. The mean % volume (± 1 SE) of aquatic invertebrates and leaf detritus consumed by two size classes of native forest (A) and pasture (B) stream crayfish; < 20 mm OCL (n=195 (A), 200 (B)) and ≥ 20 mm OCL (n=54 (A), 36 (B)). Asterisks indicate significant differences between size classes (* = P < 0.05, ** = P < 0.01, ns = not significant). Data are pooled for three sites and four seasons for each land use.

Table 5.1. The six most frequently occurring taxa found in crayfish stomachs from native (n = 236) and pasture (n = 222) streams. Data are pooled over four seasons and presented as a mean (± 1 SE) of three sites per land use.

Native		Pasture	
Group	Frequency occurrence (%)	Group	Frequency occurrence (%)
Ephemeroptera	54.6 ± 4.1	Gastropoda	48.0 ± 11.1
Gastropoda	30.5 ± 11.3	Chironomidae	34.3 ± 4.1
Chironomidae	18.0 ± 9.3	Ephemeroptera	30.2 ± 2.5
Cased caddisfly	5.5 ± 2.6	Cased caddisfly	22.8 ± 17.0
Coleoptera	5.5 ± 0.3	Hydrobiosidae	13.1 ± 3.8
Other Diptera	5.1± 2.2	Other Diptera	12.5 ± 1.8

The percentages of invertebrate groups found in crayfish guts and in the environment are shown in Figures 5.5A and B. In native forest streams, mayflies (Ephemeroptera) were the most abundant invertebrate taxon in the invertebrate community ($P < 0.0001$), and this dominance is reflected in the high percentage of mayflies in the diet of crayfish from native forest streams. However, the percentage of chironomids and gastropod snails consumed by native stream crayfish appeared to be greater than that found in the environment. Mayflies, snails, and chironomids had significantly higher percentages in stomach contents than any other invertebrate group ($P < 0.01$), but were not significantly different from each other.

The percentage of invertebrates in pasture stream crayfish stomachs reflected the abundance of a wide range of invertebrate groups found in the environment. Snails, chironomids, cased caddisflies and mayflies constituted a significantly higher percentage of the diet than any other taxon ($P < 0.05$). Snails also appeared to form a higher proportion of crayfish diet than the proportion available in pasture streams.

Table 5.2 displays the taxonomic groups that were considered preferred using the electivity index E^* of Vanderploeg and Scavia (1979) by either native forest or pasture stream crayfish during at least one season. All other taxa from Figure 5.5 that are not listed were not preferred in relation to their availability in the environment. However, the frequently occurring mayflies, which scored negatively, have also been included in this table. Electivity indices are best considered in conjunction with abundance data. For instance, mayflies constituted one-third of all invertebrate taxa found in crayfish stomachs and therefore could not be referred to as "avoided" despite their negative score. Rather, mayflies occurred in lower percentages in crayfish diets than would be expected from their abundance in the environment. The dominance of mayflies in native forest stream crayfish diets was probably a result of their high availability rather than from selective predation.

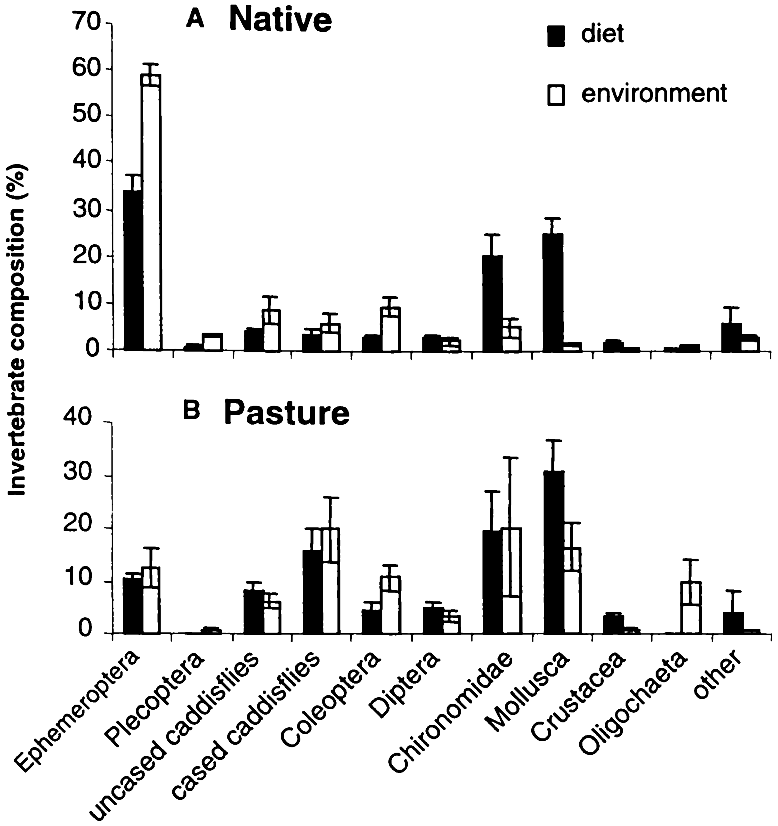


Figure 5.5. The mean (± 1 SE) percentage of each taxa group found in crayfish stomachs and in the stream environment at three native forest (A) and three pasture (B) sites (pooled over all dates). The invertebrate group Diptera excludes Chironomidae.

Table 5.2. Results of the electivity index *E (Vanderploeg & Scavia 1979) for five taxa found in crayfish guts from native and pasture sites over the four sampling dates. Shaded values indicate the taxa that were strongly positively selected (> 0.5) by crayfish relative to their availability in the environment.**

	Pasture					Native				
Taxa	Dec	Mar	Jun	Sep	**Total**	Dec	Mar	Jun	Sep	**Total**
Ephemeroptera	-0.60	-0.81	-0.37	0.38	0.03	-0.56	-0.50	-0.82	-0.73	-0.63
Diptera	-0.38	-0.39	-0.71	0.56	0.30	-0.62	-0.37	0.31	-0.41	-0.28
Chironomidae	-0.79	-0.71	0.73	0.55	0.06	0.20	0.16	0.64	0.01	0.21
Gastropoda	0.40	-0.06	-0.25	-0.44	0.25	0.65	0.73	0.60	0.77	0.75
Crustacea	0.73	0.79	0.40	-0.77	0.48	0.52	0.07	-1	-0.14	-0.06

Gastropod molluscs (*P. antipodarum*) appeared to be selected by crayfish in native forest streams above their availability in all seasons, suggesting that crayfish target snails as prey, either because they provide important nutrients or are easy to catch. In pasture streams, any preference for snails may be difficult to distinguish due to their high natural abundance. Over the winter months (June and September) in pasture streams and June in native forest streams, chironomids were positively selected for by crayfish. Crayfish may also show selective predation for Crustacea such as amphipods and ostracods, particularly in pasture streams. Although Crustacea were found in relatively low numbers in crayfish stomachs their abundance in the environment was also very low suggesting that crayfish may actively seek them out in certain months, or they are more abundant in habitats where crayfish forage.

Most taxa found in crayfish stomachs appeared to occur in similar proportions to their presence in the environment, although the core groups of snails and chironomids appeared to be selected by crayfish even when their natural availability was low. However, oligochaetes were rarely found in crayfish stomachs, but were often present in the environment, particularly in pasture streams. Oligochaetes may not have been detected in stomach contents due to quick digestion and a lack of chitinous remains, or they may be unavailable to crayfish as they burrow into fine sediments.

Stable isotope analysis

The energy base of the food web in these native forest streams was allochthonous detritus, but crayfish did not appear to obtain energy directly from this source (Fig. 5.6). Crayfish were enriched in both $\delta^{13}C$ and $\delta^{15}N$ above predatory (large *Hydrobiosis* sp.), omnivorous (Hydropsychidae), and non-predatory (snails and most mayflies) invertebrates, indicating that they were top invertebrate predators, but were a trophic step below eels.

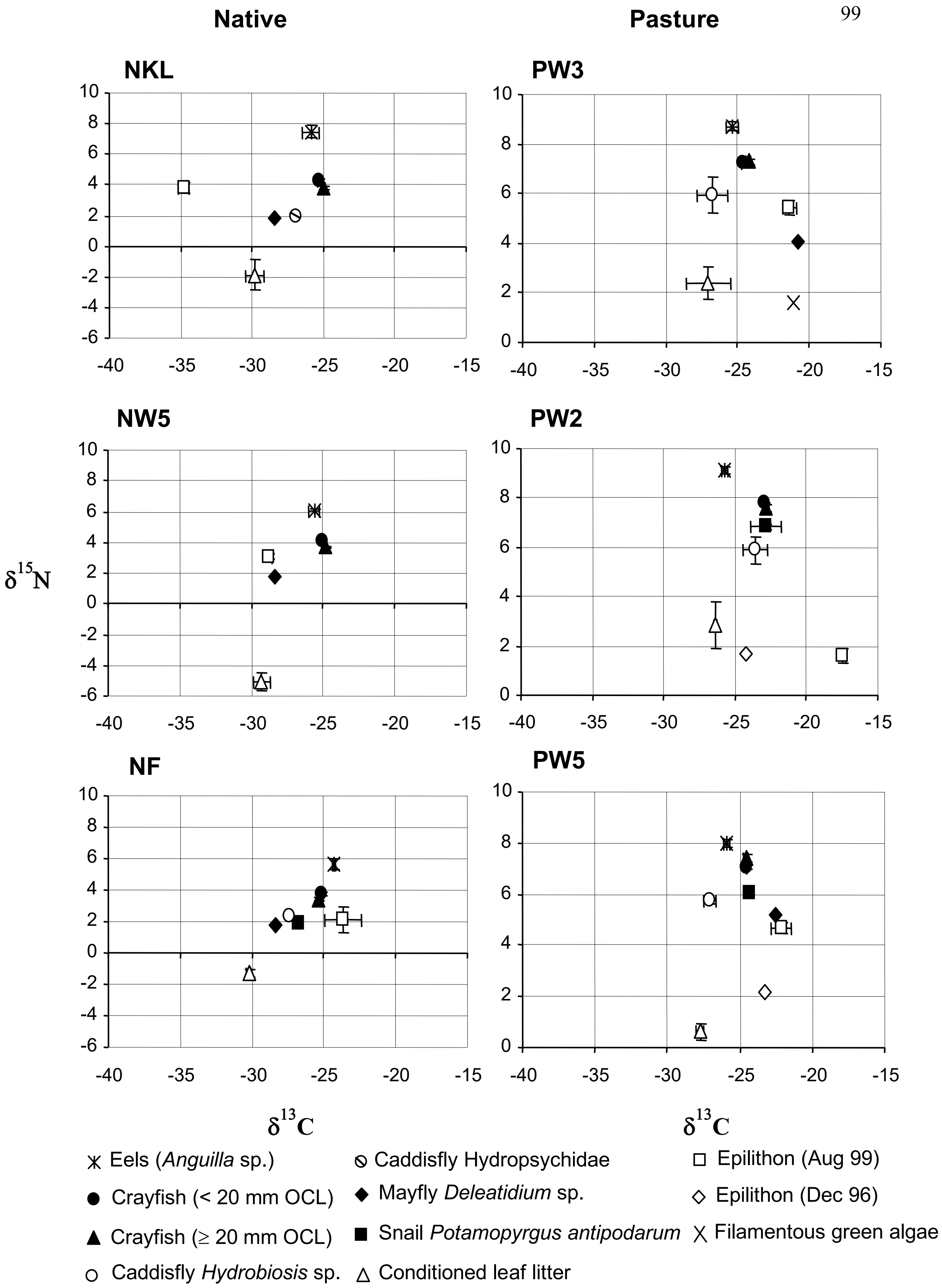


Figure 5.6. Mean (± 1 SE) stable isotope signatures ($\delta^{13}C$ and $\delta^{15}N$) of two crayfish size classes (pooled over four seasonal sampling dates from December 1996 – September 1997) and those of a predator (eels) and potential food sources for each study site. Mayfly, snail, filamentous green algae and epilithon (Dec 96) were collected at the time of koura sampling in December 1996. Additional epilithon samples were taken at all sites (n = 5) in August 1999. Conditioned leaf litter, caddisfly larvae and eel data were collected by Hicks (unpubl. data) in January 1993 and 94.

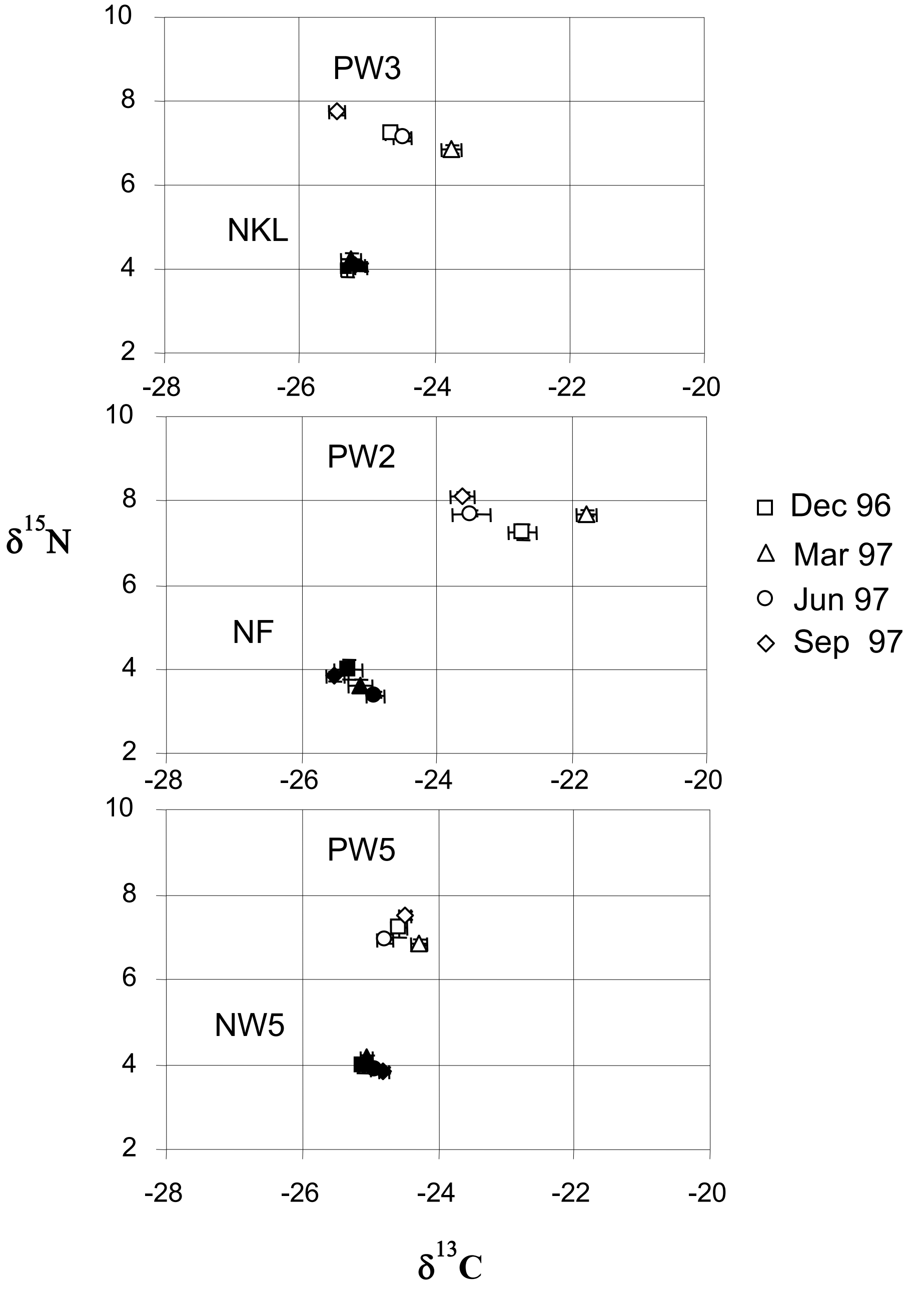


Figure 5.7. Temporal differences in the mean (± 1 SE) $\delta^{13}C$ and $\delta^{15}N$ signatures of crayfish from each of the six sampling sites on four dates between December 1996 and September 1997. Open symbols are pasture streams and closed symbols are native forest streams.

In pasture streams, food webs were greatly enriched in $\delta^{15}N$ compared to native forest streams, which was also found by Hicks (1997) who attributed this to the increased nitrogenous fertilisers and wastes generated by pastoral land use. Conditioned leaf litter was also enriched in nitrogen in pasture streams, but crayfish remained the top invertebrate predators in these streams. Crayfish at one pasture stream (PW2) were considerably more enriched in carbon than at the other pasture sites, but snails and other invertebrates were similarly enriched suggesting a difference at the base of the food web. Crayfish appeared to receive energy both from autochthonous and allochthonous pathways in pasture streams as they had intermediate values of $\delta^{13}C$ between epilithon and filamentous algae (through consumption of mayflies and snails) and that of conditioned leaf litter. Snails were identified as an important source of energy in the streams where they could be sampled (NF, PW2, PW5), as their $\delta^{15}N$ was below crayfish and their $\delta^{13}C$ values were within 0.1 – 1.5 ‰ of crayfish.

The differences between the $\delta^{13}C$ signatures of juvenile (< 20 mm OCL) and adult (≥ 20 mm OCL) crayfish in native forest or pasture streams were very small indicating that there was no substantial change in the energy source that contributes to tissue production, associated with age. The $\delta^{15}N$ signature of adult native stream crayfish was slightly lower than that of juvenile crayfish, although the decrease in $\delta^{15}N$ was not consistent with a change in trophic level.

Temporal changes in the $\delta^{13}C$ signature of crayfish were most pronounced in the small pasture streams PW2 and PW3 (Fig. 5.7). PW2 and PW3 have greater amounts of light reaching the water surface and more periphyton than the other pasture stream (PW5) and the native forest sites (Chapter 2). Greatest enrichment occurred in March ($P < 0.001$) and it is likely that this corresponds with changes in the algal carbon signatures (SMP unpubl. data). Algal biomass is greatest during summer in these streams and crayfish in the smaller pasture streams may therefore obtain most of their energy from an autochthonous pathway. PW5 has some riparian shading and this is reflected in the lower variablity of $\delta^{13}C$, similar to that of the native forest stream sites. $\delta^{15}N$ appeared to be fairly constant throughout the year but was significantly higher in all pasture streams in September ($P < 0.01$).

Discussion

Energy sources for crayfish in native forest and pasture streams

Crayfish in the study streams are true omnivores, acting as both predators and detritivores. The dominant food sources, by both volume and frequency of occurrence, in the stomachs of *P. planifrons* were aquatic invertebrates and terrestrial leaf detritus in native forest and pasture streams. Evidence from $\delta^{13}C$ and $\delta^{15}N$ data in this study showed that crayfish obtained most of their energy for tissue production from aquatic invertebrates, in particular snails (*Potamopyrgus antipodarum*). In pasture streams, crayfish were not as enriched in $\delta^{13}C$ as the epilithon and filamentous algae, and appeared to be obtaining energy from the invertebrates that consumed autochthonous material, as well as those that obtained energy primarily from an allochthonous pathway. However, temporal changes in $\delta^{13}C$ at the most open pasture sites suggested that crayfish may obtain energy primarily from an autochthonous pathway in these streams where riparian shading and litter inputs were greatly reduced. In native forest streams, the energy pathway was clearly based on allochthonous material, but crayfish gained energy for growth via the invertebrates rather than from the leaf litter itself.

Carbon values of terrestrially derived leaf detritus were well separated from algal carbon signatures in these streams even though epilithon varied greatly in both $\delta^{13}C$ and $\delta^{15}N$ between streams and also between dates (August 1999 and December 1996). Although variation in algal $\delta^{13}C$ may limit the use of stable isotope analysis for distinguishing autochthonous and allocthonous sources of carbon (France 1995, 1996a), the use of dual isotopes (France1996b, 1999, Winterbourn in press) and site specific $\delta^{13}C$ values (Doucett et al. 1996a) appeared to provide reliable identification of crayfish energy sources.

There is increasing evidence that the long-held belief that crayfish gain most of their nutritional needs from detritus and plant material has been overemphasised (Momot 1995). Food choice (Ilheu & Bernardo 1993) and growth experiments (Jones &

Momot 1983, McLain et al.1992), with a range of crayfish species fed on natural foods clearly show a preference for animal over detrital food (see also Chapter 6). Bioenergetic studies of crayfish show much higher rates of assimilation for animal versus detrital material (Whitledge & Rabeni 1997, Chapter 7) and experiments with crayfish species used in aquaculture have shown that fish meat (Oliveira & Fabião 1998) and zooplankton (Verhoef et al. 1998b) promote the best growth rates in juveniles.

The three main invertebrate groups, gastropod snails (*Potamopyrgus antipodarum*), Ephemeroptera (Leptophlebiidae) and Chironomidae, found in crayfish stomachs from native and pasture streams are also the taxa commonly found in the guts of other crayfish species (Hollows 1998, Whitledge & Rabeni 1997, Guan & Wiles 1998). Snails in particular appear to be very important to crayfish diet in general and many studies have shown significant impacts of crayfish on snail populations (Hanson et al. 1990, Matthews & Reynolds 1992, Lodge et al. 1998).

Most snails consumed by *P. planifrons* in these streams were small and included the shells. *P. antipodarum* have to be crushed upon consumption by rainbow trout to allow digestive enzymes to pass the operculum (McDowall 1990), and this may also explain why shell fragments rather than intact shells are often found in crayfish guts. There is a high probability of encountering (particularly in pasture streams) and capturing slow moving snails, and snails may be more abundant in microhabitats where crayfish prefer to forage, such as pools and edge habitats. Snails may also be an important source of calcium (Goddard 1988) and have been shown to accumulate amino acids (Eaton & Thomas 1999). A major source of amino acids for crayfish is other crustaceans and it has been suggested that cannibalism in crayfish is a response to the need for amino acids (Momot 1995). Snails were shown to be strongly positively selected by native stream crayfish, and the low numbers of snails found in these native forest stream environments suggests that crayfish may actively be seeking them out, presumably for some nutritional benefit.

Detritus is a major component of the diets of many crayfish species (Whitledge & Rabeni 1997, Turvey & Merrick 1997b) and also of *P. zealandicus* in the South

Island of New Zealand (Whitmore 1997, Hollows 1998). Although detritus made up a substantial part of *P. planifrons* diet, particularly in native streams, the energetic value of this material is likely to be low. Consuming leaf detritus requires little energetic expenditure and it is likely to provide energy for respiration and maintenance, but it appears to contribute little or no energy towards growth (Momot 1995, Chapter 6). Detritus may be a source of non-protein nutrients or carotenoids unavailable to crayfish from animal foods, however studies of growth and survival have found detritus to be a very poor food source overall (McLain et al. 1992, Momot 1995, Oliveira & Fabião 1998). Much of the nutritional value of detitus is thought to be derived from the microbial flora (fungi and bacteria) colonising leaf litter (Goddard 1988), however crayfish may need to consume large amounts of leaf detritus to gain any nutritional benefit from the microbial flora (Jones & Momot 1983, McLain et al 1992). Alternatively, detritus may be a safer mode of obtaining energy while avoiding predation. In aquaria, *P. planifrons* have been observed to venture out of shelter, grasp pieces of leaf detritus in both chelae and the 1st two pairs of walking legs, and then return to shelter to consume them (SMP personal observation). Hill & Lodge (1994) found that crayfish (*Orconectes* spp.) chose habitat on the basis of food availability when predation risk was low and on the basis of shelter availability when risk was high.

In pasture streams, crayfish were often found amidst macrophyte beds (Chapter 4), however the abundant food sources of macrophytes and algae were rarely present in gut contents, suggesting that crayfish were choosing invertebrates and leaf detritus above these food sources. Macrophytes are commonly found in diets of many other crayfish species particularly in lakes and wetlands (Hessen & Skurdal 1986, Momot 1995, Gutiérrez-Yurrita et al. 1998) and crayfish have been found to significantly affect densities of macrophytes (Chambers et al. 1990, Lodge et al. 1994, Nyström & Strand 1996, Nyström et al. 1996). Lake dwelling *Paranephrops* species also consume macrophytes (Musgrove 1988a, *P. zealandicus*) and limit the abundance of charophytes and bryophytes (Coffey & Clayton 1988, *P. planifrons*). Although abundant in two of the pasture streams in this study, the chemical defenses of the macrophytes (predominantly watercress) may explain their absence from the diet of *P. planifrons*. Crayfish have been shown to respond to macrophyte chemical and structural defenses in food choice experiments (Bolser et al. 1998) and macrophytes are often present in stomach contents partially decayed (Hessen & Skurdal 1986, Musgrove 1988a, Guan & Wiles 1998) which may reduce the effects of chemical defences (Kerfoot et al. 1998). However, watercress detritus was not recognised in stomach contents of *P. planifrons* indicating that crayfish did not utilise macrophytes in any form as a food resource in these streams.

Periphyton and filamentous algae are also abundant potential food resources in pasture streams. Although utilisation of periphyton is difficult to detect in gut content analysis, filamentous algae would be clearly evident in stomach contents if present. Other crayfish do consume filamentous algae (e.g. *Cladophora*; Creed 1994) and have been found to influence periphyton abundance both negatively through direct grazing or removal (Charlebois & Lamberti 1996, Keller & Ruman 1998) and positively by preying on periphytic grazers (Luttenton et al. 1998) or by reducing competition among algae (Creed 1994). *P. planifrons* appears not to utilise this resource directly as very little filamentous algae occurred in stomach contents.

Hollows (1998) and Hicks (1997) could not explain the ^{13}C-enrichment found in *P. zealandicus* and *P. planifrons*, respectively, relative to the food sources tested in their study streams. *P. zealandicus* was greatly enriched compared to the allochthonous detritus that was identified as the major component of its diet. Hicks (1997) attributed the ^{13}C-enrichment of *P. planifrons*, which was beyond that of the top consumers (fish), to either assimilation of microorganisms present in the gut (see also Musgrove 1988b) or assimilation of filamentous green algae. *P. planifrons* was also enriched in carbon in this study beyond that of eel predators, particularly in pasture streams, but not beyond that of autochthonous material. However, as filamentous green algae were not identified as a significant food source in gut content analyses, I suggest that this is unlikely to form a major energy source. Crayfish may show greater fractionation of δ^{13}C between themselves and their food than the average enrichment ($\approx$ 1 ‰; DeNiro & Epstein 1978), which may account for the observed ^{13}C-enrichment, although koura were within 0.1 – 1.5 ‰ of snail prey. This enrichment may also be a reflection of the variety of invertebrates consumed by both eels and crayfish or it may indicate that crayfish are not a significant food source for eels in these streams.

Ontogenetic shifts in diet

Many crayfish species appear to exhibit an ontogenetic shift in diet, whereby juvenile crayfish feed predominantly on aquatic invertebrates, and adults feed mainly on detritus (Goddard 1988, France 1996c, Guan & Wiles 1998). In crayfish from native forest streams this trend was evident with a significantly greater volume of detritus in the guts of adult crayfish (≥ 20 mm OCL) and significantly more invertebrates in the stomachs of juvenile (< 20 mm OCL) crayfish. This shift has been explained both in terms of an increased need for protein for growth by juvenile crayfish (Momot 1995) and an inability of larger crayfish to catch fast moving invertebrate prey (Abrahamsson 1966).

Adult crayfish are thought to have slower, less precise movements, and difficulty exploring small crevices, and the larger size of their chelate walking legs has been suggested to reduce their ability to grasp invertebrate prey compared to juvenile crayfish (Whitmore 1997). There appears to be little testing of whether larger crayfish are less effective predators of invertebrates and most suggestions along these lines seem to stem from one early study by Abrahamsson (1966) where he was referring to mobile zooplankton prey.

Stable isotope analyses of different size classes of *P. zealandicus* (Hollows 1998) and *P. planifrons* in this study, did not show any difference in nutritional pathway with size. France (1996c) found that $\delta^{13}C$ values for *Orconectes virilis* in oligotrophic Canadian lakes decreased from –18 to –27 ‰ with increasing size, which was attributed to a change from eating algal particles to leaf detritus. Aquatic invertebrates remained the major source of energy for adult *P. planifrons* in these native forest streams, despite the high consumption of leaf detritus that apparently offered little direct energetic benefit. The ontogenetic shift in diet, detected from gut analyses, could be an indication that lower volumes of invertebrates were able to supply the energetic requirements of adults, which require less energy for growth.

Growth rates were highest for juvenile crayfish and the size at which changes in diet were detected (c. 20 mm OCL) appeared to be the age (1 year in pasture streams and 2 years in native forest streams) where crayfish reached reproductive maturity (Chapter 3). However, in pasture streams similar volumes of aquatic invertebrates were found in the diet of adult and juvenile crayfish, which does not support the suggestions that large crayfish have difficulty catching invertebrates and that juveniles require more protein. Ilheu & Bernado (1993) demonstrated that adult crayfish (*Procambarus clarkii*) were easily able to capture macroinvertebrates in laboratory experiments, and consumption of invertebrates was several times greater than that of detritus.

The increased volumes of detritus in adult crayfish diet from native forest streams may be a function of habitat preferences and the availability of local food resources. Fern leaves are the most abundant food source in native streams and they are much tougher than the deciduous tree leaves that can be abundant at certain times of the year in pasture streams (Quinn et al. in press a), and young-of-the-year crayfish are unable to utilise fern leaves effectively (Chapter 6). Habitat choice can also be influenced by the differential predation risk between different size classes of crayfish (Stein 1977). Small crayfish may be better equipped to find cover amongst smaller cobbles and gravels to exploit the food resources in water currents. Equally, the crayfish that survive to maturity may have done so by acquiring "good" habitat and utilising leaf detritus as a low energy but low risk food source.

In contrast, adult crayfish in pasture streams had significantly less detritus in their diet than juvenile crayfish. The probability of encountering invertebrates is greater in pasture streams, as invertebrate densities are much higher than in native streams, particularly for slow moving snails, and there is less accumulated leaf litter there (Chapter 2). Therefore, the most abundant food source for crayfish in pasture streams is likely to be invertebrates. In addition, crayfish show no preference for pool over run or riffle habitats (Chapter 4), and may utilise more invertebrates in their diet from areas of high invertebrate density, such as riffles. Younger crayfish may also assimilate microorganisms and plant material more readily than older crayfish (Momot 1995, Guan & Wiles 1998) suggesting they would be more likely to utilise plant material. *P. planifrons* showed greater assimilation efficiencies with decreasing size for soft, deciduous tree leaves (willow, *Salix fragilis*) commonly found in pasture streams, but not with fern leaves which are abundant in native forest streams (Chapter 7). Therefore the type of leaf litter available and the ability of different sized crayfish to consume tough or soft leaf material may explain the greater utilisation of leaf detritus by small crayfish in pasture streams than in native forest streams.

It appears that the choice of food by *P. planifrons* may depend on a range of interacting factors including food availability, habitat choice, and possible predator avoidance tactics. Juvenile crayfish show a reduced ability to utilise leaf detritus in native forest streams whereas adults appear to utilise low energy foods predominantly. However, in pasture streams, where invertebrates were more abundant, adult crayfish consumed similar amounts of invertebrates as juvenile crayfish. Stable isotope analyses indicated that invertebrates were the most important food source for both juvenile and adult crayfish. Apparent ontogenetic shifts in diet were not consistent across land use, suggesting that changes to the local habitat and food resources, as a result of land use change, affect crayfish food choice more than age and size.

Functional role of crayfish in hill-country streams

Gut content and stable isotope analyses are valuable tools for elucidating the trophic and functional roles of crayfish in the stream environment. Crayfish have been labelled as detritivores or herbivores mainly on the basis of gut content analysis which tends to overemphasise the importance of items such as detritus that are slow to break down (Momot 1995). Stable isotope analysis in isolation would identify crayfish as top invertebrate consumers but would not have identified their role in processing organic matter.

Clearly the trophic and functional roles of crayfish differ. Crayfish appear to gain most or all of their energy for tissue production from aquatic invertebrates, however they and other crayfish species consume significant amounts of detritus. This detritus may often be tough, woody material that would be difficult for most invertebrates to break down (Turvey & Merrick 1997b). Evidence from the stable isotope analyses suggest it is unlikely that crayfish convert leaf litter into their own body tissue, and therefore do not pass energy from detritus to higher trophic levels. However, a major functional role of crayfish may be as detritivores that breakdown leaves into FPOM that can be utilised by other stream invertebrates. This may be more important in native forest streams, where the energy base is allochthonous, and tough leaf species such as tree ferns are abundant leaf litter.

Despite the common classification of crayfish as detritivores they have largely been overlooked in both the design and interpretation of leaf breakdown studies. Several studies have specifically looked at the organic matter ingestion budgets of crayfish (Huryn & Wallace 1987, Hessen & Skurdal 1989), however in conventional studies of leaf breakdown, the role of crayfish may be underestimated as they do not colonise leaf packs in the same way as other invertebrate shredders. Few studies appear to have sampled the crayfish population in the streams where leaf packs have been placed.

The role of crayfish as shredders may be particularly important in some New Zealand streams, as the invertebrate fauna is generally depauperate in specialised shredders in comparison to Northern Hemisphere temperate streams (Winterbourn 1995). However, the degree of leaf breakdown facilitated by crayfish, and the potential contribution of FPOM to other invertebrates, have yet to be measured in New Zealand streams. Parkyn et al. (1997) demonstrated that *P. planifrons* significantly increased the weight loss of wineberry (*Aristotelia serrata*) leaves, a soft-leaved native species, in artificial stream channels. However, Whitmore (1997) did not find a significant decline in CPOM in instream enclosures with *P. zealandicus,* relative to controls without crayfish, although in gut content analysis he found detritus to be the major component of *P. zealandicus* diet. Huryn and Wallace (1987) studied the litter processing ability of *Cambarus* sp. and found it to process 4 – 6% of the annual litter input in a North American mountain stream.

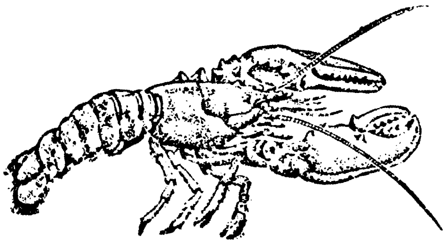
Perhaps more importantly, the potential role of crayfish as major predators in stream ecosystems has been overlooked in contemporary studies (Momot 1995). *P. planifrons* relies on invertebrate food for growth in both native and pasture streams suggesting that they are significant predators. Direct effects of crayfish predation are difficult to demonstrate with the interaction of indirect effects from polytrophic feeding and bioturbation of the physical environment. For instance, Ephemeroptera are frequently present in crayfish gut contents, but their population densities were found to increase significantly in experimental enclosures and channels, where the presence of *P. zealandicus* (Whitmore 1997) and *P. planifrons* (Parkyn et al. 1997) significantly reduced silt accumulation.

Crayfish in these streams tended to feed on the invertebrate taxa that were commonly available. However, chironomids and Crustacea (amphipods and ostracods) appeared to be positively selected in some months of the year and crayfish may exert predation pressure on snail populations particularly in native forest streams where they were strongly selected for. Direct effects of crayfish predation on snail populations have been demonstrated with many crayfish species (Hanson et al. 1990, Lodge et al. 1994, Nystrom et al. 1996), and crayfish have been shown to have significant effects on both the behaviour and morphology of snails. Alexander and Covich (1991) found that snails would actively leave the water in the presence of crayfish to avoid predation and Crowl and Covich (1990) found that snails altered their life history traits, by channelling energy into growth rather than reproduction, to achieve a size that was less attractive to crayfish.

Omnivorous feeding habits allow crayfish to exploit a variety of food resources, however, aquatic invertebrates were the major energy source for crayfish in these hill-country native forest and pasture streams, and snails, mayflies and chironomids were the most important invertebrate taxa in the diet. By acting largely as a predator of a wide range of invertebrate taxa in pasture streams, crayfish were able to take advantage of both allochthonous and autochthonous pathways of energy transfer. Diet appears to be largely controlled by the relative availability and abundance of food sources in conjunction with crayfish habitat choice and possibly the interaction of predator avoidance tactics. Apparent ontogenetic shifts in diet were not consistent between land uses, and therefore it is suggested that these may be mainly due to differential use of local habitat, and the ability to utilise local food resources, by crayfish of different ages. As omnivores, crayfish may have dual functional roles as both predators and processors of organic matter, and directly and indirectly affect other invertebrates in stream ecosystems. The degree of their functional importance to the stream community may differ between land uses as crayfish food choice appears to be closely related to the abundance of local food resources.

Appendix 5.1. Taxa found in crayfish gut contents sampled seasonally between December 1996 and September 1997 in pasture (PW3, PW2, PW5) and native forest (NKL, NW5, NF) streams.

Order	Family	Species	Stream sites					
			PW3	PW2	PW5	NKL	NW5	NF
Megaloptera	Corydalidae	*Archichauliodes diversus*	0	0	0	1	2	1
Odonata	Zygoptera	unidentified	0	0	0	0	1	0
Ephemeroptera	Coloburiscidae	*Coloburiscus humeralis*	0	0	0	0	5	2
	Ephemeridae	*Icthybotus hudsoni*	0	0	0	2	1	0
	Nesameletidae	*Nesameletus* sp.	1	0	0	1	0	1
	Leptophlebiidae	*Acanthophlebia cruentata*	0	0	0	1	2	2
		unidentified	5	6	9	14	11	18
		Austroclima sepia	3	1	1	1	0	0
		A. jollyae	0	0	1	0	0	0
		Zephlebia sp.	0	1	3	1	3	5
		Z. borealis	0	0	0	9	2	3
		Z. versicolor	0	0	0	0	1	0
		Z. dentata	3	3	4	5	3	3
		Neozephlebia scita	1	0	0	0	1	1
		Deleatidium spp.	10	12	15	18	9	16
Plecoptera	Gripopterygidae	*Zelandobius* sp.	0	0	0	0	1	1
	Eustheniidae	*Stenoperla prasina*	0	0	0	0	0	1
Trichoptera	Polycentropodidae	*Polyplectropus* sp.	2	0	1	1	0	1
		Plectrocnemia sp.	0	0	0	0	0	2
	Hydropsychidae	unidentified	0	2	0	0	1	0
		Aoteopsyche sp.	4	4	4	0	1	1
		Orthopsyche sp.	1	1	1	0	2	0
	Hydroptilidae	*Oxyethira albiceps*	0	7	2	0	1	0
	Hydrobiosidae	*Hydrobiosis* sp.	1	2	4	0	2	1
		H. umbripennis	1	4	3	0	0	0
		H. parumbripennis	1	0	7	0	1	0
		Psilochorema sp.	2	3	3	2	0	1
	Conoesucidae	unidentified	0	2	2	0	4	0
		Olinga feredayi	0	1	4	0	4	0
		Pycnocentria sp.	0	0	3	0	0	0
		Pycnocentrodes sp.	1	0	59	1	0	0
	Helicopsychidae	*Helicopsyche* sp.	0	0	13	0	0	2
	Leptoceridae	*Hudsonema amabilis*	0	0	4	0	0	0
		Triplectides obsoleta	0	0	7	0	1	2
	Helicophidae	*Zelolessica* sp.	0	0	2	0	0	1
Coleoptera		unidentified larvae	0	0	0	0	0	1
		unidentified adult	0	0	0	2	1	0
	Elmidae		2	0	29	0	1	0
	Hydraenidae		0	0	0	0	1	2
	Hydrophilidae		0	0	0	1	0	0
	Scirtidae		0	0	0	1	1	1
	Ptilodactylidae		0	0	0	1	0	0
Diptera		unidentified	0	0	0	0	5	0
	Tipulidae	unidentified	0	1	0	0	0	0
		Aphrophila neozelandica	0	0	8	1	0	1
		Paralimnophila skusei	3	0	0	0	2	0
		Zelandotipula sp.	0	0	1	0	0	0
	Muscidae		0	1	0	0	0	0
	Empididae		0	0	0	0	0	1
	Simuliidae	*Austrosimulium* sp.	16	5	7	0	1	1
	Chironomidae	unidentified	0	3	6	5	1	0
		Orthocladiinae	0	1	0	0	0	1
		Eukiefferiella sp.	20	17	11	2	0	0
		Naonella forsythi	3	0	1	1	0	0
		Cricotopus sp.	12	76	12	5	0	2
		Tanytarsus sp.	0	0	4	0	0	1
		Polypedilum sp.	1	0	1	2	1	18
		Paucispinigera sp.	0	0	0	0	0	39
		Chironomus sp.	3	0	2	0	0	0
		Macropelopiini	7	1	3	0	1	5
		Diamesinae	0	3	2	0	0	0
	Stratiomyidae		0	0	0	0	0	1
Mollusca	Hydrobiidae	*Potamopyrgus antipodarum*	67	88	65	12	34	59
	Planorbidae	*Gyraulus* sp.	0	0	1	0	0	0
Oligochaeta	Lumbricidae	*Eiseniella tetrahedra*	0	0	1	0	0	1
Acarina			1	0	0	1	2	2
Crustacea	Ostracoda		5	7	0	0	0	1
	Copepoda		0	0	0	0	0	1
	Amphipod (large)		4	1	0	0	0	0
Decapoda	Parastacidae	*Paranephrops planifrons* carapace	3	4	9	18	8	6
Nematomorpha	Gordiidae		10	6	0	16	2	2
Perciformes (fish)	Eleotridae	*Gobiomorphus* sp.	0	0	7	0	0	0
		Total	190	258	312	107	110	205
		No. of taxa	28	27	40	27	36	39



Chapter 6

Effect of diet and temperature on juvenile crayfish (*Paranephrops planifrons)* growth: experimental comparison of leaf detritus and invertebrate food sources at two diurnally fluctuating temperatures.

Abstract

In field populations of the New Zealand crayfish *Paranephrops planifrons*, growth was faster in pasture streams than native forest streams, possibly due to differences in temperature and diet. To investigate the effect of leaf detritus vs. invertebrate food sources and temperature on crayfish growth, juveniles were collected from native forest and pasture streams and reared in individual chambers for 9 weeks to assess the variation in moult increment and intermoult period. Temperature treatments were representative of native forest (12 - 15°C) and pasture (16 - 23°C) streams in summer. Survival was low in the leaf (fern and elm) detritus treatments at both temperature regimes, and growth rates were significantly lower than for juveniles fed invertebrate (*Chironomus* sp.) food. Growth rates between temperature treatments were not significantly different, however, juveniles in the cool treatment had a longer intermoult period. Analysis of stable carbon isotopes in juveniles at the end of the experiment showed that leaf detritus was not assimilated into crayfish tissue, unlike the chironomid food source that directly contributed to growth. Diet affected both the size increase at moult as well as the frequency of moulting in *P. planifrons* juveniles, whereas temperature only affected moult frequency. However, in field populations of crayfish, temperature is likely to be the primary determinant of growth unless invertebrate food resources are limited.

Introduction

Growth in crayfish is a stepwise process involving a series of moults, and variation in growth rate is the result of differences in both size increase at moult (moult increment) and the length of time between succesive moults (intermoult period). A range of factors can influence growth rates, and of these factors temperature has been described as the primary determinant of growth (Lowery 1988, Musgrove and Geddes 1995, Whitmore 1997). Growth can also be density dependent (Hopkins 1966, Morrissy et al. 1995) and can be influenced by water chemistry (particularly calcium content, which is required during the moult process; Lowery 1988), shelter availability (Figler et al. 1999), and environmental stress from water currents (Flint 1975). Food sources have also been shown to significantly affect growth rates of many species of crayfish (Ackefors et al. 1992, McClain et al. 1992) and best growth and survival has been achieved with animal protein (Oliviera & Fabião 1998) and zooplankton diets (Brown et al. 1992, Verhoef et al. 1998b).

Field growth data showed that the New Zealand crayfish *P. planifrons* grew faster in pasture streams than in native forest streams in the Waikato region, and the difference in growth rates was greatest for crayfish less than 1 year old (Chapter 3). The main differences between these streams were the increased shading and consequently lower water temperature in native forest streams (Chapter 2), increased biomass of invertebrates in pasture streams (Quinn et al. 1997), and greater volumes of aquatic invertebrates in the diets of pasture stream crayfish (Chapter 5). Pasture streams were on average 2°C warmer than native forest streams and mean temperatures fell below the 10°C threshold identified as limiting growth in *Paranephrops zealandicus* (Whitmore 1997, Hollows 1998) in only one month. However, in native forest streams mean water temperatures were below 10°C between June and September.

The main food sources for all sizes of crayfish in both native forest and pasture streams were leaf detritus and aquatic invertebrates. The relative proportions of these differed in native and pasture streams such that juveniles (< 10 mm OCL) from native forest streams had higher volumes of detritus (62%) in their stomachs, than invertebrates (23%), whereas crayfish in pasture streams had lower volumes of detritus (25%) than invertebrates (42%) (Parkyn unpubl. data but see Chapter 5).

The factors that affect growth may differentially affect the moult increment and intermoult period, but few studies have looked at the effect of temperature or food quality on the separate components of growth (but see Verhoef et al. 1998a). The aim of this study was to measure growth (moult increment and frequency) of crayfish at temperature regimes characteristic of native forest or pasture streams, fed on a diet of leaf detritus or invertebrate food, to differentiate the effects of diet and temperature on the growth and survival of juvenile crayfish. Growth of juvenile crayfish was investigated in this study, as the greatest influence on overall growth appeared to occur in the 0 - 1 year age class (Chapter 3). Crayfish from both native forest and pasture streams were used in the experiment to assess whether there were any adaptive differences between the populations for either temperature or food source. The effect of temperature on growth was studied using diurnally varying rather than constant temperatures, as the intention of the study was to imitate the natural thermal conditions of native and pasture streams as closely as possible. In addition, rates of growth, development and feeding (Sweeney 1984) and survival (Cox & Rutherford 1998) may differ for stream invertebrates when studied at constant rather than variable temperatures.

Methods

Crayfish collection

Juvenile crayfish were collected using electrofishing from a native (NF) and a pasture stream (Ahirau Stream, NZMS260 S14 947916) in the Hakarimata Range, in January 1999, and in February 1999 from a native (NW5) and pasture stream (PW5) at the Whatawhata Research Station. Crayfish sizes for the experiment ranged from 4.9 – 9.3 (pasture) and 4.6 – 9.3 (native) mm OCL, however the median size of crayfish from pasture streams (7.7) was larger than from native streams (6.4) as the timing of the breeding cycle differed between the two populations (Chapter 3).

Experimental Design

Eight crayfish were randomly assigned to two food treatments, invertebrate food or conditioned leaf litter, at two experimental temperatures. These temperatures mimicked summer diurnal temperature fluctuations in native forest and pasture streams as determined from visual examination of continuous temperature data for three native forest and three pasture streams over two years (Parkyn unpubl. data). The thermal regimes ranged from 12 - 15 °C ("cool" treatment), and from 16 - 23°C ("warm" treatment) (Fig. 6.1).

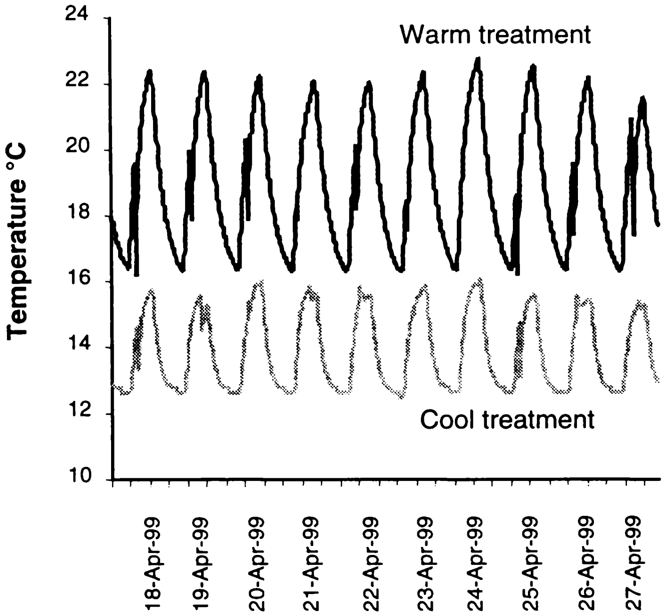


Figure 6.1. An example of temperature profiles for one week of the study measured by continuous data loggers.

For each temperature treatment, four aquaria with eight crayfish chambers in each were placed in water baths within a 12°C (cool) or 15°C (warm) constant temperature room (Fig. 6.2). Heaters in each water bath were set by timer to heat from 8 am to 6 pm and reach a maximum of 15°C or 23°C in the cool and warm rooms, respectively. Water in both the aquaria and water baths was topped up regularly to a constant level to maintain volume, and temperatures were monitored periodically in all aquaria with temperature loggers at several different locations to check that temperatures were similar throughout the aquaria. Diffuse lighting was provided by a 100 W incandescent lamp pointed away from the experimental area on a 10:14 h light:dark cycle synchronised with temperature regime. Crayfish aquaria were also covered from above with shade cloth (5 mm mesh) to reduce direct exposure to light.

Crayfish were reared individually to avoid density dependent effects on growth and so that intermoult periods and moult increments for each individual could be measured. Each individual was housed in a 70x70x120 mm plastic chamber and supplied with a small piece of hose (c. 3 – 4 cm long, 15 mm diameter) as cover. The chambers had three plastic netting (1 mm mesh) sides to facilitate circulation of aerated water between them, with one aerator supplying four chambers (Fig. 6.2). Dissolved oxygen in each chamber was measured on three occasions and the averages (± 1 SE) for the cold and warm treatments were 9.3 ± 0.1 and 9.1 ± 0.05 mg L^{-1}, respectively. The positions of chambers were re-randomised within each temperature treatment on three occasions to minimise the effects of any unknown heterogeneity in the experimental aquaria on crayfish growth.

Crayfish were fed *ad libitum* each day with either a small amount of commercially prepared frozen *Chironomus* sp. larvae, or a small piece of abscissed tree fern (*Dicksonia* sp.) leaf that had been conditioned in aerated stream water for 6 weeks at 15°C prior to the start of the experiment. Leaves of the introduced elm (*Ulmus* sp.) replaced fern leaves as a detrital food source after 5 weeks of the experiment as fern leaves proved to be an inadequate food source (see results). Recently abscised elm leaves were air dried for 48 h and conditioned in aerated stream water at 15°C for 5 days prior to introduction to crayfish. Crayfish were supplied with fresh food daily and uneaten food and faeces were sucked out of the chambers using a plastic pipette.

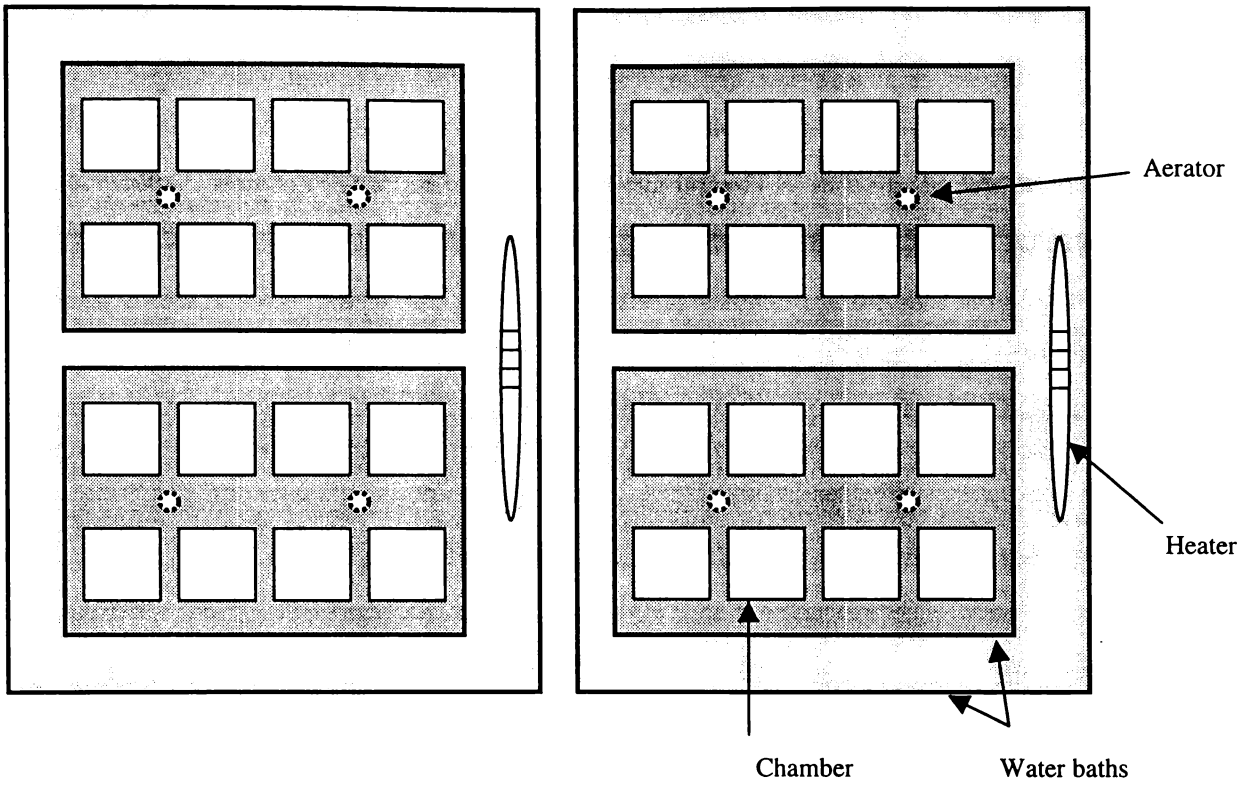


Figure 6.2. Experimental set-up for one temperature treatment. Crayfish were individually housed in chambers within water baths that were heated using timers to create a diurnal temperature cycle.

An initial pilot study, conducted in January, was abandoned due to high initial crayfish mortalility, particularly in the warm treatment. The combination of high temperatures and high ammonia concentrations, as the water was replaced only once per week, may have caused greater stress and ultimately deaths in the warm treatment. Surviving crayfish in the cool treatment were used in subsequent experiments, with some replacements where deaths had occurred, and these crayfish therefore had been acclimated to experimental conditions for one month longer than other crayfish.

To control ammonia build-up, 80 – 90% of aquaria water was subsequently replaced each morning with dechlorinated water which had been aerated and acclimated to the constant temperature overnight so that diurnal temperature regimes were not significantly affected. All water in the aquaria was exchanged at the end of each week. Maximum ammonium concentrations in each aquarium were tested on two occasions. Mean concentrations were 0.04 mg NH_4-N l^{-1} in both the warm and cold treatments. These values are below other reported experimental levels of ammonium (e.g. 0.5 mg l^{-1}, Karplus et al. 1995). The average pH for both hot and cold treatments was 7.8, measured at the same time as ammonium, which was similar to the pH measurements (7.3 – 7.5) for streams containing crayfish in the Waikato region (Chapter 2).

Crayfish were observed daily to record ecdysis and remove exuviae before consumption by the crayfish. Each week for ten weeks, crayfish were measured (orbit-carapace length (OCL)) with electronic calipers to the nearest 0.1 mm, and wet weighed to the nearest 0.001 mg, after blotting dry with soft tissue, in a small amount of pre-weighed water.

Stable carbon isotope analysis

At the end of the experiment, two crayfish from each source and food treatment were sacrificed for analysis of stable carbon isotopes to determine whether the food sources had been assimilated into tissue. High temperatures may increase the rate of carbon and nitrogen assimilation into body tissue, so only crayfish from the warm temperature treatment were used, as their isotopic signatures were more likely to reflect their experimental food source. Where possible, crayfish that had moulted twice were chosen, as they were more likely to have assimilated experimental food source carbon. The average $\delta^{13}C$ signatures for field populations of crayfish in native and pasture streams were used as an indication of initial $\delta^{13}C$ for the experimental crayfish (from Chapter 5).

For analysis of carbon stable isotopes, crayfish tail muscle was removed from the carapace, and three samples each of chironomid larvae, elm, and fern leaves were dried at 50°C for 24 hours and ground separately with a glass rod in a ceramic crucible. Samples were analysed by the Waikato Stable Isotope unit using methods described in Chapter 5. Due to the amount of material required for analysis, the replicate crayfish samples within source and food treatment had to be pooled.

Statistical analysis

In order to assess the growth of crayfish with differing initial sizes, growth rates (% weight gain day^{-1}; Ackerfors et al. 1992) were calculated for each of the crayfish. Differences between crayfish land use source (native forest and pasture streams) were tested with ANCOVA for each food source at each temperature, using size (mm OCL) as a covariate to test whether size affected differences between sources. Differences between growth of crayfish fed the two experimental foods under the two temperatures were analysed with a two-way ANOVA in SYSTAT 7.0 for each crayfish source. Probability plots showed that the growth data did not require transformation. Differences in the mean intermoult period for crayfish in the temperature treatments were analysed using a paired t-test in Excel 7.0. Differences in moult increments (mm OCL) between crayfish treatments were assessed using homogeneity of slopes analysis (Wilkinson 1997) in SYSTAT 7.0. The difference in moult increment between temperatures and crayfish source were tested using data from the invertebrate food treatment only due to a limited number of moults in the leaf detritus treatment.

Results and Discussion

Survival

Survival of juvenile crayfish in the invertebrate treatments was high (75 – 100%) at both cool and warm temperatures (Table 6.1). Survival of crayfish in the leaf detritus treatments however, was low (13 – 63%), particularly for very small crayfish (c. < 0.5 g wet weight) (Fig. 6.3) and may have been caused by low food quality or unpalatability of the leaves provided. Very little fern leaf matter appeared to have been consumed (although leaf surfaces could have been scraped) whereas consumption of elm leaf matter was visibly greater (pers. obs. SMP). Fern leaves alone were evidently unable to sustain juvenile crayfish, despite being an abundant litter source in native forest streams and occurring in 20% of all crayfish stomachs from native forest streams (Chapter 5). Elm leaves are much softer and have been found to be preferred over tougher leaf species in food choice experiments with other New Zealand invertebrate leaf shredders (Parkyn & Winterbourn 1997). However, even after the introduction of elm leaves, the juvenile crayfish in the leaf detritus treatment did not gain weight and deaths continued (Fig. 6.3). Plants and algae may be important sources of carotenoids that are required for good pigmentation in crayfish (Goddard 1988). Pigmentation of juveniles in all treatment groups was similar, although juveniles in leaf detritus treatments were generally paler than those fed chironomids, particularly prior to death. Deaths were more likely to occur during or after handling, which may suggest juvenile crayfish were already under stress from an inadequate food source.

Table 6.1. Survival and moult frequency of juvenile crayfish from native forest or pasture streams held for nine weeks under two experimental temperature regimes (cool, 12 – 15°C and warm, 16 – 23 °C) and fed leaf detritus or invertebrate foods (n = 8 for each treatment).

Treatment	Source	Survival (%)	Moulted once (%)	Moulted twice (%)
Cool				
Leaf detritus	Native	50	13	0
	Pasture	13	0	0
Invertebrate	Native	100	75	13
	Pasture	100	100	63
Warm				
Leaf detritus	Native	13	25	0
	Pasture	63	25	0
Invertebrate	Native	100	63	25
	Pasture	75	75	38

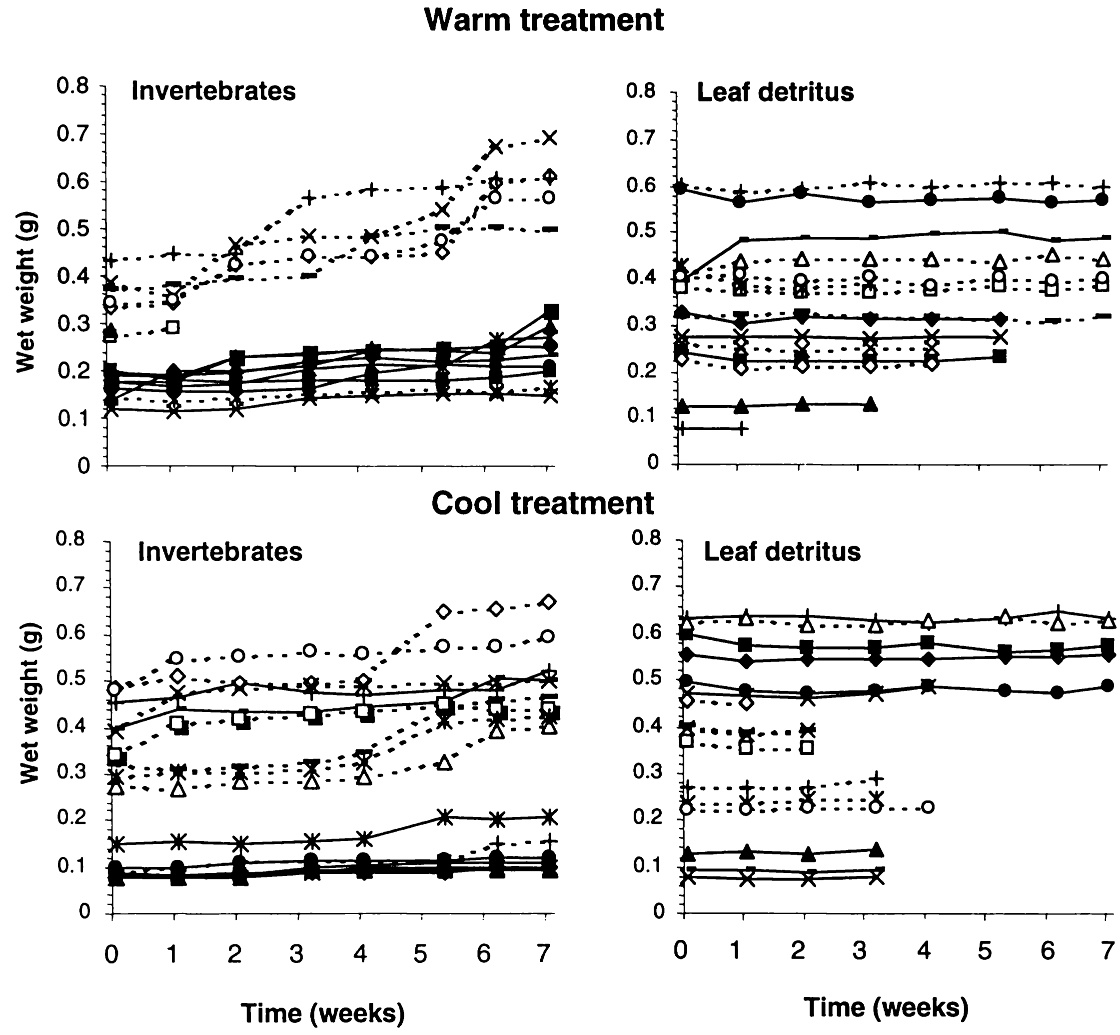


Figure 6.3. Wet weights (g) of individual juvenile crayfish in the warm and cool treatments fed invertebrates or leaf detritus. Solid lines are juveniles from native forest streams and dashed lines are juveniles from pasture streams. Initial weights (T_0) were taken two weeks after the start of the experiment in February as all crayfish lost weight initially.

Growth

The initial weight (T_0) of crayfish was taken to be the weight after at least two weeks of acclimation to experimental conditions, as all crayfish lost weight initially. Wet weights of crayfish fed chironomids at both temperatures increased over the subsequent seven weeks, whereas wet weights of crayfish in the leaf detritus treatment remained constant and did not increase despite the introduction of elm leaves after three weeks (Fig. 6.3). A small percentage of crayfish moulted once in the detritus treatment, but the only crayfish to moult twice during the course of the experiment were from the invertebrate treatment (Table 6.1).

Growth rates for both native forest and pasture stream crayfish, calculated from the % difference between the final weight of crayfish (either at the end of the experiment or the last live measurement) and the initial weight (after 2 weeks acclimation), were not significantly different between temperature treatments, due in part to high individual variation in growth rates (Fig. 6.4). However, food source had a greater effect on growth rates than temperature ($P < 0.0001$). Crayfish from both native and pasture streams that were fed detritus showed no appreciable growth over the course of the experiment and many had negative growth rates, whereas crayfish fed chironomids had growth rates of 0.5 – 1.1% weight gain day^{-1}. McClain et al. (1992) also found that the ability of juvenile *Procambarus clarkii* to use plant components for weight gain was extremely limited and that juveniles relied on a high microbial biomass associated with detritus for growth. However, weight gain on microbially enriched detritus was still less than on commercially prepared crayfish feed.

It seems unlikely that there is any genetic or adaptive difference between crayfish from pasture or native forest streams (Fig. 6.3, 6.4). There was a significant difference between the source of crayfish in the cool treatment, where pasture stream crayfish that were fed chironomids had significantly higher growth rates than comparable native stream crayfish ($P < 0.01$). However, there were no significant differences between crayfish from native forest or pasture streams in any other food source and temperature treatment. The lower growth rates for native forest stream crayfish than pasture stream crayfish in the cool, chironomid treatment may be due to the smaller size of the randomly selected native forest stream crayfish in that treatment. Four of the eight crayfish from native forest streams selected for this treatment were < 0.1 g wet weight (Fig. 6.3) and small juvenile crayfish may be affected by stress from handling or containment more than larger juveniles. There was a weakly significant effect of size on source of crayfish ($P < 0.1$) in the cool, chironomid treatment (assessed by using size as a covariate when testing between crayfish source), but no significant effect of size was detected in any other treatment.

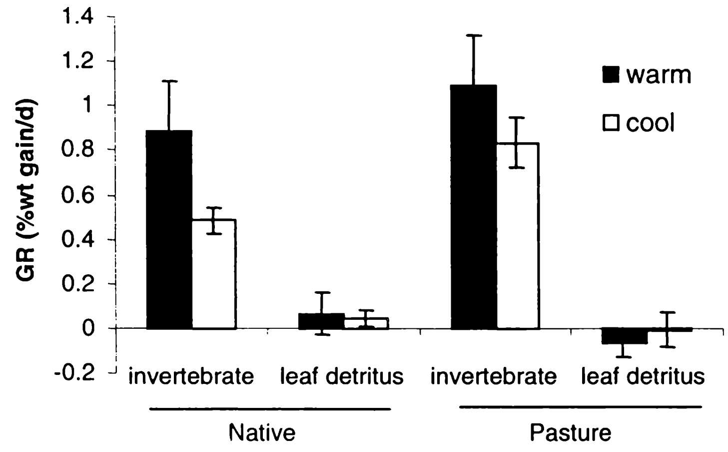


Figure 6.4. Mean growth rates (± 1SE) for juvenile crayfish from native forest or pasture streams and fed invertebrates or leaf detitus, that survived for at least four weeks in the warm and cool temperature treatments.

Moult increment and intermoult period

Temperature had no effect on size increase (mm OCL) at moult of juvenile crayfish in this study (homogeneity of slopes analysis, chironomid treatment only, Fig. 6.5A). However, there was a significant decrease in the moult increment of crayfish in the leaf detritus treatment relative to crayfish fed chironomids when data from both temperatures were combined ($F = 9.7_{35,4}$, $P < 0.01$, Fig. 6.5B). There was no difference in moult increment between crayfish from native and pasture land use sources (Fig. 6.5C), although this was tested with crayfish in the invertebrate treatment only, as there were too few moults in the detritus treatment to compare land use source.

Although there was no difference in moult increment between crayfish in cool and warm temperature treatments, there was a noticeable difference in the length of the intermoult period. The mean intermoult period of crayfish that had moulted twice from both temperature treatments was calculated for three crayfish size classes: 4 – 5.9 mm OCL, 6 – 7.9 mm OCL, 8 – 10 mm OCL (Fig. 6.6) as intermoult period differs with age and thus size of crayfish (Lowery 1988). No comparison of food treatment was possible as only crayfish fed invertebrates moulted twice and the only comparison of intermoult period possible between temperature treatments was in the 6 – 7.9 mm size classes. The intermoult period in the cold treatment was significantly longer than in the warm treatment for this size class (t test; $P < 0.01$) at an average of 41 and 29 days, respectively.

P. planifrons demonstrated greater annual growth in pasture streams than in native forest streams as a consequence of a greater moult increment and higher frequency of moults throughout the year (Chapter 3). Based on the results of this experiment, designed to represent summer temperatures for native forest and pasture streams, temperature is unlikely to cause the observed differences in moult increment for field crayfish. However, the greatest effect of temperature on crayfish growth appeared to be on the length of intermoult period. Verhoef et al. (1998a) found that the moult increment of *C. destructor* decreased with increasing temperature, but the increase in moult frequency resulted in greater overall growth at higher temperatures.

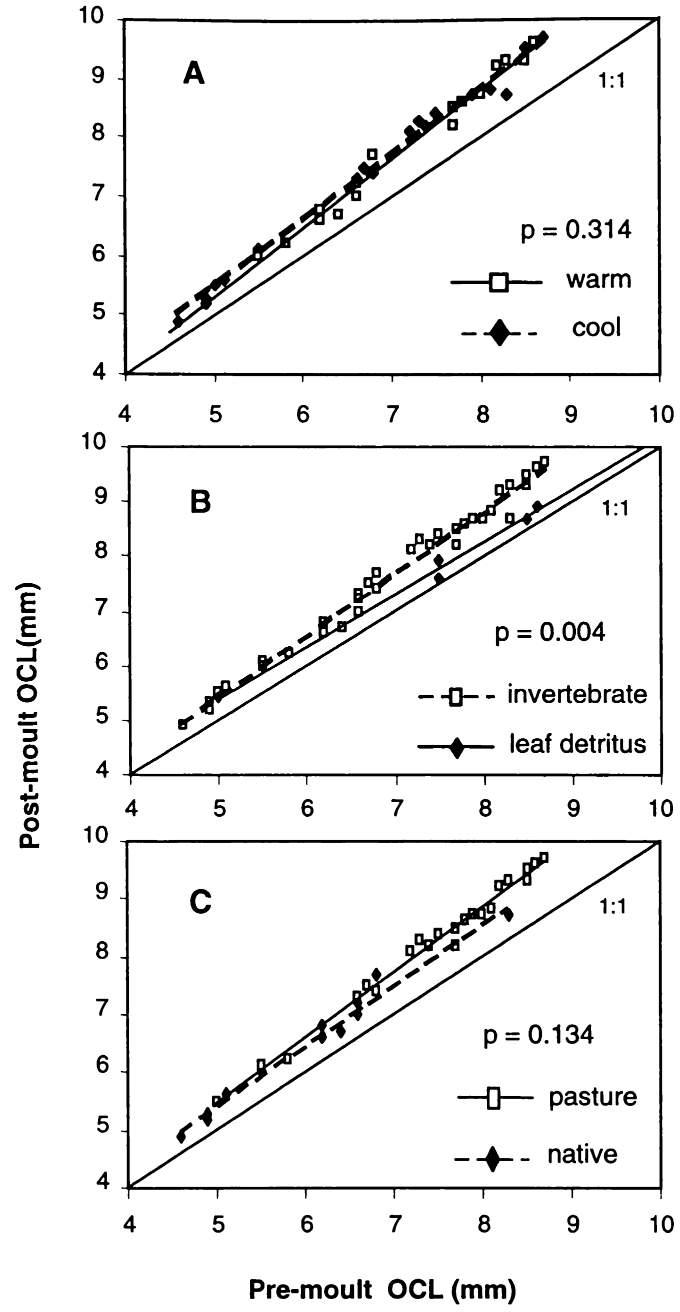


Figure 6.5. Pre-moult to post-moult orbit-carapace length (OCL) regressions ($R^2 > 0.95$) for all crayfish in warm (16 - 23°C) and cool (12 - 15°C) treatments (invertebrate treatment only, both sources combined; A); in invertebrate or leaf detritus treatments (both temperatures and sources combined; B); and from native forest or pasture streams (invertebrate treatment only, both temperatures combined; C). P values for each comparison are from homogeneity of slopes analysis.

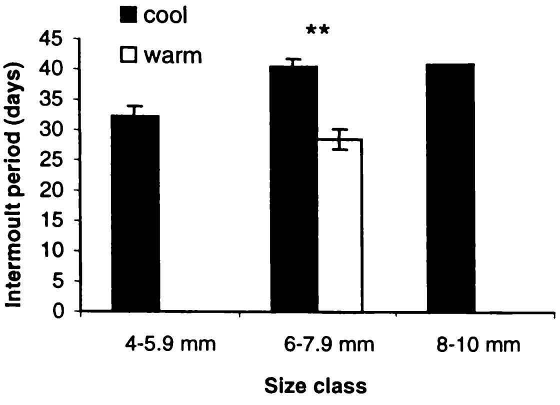


Figure 6.6. Mean (± 1SE) intermoult period for three size classes of crayfish and a comparison between cool (12 - 15°C, n = 3) and warm (16 - 23°C, n = 4) treatments in the 6 – 7.9 mm orbit-carapace length size class. ** = P < 0.01.

Growth rates over the length of this experiment did not reflect the difference in intermoult period length, as crayfish from both temperature treatments had time to moult twice and there was no difference in moult increment. However, it is likely that the shortened intermoult period results in greater annual growth of crayfish in warm pasture streams than those in cooler native forest streams. Jones (1981b) reared juvenile *P. planifrons* that were sourced from two different stream systems in laboratory aquaria at 10 - 21°C and 18 - 21°C for 18 months. The crayfish that were reared at the higher temperature had a faster growth rate, but the moult increments did not differ from crayfish that were reared at the lower temperature. Jones was unable to determine whether temperature or genetic factors caused the greater moult frequency, but evidence from my study suggests that temperature would be the primary influence.

A high amount of individual variation in annual growth increment has been found in many field populations of crayfish (Morey 1998, Chapter 3), even within streams

(Turvey & Merrick 1997a,c, Whitmore 1997, Hollows 1998). Discrete moult increments have been shown to vary greatly for *P. planifrons* (Chapter 3) and it appears that differences in temperature, of the ranges tested in this experiment, did not affect individual moult increment. In addition, temperature is unlikely to vary greatly within the sections of stream sampled for crayfish with the same adjacent land use. Therefore the variation in individual moult increments from within sites is more likely to be attributed to differential use of food resources, although differences in energy expenditure from the use of differing flow habitats in streams (Hopkins 1967b, Flint 1975) and density-dependent factors (e.g. resource limitation; Hopkins 1966) may also influence growth increments in field situations. Genetic variability between individuals or broods is likely to be a major cause of variation in growth rates, although Austin et al. (1997) found that diet had a greater effect on growth than phenotypic variation in *Cherax destructor*. However, greatest variation in annual growth rates for crayfish from the same year class may result from the timing of release from the mother. Juveniles that become free-living earlier in the summer are likely to undergo many more moults, with the longer exposure to warmer temperatures, than those released at the end of summer.

Assimilation of dietary carbon

Stable isotope analysis of muscle tissue of crayfish from the detritus and invertebrate treatments in the warm temperature treatment, provided further evidence that juvenile crayfish in this study did not utilise detrital material (Fig. 6.7). The $\delta^{13}C$ signature of an animal will be the same or slightly enriched from that of its food source (Peterson & Fry 1987). Crayfish that were fed detritus had $\delta^{13}C$ signatures of between -23 and –25 ‰, which were in the same range as mean signatures for field crayfish (Chapter 5). The $\delta^{13}C$ signatures for field crayfish are used in this study as an indication of the initial $\delta^{13}C$ signature of juveniles. Elm and fern leaves had $\delta^{13}C$ signatures of around –30 ‰, thus crayfish in the detritus treatment had not assimilated any of the leaf matter over this time period. On the other hand, crayfish in the invertebrate treatment had $\delta^{13}C$ signatures that were enriched compared to that of field crayfish (-19 and – 20 ‰) and close to the chironomid food source signature of –19 ‰ $\delta^{13}C$. Therefore, the observed growth in juvenile crayfish in the invertebrate treatment is directly related to the assimilation of the chironomid food source, and the lack of growth for crayfish fed detritus is due to their inability to incorporate the leaf matter used in this study into muscle tissue.

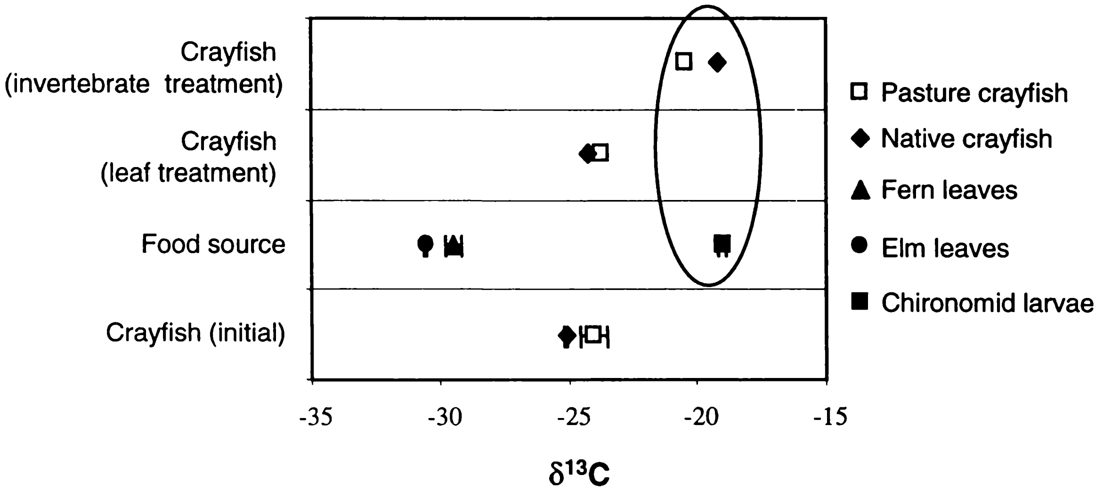
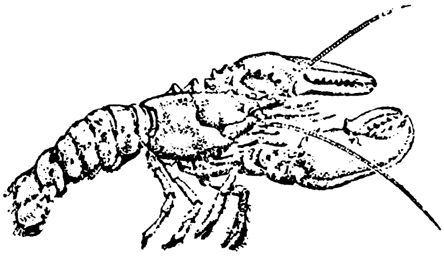


Figure 6.7. The $\delta^{13}C$ signatures of warm treatment crayfish (16 - 23°C) from native and pasture stream sources fed on leaf detritus or chironomid larvae (n = 2 per sample, pooled). Mean (± 1SE) $\delta^{13}C$ of chironomid, elm (n = 3) and fern leaf (n = 2) food sources. Initial crayfish $\delta^{13}C$ taken from means of field crayfish (Chapter 5).

Conclusion

The importance of diet to growth and survival of crayfish juveniles was evident from this study as no crayfish in the leaf detritus treatment moulted twice, mortality was high and the moult increment was significantly lower than for juveniles fed invertebrate food. Furthermore, stable carbon isotope analysis showed that leaf detritus was not assimilated into the body tissue over the nine week period, unlike the chironomid food source that directly contributed to growth. Diet affected both the size increase at moult as well as the frequency of moulting in *P. planifrons* juveniles. Temperature did not affect the size increase at moult for juvenile crayfish, although warmer temperatures significantly decreased the intermoult period. Increased moult frequency is likely to result in greater annual growth rates for crayfish, and warm temperatures coupled with a high proportion of invertebrates in the diet may result in rapid growth over the long term. Temperature is likely to be the primary determinant of growth for crayfish in these streams, but temperature may be less important than diet in environments where invertebrate food resources are limited.



Chapter 7

Trophic basis of omnivorous crayfish (*Paranephrops planifrons*) production in New Zealand native forest and pasture streams

Abstract

Crayfish annual production estimates and the volumes of food items found in crayfish stomach contents were combined with bioenergetic efficiency values to assess the basis of crayfish production and to quantify the trophic role of crayfish within streams that had experienced significant land use change. Crayfish assimilation efficiencies were determined experimentally and were higher for invertebrate foods than leaf detritus. The ability of crayfish to assimilate leaf detritus decreased with crayfish size and similarly, the ingestion rates of all food types decreased exponentially with size. Invertebrate food contributed the most to crayfish production in both native forest and pasture streams, despite high annual ingestion of leaf litter in native forest streams. This apparent anomaly was due to the high annual production of juvenile crayfish in both land uses. By investigating ontogenetic effects on bioenergetics, juveniles were shown to attain most of their production from consuming invertebrates, whereas adult crayfish in native forest streams apparently ingested more leaf litter in order to attain sufficient energy for production. Annual ingestion of invertebrates that contributed to production was up to 5.5 g m^{-2} y^{-1} in one pasture stream, but the transfer of energy from aquatic invertebrates to higher trophic levels through crayfish may be more significant in native forest streams where densities of invertebrates are lower. Flexible feeding strategies have allowed crayfish populations in these hill-country pasture streams to maintain similar annual production to those in native forest streams despite deforestation. Therefore, the role of crayfish as omnivores may have a stabilising effect on food webs through their ability to switch food sources in response to land use disturbance.

Introduction

The role of crayfish in streams is difficult to demonstrate, as they are omnivorous and can have direct and indirect effects on the stream community (Creed 1994, Parkyn et al. 1997, Nystrom et al. 1999). Omnivores utilise resources from more than one trophic level, including basal resources, and may therefore decouple classic trophic cascades, where predation from top predators has cascading effects on each trophic level below (Nyström et al. 1996, Pringle & Hamazaki 1998).

Crayfish have been labelled as primarily herbivores or detritivores on the basis of gut content analysis alone. This approach may overestimate the importance of items that are slow to digest and does not provide information on the energetic value of food sources. Understanding the role of crayfish in aquatic ecosystems requires measurement of the bioenergetic efficiencies of crayfish food sources relative to their contribution to growth and an understanding of how environmental conditions modify these processes (Momot 1995).

In New Zealand, large areas of land have undergone deforestation and conversion to farmland, particularly over the past 150 years. Streams have been strongly affected by the change in land use from forest to pasture, including effects on water quality and temperature, sedimentation, periphyton biomass, benthic invertebrate community composition (Scott et al. 1994, Quinn et al. 1997), and fish (Hanchet 1990, Hicks & McCaughan 1997). Deforestation has the potential to greatly affect populations of crayfish *Paranephrops planifrons* if, as detritivores, they obtain most of their energy from leaf litter.

As a result of deforestation, the abundance of aquatic invertebrates in pasture streams has increased and leaf litter inputs have decreased (Chapter 2). *P. planifrons* utilise a wide range of invertebrate species as well as leaf detritus in their diet and food choice was strongly linked to availability (Chapter 5). Consequently crayfish may have differential effects on benthic invertebrate communities depending on available food resources within streams. Similarly, ontogenetic shifts in utilisation of food resources, where juveniles consume more invertebrates than do adult crayfish, have been demonstrated for a number of crayfish species (Goddard 1988, France 1996c) including *P. planifrons* in native forest streams (Chapter 5), suggesting the role of crayfish may change with age.

In this study, production estimates and diet analyses have been combined with bioenergetic efficiencies to (1) determine the energy contribution of crayfish food sources to production and (2) quantify the role of crayfish in energy transfer through predation and organic matter processing. The lack of species-specific bioenergetics data was a major shortcoming identified by Benke & Wallace (1980) in their calculation of the trophic basis of caddisfly production, therefore assimilation efficiencies were established for *P. planifrons* when fed both invertebrate and leaf detritus food sources. The trophic basis of crayfish production was compared between populations of crayfish in native forest and pasture streams and for juvenile and adult crayfish to assess the effect of deforestation and age on the role of crayfish.

Methods

Crayfish production

Crayfish annual production (g dry weight m^{-2} y^{-1}) was estimated from quarterly samples taken between December 1996 and December 1997 at three native forest streams (NKL, NW5, NF) and three pastoral streams (PW2, PW3, PW5) in the Whatawhata AgResearch Station and Hakarimata Ranges west of Hamilton (Chapter 2). Three cohort year classes were identified in pasture streams and four in native forest streams. Size classes for each cohort present on each sampling date were identified from size frequency distributions and growth of mark-recapture crayfish (Chapter 3). Larger crayfish found in native and pasture streams were grouped as > 4 years and > 3 years, respectively, as there were too few of these crayfish to assign them to age classes reliably.

Crayfish densities were determined by electrofishing four small (6 – 8 m long) reaches at each site. Reaches were chosen using a stratified random method where 10 representative reaches comprising a pool and a run or riffle were identified within a 100 - 200 m stretch of stream, and four reaches were randomly chosen from these for sampling. A pool was included in each reach to standardise comparisons between the reaches. Each reach was fished using an EFM 300 electrofishing machine (Kainga Instrument Systems) powered by a 12 V battery, in an upstream direction using between two and four consecutive passes to achieve > 75% reduction in numbers. Wetted channel widths (mean of five equi-distant cross-sections in each reach) and reach lengths were measured on each sampling date to estimate wetted area (m^2) and length sampled. In each reach, actual numbers caught for each cohort size class on each date were expressed by area and were the mean of the four reaches was used for cohort density estimates for each stream.

Crayfish were measured with electronic Vernier calipers (0.1 mm) from the back of the eye socket to the mid-dorsal posterior border of the carapace to give orbit-carapace length (OCL) (Hopkins 1967b, Jones 1981b). Carapace lengths (OCL) were converted to dry weights (0.1 mg W) for each crayfish accounting for the number of chelae present, using power regression equations developed prior to sampling (Chapter 3). For crayfish that had two, one or no chelae the equations were: $W = 0.0001\ OCL^{3.264}$, $W = 0.0001\ OCL^{3.240}$, $W = 0.0001\ OCL^{3.125}$, respectively with $R^2 = 0.96$ for all equations. Mean individual weights were determined for each year class on each date from crayfish measured in all reaches (i.e. pooled) at each stream.

The annual density and weight (W) of each cohort was taken as the mean of the five sampling dates. Biomass (g dry weight (dw) m^{-2}) was the product of density and mean weight of each cohort. The instantaneous growth method (Benke 1984) was used to calculate the production of the interval between year classes using the equation:

$$P = GB$$

where production (P) was the product of the mean biomass (B) and instantaneous growth rate (G; $G = \ln (W_{final}/W_{initial})$ of the interval. Annual production (P) was the sum of the production between each year class present (Rabeni et al. 1995). Values of production used in the calculations in this study are shown in Chapter 3.

Volume of food consumed

Approximately twenty crayfish ranging in size from 5 - 32 mm OCL were sampled from each of the six streams in December 1996 and March, June and September 1997. The crayfish were captured from a mixture of pool, riffle or run sections of the streams soon after dark using electrofishing and handnetting, and were immediately put on ice and frozen on their return to the laboratory. Later, the stomachs of thawed crayfish were dissected out and placed into vials of 70% isopropyl alcohol (IPA). Percent volume of each food type was assessed visually through a binocular microscope by spreading the stomach contents evenly in the bottom of a small glass dish placed over a sheet of graph paper (1 mm grid). Coarse particulate organic matter (> c. 1 mm, CPOM) was identified as “leaf detritus” (including unidentified leaf species, fern leaf detritus and woody material), aquatic invertebrates, terrestrial invertebrates, seeds, macrophytes and moss, filamentous green algae, fish and unidentified flesh (Chapter 5).

Assimilation efficiency of invertebrate and leaf matter

Experiment 1: Effect of land use source. Crayfish (7.1 – 28.1 mm OCL) were collected using electrofishing in December 1997 from a pastoral stream (Tunaeke Stream, NZMS260 S14 939752) and a native forest stream (Firewood Creek, NZMS260 S14 976888) in the Hakarimata Ranges, Waikato. Crayfish were maintained in the laboratory until January 1998 at 10°C in tanks under shade cloth with gravel substrate and tiles provided as cover, and fed a range of fallen leaves and stream invertebrates.

Ten crayfish from the native stream and 11 from the pasture stream were randomly chosen from c. 15 crayfish from each site. Crayfish were placed in individually aerated containers with a circle of wire netting (1 mm mesh) pushed horizontally into them to form a false bottom in order to separate crayfish from their faeces. Each container was covered so crayfish could not escape. Crayfish were left in the dark at 15°C to empty their guts for 72 h as a preliminary experiment showed that some crayfish (particularly large ones) were still clearing their guts after 48 h.

Crayfish assimilation of invertebrates was tested using leptophlebiid mayfly nymphs collected from a pasture stream in the Hakarimata Ranges. Crayfish were moved to individual non-aerated 2-L containers filled with dechlorinated water at 15°C, and fed 10 live mayflies. Crayfish > 15 mm OCL received 10 large mayflies of similar sizes and crayfish < 15 mm OCL received 10 small mayflies, so that small crayfish were not disadvantaged by any possible difficulty in capturing or consuming large mayflies. The dry weight of mayflies given to crayfish was calculated by drying at 40°C for 24 h and taking the average weight of six groups of 10 large and 10 small mayflies. Crayfish were monitored regularly and additional mayflies, in groups of 10, were offered to crayfish that had consumed the original number. Crayfish were removed after four hours or after they had consumed 20 mayflies and the time of experimental exposure to the food source was recorded (range = 40 minutes to 4 hours). Crayfish were returned to their previous aerated containers and left to purge gut contents for 48 h when it was apparent that all food had passed through. Empty faecal membranes were removed from the faeces, which were then filtered onto previously dried and weighed (0.0001 g) glass microfibre filters. Both faeces and uneaten food were dried at 40°C for 24 h and weighed. Assimilation efficiency (AE) was determined gravimetrically according to the equation (e.g. Whitledge & Rabeni 1997):

$$AE\ (\%) = (1-(\text{faecal DW} / (\text{initial food DW} - \text{remaining food DW})))*100$$

where DW is dry weight (0.0001 g). Following collection of faeces, crayfish from native or pasture sources were returned to separate aquaria. One week later, 10 native stream and 10 pasture stream crayfish, were randomly chosen from the pool of 12 - 15 crayfish from each treatment. Assimilation efficiency of leaf detritus was tested using willow leaves (*Salix fragilis*), conditioned in stream water for 17 days. Five leaves were blotted dry and then wet weighed to the nearest 0.001 g in a container of pre-weighed water. Wet-dry weight conversion factors were established by wet weighing five groups of leaves, drying at 40°C for 48 h and re-weighing. Crayfish were left to feed for 4 h and then removed to clear guts as above and the same procedures were followed for calculating AE.

Experiment 2: Effect of temperature. A second experiment was run to investigate the effect of temperature on AE and to achieve a representative estimate of average AE for aquatic invertebrate and leaf matter using chironomid larvae (*Chironomus* sp.) and fern leaves, which provide a structural contrast to the food items used in the Experiment 1. The digestibility of chironomid larvae may differ from that of mayfly nymphs, as chironomids have a greater relative area of soft cuticle. Likewise, fern is a tougher leaf than willow, and leaf toughness has been identified as a factor affecting feeding rates of the facultative shredder *Olinga feredayi* (Quinn et al. in press b). Temperature has been shown to affect the AE of crayfish (Huryn & Wallace 1987, Musgrove 1988a) and temperatures of 15°C and 20°C were chosen for this experiment as they were representative of mean summer temperatures in native forest and pasture streams, respectively.

Crayfish were captured by electrofishing in November 1998 from a pastoral stream (Ahirau Stream, NZMS260 S14 947916), west of the Hakarimata Ranges, Waikato. Forty-eight crayfish were caught and kept for one week in the laboratory at 10°C with a 14h dark:10h light cycle prior to the experiment. They were fed mahoe (*Melicytis ramiflorus*) and fern (*Dicksonia* sp.) leaves and commercially frozen chironomids, and given PVC pipes for cover.

Twenty-four crayfish were placed in individual aerated containers (as above) at each constant temperature (15 or 20°C) and left in the dark for 72 h to acclimate to experimental conditions and clear guts fully. Twelve crayfish were randomly assigned to either chironomid or fern leaf food treatments and placed in individual, non-aerated containers filled with 1 litre of de-chlorinated water that had been aerated and equilibrated to the experimental temperatures. Food items consisted of one pre-frozen commercial cube of *Chironomus* sp. (c. 2.5 g wet weight) or one section of tree fern leaf (0.3 – 1.0 g wet weight) conditioned for 30 days in pond water. Chironomid cubes were weighed frozen and defrosted, and fern leaves were blotted dry and wet weighed, prior to presentation to crayfish. Wet to dry weight conversion factors were established previously (n = 6 for each food source) for the dry weight of each food item given to the crayfish.

Crayfish were left to feed in the dark for 4 h after which they were returned to their aerated containers. Crayfish fed fern leaves had eaten little or no leaf matter during the experiment so were returned to their aerated containers with the leaves overnight. Leaves were removed the following morning and all crayfish were left a further 48 h to clear their guts. Uneaten food was collected, dried at 70°C for at least 48 h and weighed. Empty peritrophic membranes were sorted from faeces, which were then filtered onto glass microfibre papers that had been previously dried and weighed. The filter papers with faeces were then dried at 70°C for 48 h and weighed, and AE was calculated as described above.

The trophic basis of crayfish production

Production estimates (Chapter 3) were combined with diet analyses (Chapter 5) and bioenergetic efficiencies using the calculations of Benke & Wallace (1980). Bioenergetic efficiencies were determined from the literature and from the assimilation efficiency experiments for *P. planifrons* when fed aquatic invertebrates and leaf detritus (this study). Calculations were based on assimilation efficiencies of 80% for aquatic and terrestrial invertebrates, fish and unidentified animal flesh, 20% for leaf detritus, seeds, macrophytes and mosses and 30% for filamentous algae (Benke & Wallace 1980, 1997). The assimilation efficiency for animal foods was determined from the mean AE for mayfly and chironomid foods for both juvenile and adult crayfish (see results). For leaf detritus, the mean value for willow leaves (a soft leaf type) was 50%, but AE for fern leaves (a tough leaf type) was likely to be very low (unmeasurable in experiment 2). Values of AE for willow leaves were much higher than those determined for other crayfish fed leaf detritus (e.g. maximum of 33% for *Cambarus bartonii*, Huryn & Wallace 1987; 14% for *Orconectes luteus*, Whitledge & Rabeni 1997) or macrophyte detritus (e.g. 21% for *P. zealandicus*, Musgrove 1988b; 16% for *Astacus astacus*, Hessen and Skurdal 1989). Furthermore, the assimilation efficiency of vascular plant detritus used in the calculation of the trophic basis of caddisfly production was 10% and assumed to be constant for all consumers by Benke & Wallace (1980, 1997). In this study, the value of 20% was chosen for vascular plant detritus, as it represented a conservative estimate of AE based on the variation in digestibility of the mixture of tough and soft leaf types that is present in streams, and the low values of assimilation efficiency for other types of detritus by crayfish recorded in other studies. Support for the use of a conservative AE estimate was provided by the stable isotope analyses, which indicated that *P. planifrons* assimilated little or no energy for growth from leaf litter (Chapter 5).

Calculated percentages of the amount of ingested energy used for growth (net growth efficiency, K_2) by a range of crayfish species generally varied from 20 – 50%, although values for crayfish < 1 year old when fed chironomids and high protein diets can be as high as 75% (Jones & Momot 1983, Momot 1995). Therefore, in the absence of experimental growth efficiencies for *P. planifrons*, net production efficiency (NPE; the amount of assimilated energy that is incorporated into body tissue), for each stream population was assumed to be 50%, as used in the evaluation of the trophic basis of production for caddisflies (Benke & Wallace 1980) and crayfish (*Orconectes* sp.; Whitledge & Rabeni 1997).

Effect of age on the trophic basis of production

The contributions of the two main food groups, leaf detritus and aquatic invertebrates, to the production of juvenile (c. < 20 mm OCL) and adult (c. ≥ 20 mm OCL) crayfish were calculated separately because differences in growth (Chapter 3) and diet (Chapter 5) were observed as crayfish became reproductively mature. Estimates of annual cohort production for juveniles (0 - 1 year old in pasture, and 0 - 2 years old in native forest streams) and adults, were combined with average volumes (%) of the food types consumed and bioenergetic efficiencies as done previously for crayfish of all ages combined. Assimilation efficiencies of leaf detritus changed with crayfish age, and mean AE of adult crayfish (≥ 20 mm OCL) was two-thirds of that of juvenile crayfish (< 20 mm OCL) (see results), therefore an AE of 20% was used for adult crayfish as above, and 30% for juvenile crayfish. AE of invertebrate food did not change with size, so 80% was used as above. Net production efficiency is also likely to change with crayfish size (Jones and Momot 1983), therefore a value of 70% was estimated for juveniles and 30% for adults, as juveniles would be likely to utilise more energy for growth than adult crayfish.

Statistical analysis

Estimates of assimilation efficiences from crayfish that moulted during the experiments or had consumed very little food were not included in analyses. Assimilation efficiencies were transformed using an arcsine square root transformation before statistical analysis and all analyses were performed in SYSTAT 7.0. The effects of crayfish size, land use source and temperature on AE were tested with ANCOVA using carapace length (mm OCL) as the covariate and land use source as the variable for willow leaves and mayfly nymphs (experiment 1) and temperature as the variable for chironomids (experiment 2). ANCOVA could not be used to compare crayfish AE between food sources as size affected AE differently depending on the food source (i.e. the slopes were not parallel). Therefore crayfish AEs were separated into size classes (< 20 mm and ≥ 20 mm OCL, that correspond to juvenile and adult (reproductively mature) crayfish) to account for the influence of size, so that differences between the food sources within each size class could be compared with a two-way ANOVA. Ingestion rates (mg dw g^{-1} body dw h^{-1}) were calculated for each food source offered to crayfish and compared using ANCOVA after log transformation. Crayfish dry weight was estimated from the length – weight regression equation for crayfish with two chelae used in the production analyses described above.

Annual ingestion (log transformed) and the percentage of production attributed to each food source (arcsine square root transformed) were tested with two-way ANOVAs for differences between land use (native forest or pasture streams) and food source. Annual ingestion, egestion (log transformed) and the percentage of production attributed to aquatic invertebrate or leaf detritus food sources (arcsine square root transformed) were tested using a series of one-way ANOVAs for the difference between age of crayfish (juvenile or adult) within each land use and food source.

Results

Feeding rates and assimilation efficiency

Assimilation efficiencies were greatest for crayfish fed chironomid larvae (Fig. 7.1.) The AE for crayfish that were fed tree fern leaves were largely meaningless and are not reported, as very little leaf matter was consumed (mean = 0.03 g dry weight) and the amount egested was relatively high (mean = 0.02 g dry weight). The amounts of fern leaf utilised by crayfish were considered small enough to be within the error produced by measurement (e.g. wet-dry weight conversions) or other weight loss errors (e.g. leaching) during the experiment. However, this result does indicate that AE values for fern leaves are likely to be very low.

No significant differences in AE were detected between crayfish from native forest or pasture streams (experiment 1; Fig. 7.1 A and B) or between experimental temperatures of 15°C and 20°C (experiment 2; Fig. 7.1 C) for any food source. However, assimilation efficiences for crayfish fed willow leaves (22 – 97%) decreased with increasing crayfish size (ANCOVA, $P < 0.01$). Although AE for crayfish fed chironomid larvae also declined with size ($P < 0.05$), values were generally above 90%. There was no effect of size on the AE of crayfish fed mayfly nymphs where the majority of crayfish had AE values between 70 - 90%.

Assimilation efficiencies for crayfish from land use and temperature treatments were therefore pooled for each food type, and mean AE for each food type was calculated for juvenile (< 20 mm OCL) and adult (≥ 20 mm OCL) crayfish (Table 7.1). Juvenile crayfish had a greater assimilation efficiency for chironomids than for mayflies or willow leaves ($P < 0.001$), which did not differ significantly from each other. For adult crayfish, the AE of chironomids was greater than that of mayflies ($P < 0.01$), which in turn was greater than that of willow leaves ($P < 0.05$).

Table 7.1. Mean (± 1 SE) consumption (mg dry weight h^{-1}) and assimilation efficiencies (AE) and the range of ingestion rates (mg h^{-1}) expressed as a percentage of crayfish body weight (mg dry weight) for juvenile (< 20 mm OCL) and adult (≥ 20 mm OCL) crayfish fed chironomid larvae (*Chironomus* sp.), leptophlebiid mayfly nymphs and willow (*Salix fragilis*) leaves.

Food Item	Crayfish	n	Mean consumption (mg dw h^{-1})	% of body weight ingested h^{-1}	AE (%)
Chironomid larvae	Juvenile	10	23.8 ± 1.5	1.2 – 9.4	96.9 ± 0.4
	Adult	8	26.4 ± 1.5	0.3 – 1.6	92.4 ± 1.2
Mayfly nymphs	Juvenile	11	4.5 ± 2.2	0.1 – 3.6	68.5 ± 5.6
	Adult	10	3.9 ± 1.9	0.03 – 0.9	65.6 ± 7.9
Willow leaves	Juvenile	8	7.2 ± 0.9	0.6 – 5.6	60.9 ± 7.6
	Adult	7	14.3 ± 2.0	0.3 – 0.8	39.6 ± 7.6

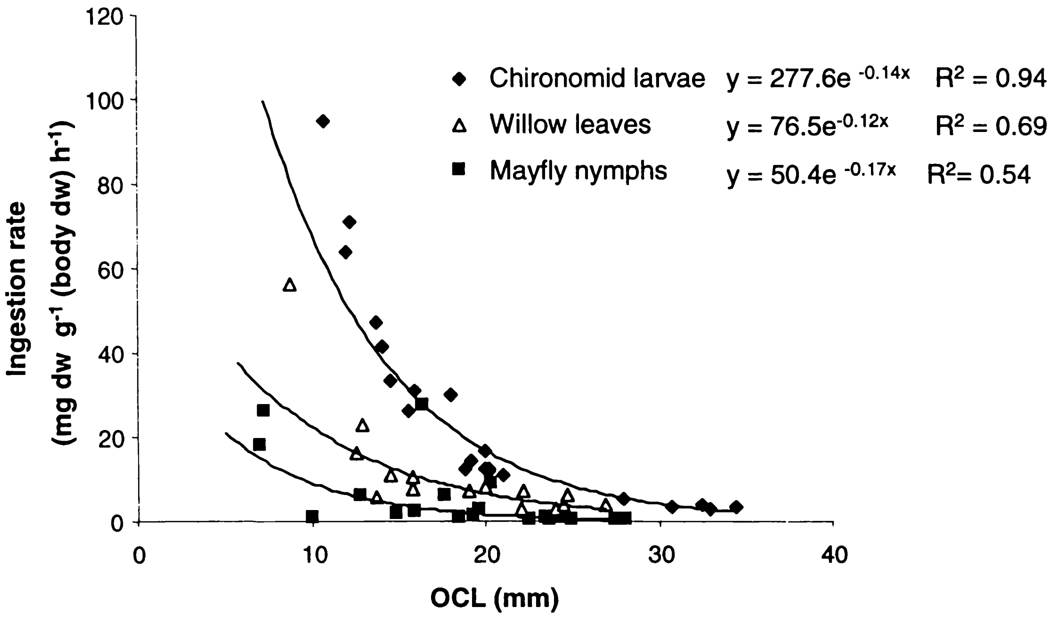


Figure 7.2. Ingestion rates of different-sized crayfish expressed as amount ingested per hour (mg dry weight (dw)) per gram of crayfish body dry weight, fed willow leaves and mayfly nymphs (experiment 1), and chironomid larvae (experiment 2). OCL = orbit-carapace length.

Ingestion rates (Fig. 7.2.) were significantly different between all food types ($P < 0.001$) in the sequence chironomids > willow leaves > mayflies. Juvenile and adult crayfish consumed similar amounts during the experiment (mg dry weight h^{-1}; Table 7.1), but the ingestion rates when expressed per gram of crayfish body dry weight (dw) were much greater for juvenile crayfish for all food types and decreased exponentially with size (Fig. 7.2). Very small crayfish (< 10 mm OCL) were found to ingest chironomids, willow leaves and mayflies at a rate of 9, 6 and 4% of their body weight per hour, respectively, whereas adult crayfish (≥ 20 mm OCL) ingested ≤ 1.6% of their body weight per hour (Table 7.1).

The trophic basis of production

Annual ingestion of leaf detritus and aquatic invertebrates was greater than for all other food types consumed by crayfish in both native forest and pasture streams ($P < 0.001$, Fig. 7.3 A). There was no significant difference between the amounts of invertebrate food and leaf detritus consumed by crayfish in either land use, due in part to the high variation in production estimates between sites used to derive the estimates of ingestion. The majority of crayfish production was due to consumption of invertebrates rather than leaf detritus for crayfish in both native forest (50%; $P < 0.05$) and pasture (70%; $P < 0.001$) streams (Fig. 7.3 B). In native forest streams, a significantly higher amount of crayfish production (35%) was attributed to consumption of leaf detritus compared to 15% of crayfish production in pasture streams ($P < 0.01$). All other food sources contributed to < 10% of production in both native forest and pasture streams.

To achieve their production, crayfish annual ingestion of aquatic invertebrates ranged from 0.9 – 1.8 g m^{-2} y^{-1} in the native forest streams and from 1.5 – 5.5 g m^{-2} y^{-1} in the pasture streams (Table 7.2). Amounts of leaf litter ingested were higher than for aquatic invertebrates at most sites, particularly in native forest streams (2.5 – 6.5 g m^{-2} y^{-1}), but were not significantly different due to the high variability between production estimates for the sites within each land use. The amount of leaf litter

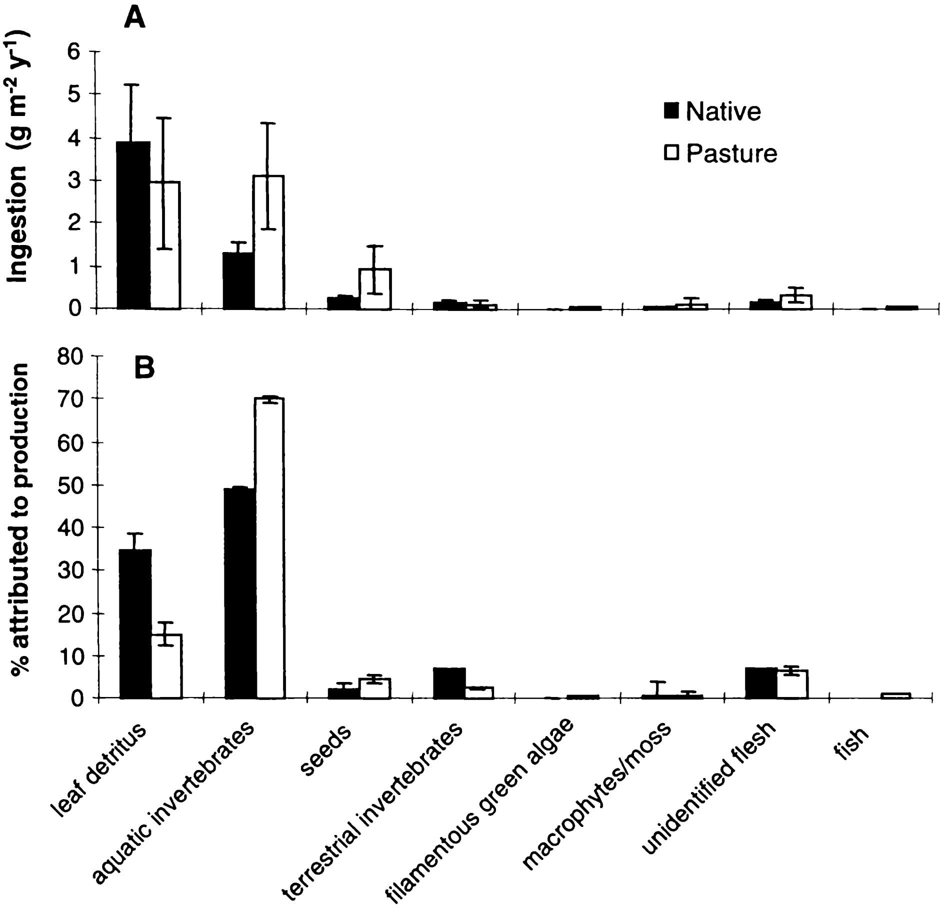


Figure 7.3. Mean (± 1 SE) annual ingestion (g m^{-2} y^{-1}) of all food sources found in crayfish gut contents (A) and the percentage that each food source attributed to crayfish production (B) in three native forest and three pasture streams.

Table 7.2. Estimated annual ingestion and egestion rates of aquatic invertebrates and leaf litter by crayfish populations from three native forest and three pasture streams. Mean percentages of the amount of each food/total amount ingested or egested are in brackets.

Site	Aquatic invertebrates ($g\ m^{-2}\ y^{-1}$)		Leaf litter ($g\ m^{-2}\ y^{-1}$)	
	Ingested	Egested	Ingested	Egested
Native forest				
NKL	1.8	0.4	6.5	5.2
NF	0.9	0.2	2.5	2.0
NW5	1.2	0.2	2.6	2.1
Mean	1.3 (22%)	0.3 (7%)	3.9 (67%)	3.1 (84%)
Pasture				
PW3	5.5	1.1	6.0	4.8
PW2	1.5	0.3	1.2	0.9
PW5	2.3	0.5	1.7	1.3
Mean	3.1 (41%)	0.6 (15%)	2.9 (39%)	2.3 (60%)

egested was correspondingly high (84% of the total egested matter from crayfish in native forest streams compared to 60% for pasture streams). In contrast, the amount of egested matter that was derived from aquatic invertebrates was very low due to the high assimilation efficiency of invertebrate matter. Estimates of the amount of leaf FPOM generated by crayfish and potentially available to other stream invertebrates, ranged from 2.1 – 5.2 $g\ m^{-2}\ y^{-1}$ for native forest streams and 0.9 - 4.8 $g\ m^{-2}\ y^{-1}$ for pasture streams.

Effect of age on the trophic basis of production

Both juvenile and adult crayfish in pasture streams derived most of their production from consumption of aquatic invertebrates (75% and 84%, respectively; Table 7.3). In contrast, adult crayfish from native forest streams gained 63% of their production from leaf detritus, while 53% of juvenile production was attributed to aquatic invertebrates. Although juveniles appeared to utilise more invertebrates in their diet than adults did in native forest streams, the annual ingestion by the juvenile population was not significantly higher than that of the adult population (mean = 0.8 and 0.4 g m^{-2} y^{-1}, respectively, P = 0.09)). Annual ingestion rates were affected by the high variability of production estimates between sites within each land use, which limited the use of statistical analyses.

Growth of juvenile crayfish was faster in pasture streams than in native forest streams (Chapter 3) possibly due in part to abundant high energy sources (aquatic invertebrates) available to crayfish in pasture streams. More juvenile crayfish production was attributed to invertebrates in pasture (75%) than in native forest (53%) streams ($P < 0.01$, Table 7.3), and annual ingestion of invertebrate matter by juvenile crayfish to achieve their production in pasture streams ranged from 0.7 – 3.2 g m^{-2} y^{-1} and from 0.5 – 1.2 g m^{-2} y^{-1} in native forest streams. Most of the litter processing and production of FPOM may be done by large crayfish in these native forest streams. Annual ingestion of leaf detritus to achieve their production in native forest streams ranged from 1.4 – 2.6 g m^{-2} y^{-1} for juveniles, and up to 1.8 g m^{-2} y^{-1} was egested, whereas ingestion by adult crayfish was higher at each stream and ranged from 1.7 – 4.6 g $m^{-2}y^{-1}$, and up to 3.7 g m^{-2} y^{-1} of leaf detritus was egested.

Table 7.3. Mean (± 1 SE) ingestion and egestion (g m^{-2} y^{-1}) of aquatic invertebrates and leaf detritus by juvenile (< 20 mm OCL) or adult (reproductively mature; ≥ 20 mm OCL) crayfish and the percentages that each food source contributed to crayfish production, from three native forest and three pasture streams.

Food source	Crayfish	Percentage attributed to crayfish production		Ingestion (g m^{-2} y^{-1})		Egestion (g m^{-2} y^{-1})	
		Pasture	Native	Pasture	Native	Pasture	Native
Aquatic invertebrates	Juvenile	74.8 ± 2.7	53.0 ± 1.6	1.7 ± 0.8	0.8 ± 0.2	0.3 ± 0.2	0.2 ± 0.0
	Adult	83.8 ± 7.6	37.0 ± 7.6	1.6 ± 0.4	0.4 ± 0.1	0.3 ± 0.1	0.1 ± 0.0
Leaf detritus	Juvenile	25.2 ± 2.7	47.0 ± 1.6	1.7 ± 1.0	1.8 ± 0.4	1.2 ± 0.7	1.3 ± 0.3
	Adult	16.2 ± 7.6	63.0 ± 7.6	1.8 ± 1.1	2.8 ± 1.0	1.4 ± 0.9	2.2 ± 0.8

Discussion

Assimilation efficiency and feeding rates

Mean assimilation efficiency of invertebrate foods ranged from 66 – 97% for juvenile and adult crayfish fed chironomid larvae or mayfly nymphs, and was similar to reported values of AE for many crayfish species fed animal foods (Jones & Momot 1983, Momot 1995, Whitledge & Rabeni 1997). Assimilation efficiencies for small crayfish fed leaf detritus were higher than for large crayfish and in general were much higher than other values found for detritus in the literature (e.g. < 33% Huryn & Wallace 1987). Jones and Momot (1983) did not find an effect of size on assimilation efficiencies of *Orconectes virilis* when fed an alginate diet, but consumption was greater for larger crayfish. During my experiments large crayfish also consumed more leaf matter than juvenile crayfish, but they assimilated much less. Consumption of animal matter was similar for adults and juveniles and the assimilation efficiency of invertebrate material remained constant with size. In addition to the decrease in AE of leaf detritus with crayfish size, ingestion rates when expressed per g of body weight also decreased with size for all foods. Younger crayfish may therefore consume higher amounts of food relative to their body size and be capable of assimilating more from detrital material, when the requirements of growth are high. Juveniles did not grow when fed leaf detritus in laboratory experiments (Chapter 6), which suggests that the amounts assimilated from leaf detritus may be used for maintenance rather than growth.

Devcich (1974) followed the nocturnal feeding patterns of lake-dwelling *P. planifrons* and found those in the shallowest waters (1 m depth; closest comparison to stream crayfish) to be actively feeding from 8 p.m. to 5 a.m. Assuming a daily feeding period of 9 hours, ingestion of chironomids by small crayfish may be up to 85% of their body weight per day, but lower for the other food types. Daily consumption of invertebrates may be more accurately expressed as a mean of chironomid (presented dead to crayfish) and mayfly (live) foods (60% of body weight per day for crayfish < 10 mm OCL). For soft willow leaves the maximum consumption for the smallest juveniles may be up to 50% of their body weight per day. Average percentages of adult body weight (≥ 20 mm OCL) consumed for all food types per day were 0.2 - 11%. These maximum values of daily food consumption (% of body weight) are higher than those reported for other crayfish species (e.g. 2.4 – 2.8% *Orconectes virilis* 12-14 mm CL; Jones and Momot 1983). In a review by Momot (1995), daily consumption for species fed a range of foods ranged from 0.4 - 16%, but no information on crayfish sizes were presented. The length of feeding period (9 h) may be an overestimate, although for the 4 h feeding experiments ingestion rates were still high, up to 38%, depending on the size of crayfish and the food type.

Trophic dynamics

Crayfish populations from native forest and pasture streams attain most of their production from consumption of aquatic invertebrates, despite the high amounts of leaf detritus consumed in native forest streams. This result concurs with stable isotope analyses of carbon and nitrogen that identified aquatic invertebrates as the major energy source for *P. planifrons* (Chapter 5). Whitledge & Rabeni (1997) identified aquatic invertebrates and leaf litter as the trophic basis of crayfish (*Orconectes* sp.) production using bioenergetic and stable isotope analyses, and concluded that crayfish were more carnivorous than previously thought. Similarly, three species of caddisflies that were thought to be primarily detritivorous obtained half of their production from animal food (Benke & Wallace 1980).

The bioenergetic analyses in this study attributed more importance to leaf detritus in native forest streams than was indicated by stable isotopes (Chapter 5), which may be an artefact of the assumption that the amount of energy used for growth (NPE) was 50% for all food sources (i.e. half of the energy from a food source is converted to production and half is used for maintenance). This assumption may not be valid for leaf matter that did not promote growth of juvenile crayfish and was not assimilated into crayfish tissue in a 9 week experiment (Chapter 6). However, in the absence of measured values of NPE for *P. planifrons* on each food source, use of a constant value for NPE would permit comparison of the trophic basis of production based largely on food volumes and assimilation efficiencies that have actually been measured in this study, and conclusions regarding the effect of land use should still be valid. The contribution of seeds may also be more important than indicated here, as seeds may have higher assimilation efficiencies than other plant material (Momot 1995) but they were not included in the assimilation efficiency experiments due to their low abundance in gut contents.

Trophic dynamics of juvenile and adult crayfish

The energetic needs of juvenile crayfish are likely to be greater than those of adults due to their rapid growth (Momot 1995). To determine the trophic basis of this growth, juvenile production (0 – 1 year in pasture, 0 – 2 years in native forest streams) was combined with size specific food consumption and bioenergetic efficiencies, and compared to data from adult crayfish. Juveniles from both native forest and pasture streams gained more of their energy for growth from aquatic invertebrates than from leaf detritus, but the contribution of invertebrates was higher for crayfish from pasture streams (75%) than native forest streams (53%). Growth of juvenile *P. planifrons* was greater in pasture streams than in native forest streams (Chapter 3) and the increased amount of animal matter converted into crayfish production in pasture streams suggests that diet could be a major factor in this accelerated growth. Surprisingly, calculations indicate that adult crayfish in pasture streams also obtained over 80% of their production from invertebrate sources, suggesting that the greater growth of juveniles than adults in pasture streams may be due to a combination of invertebrate consumption and higher ingestion rates.

Role of omnivorous crayfish

The roles of crayfish in New Zealand streams as processors of leaf litter, bioturbators and predators have been highlighted from experimental systems (Parkyn et al. 1997, Whitmore 1997), but the extent in which they influence energy pathways in streams has not been quantified. Calculation of the trophic basis of crayfish production and the amounts of the food sources consumed to achieve this production, enable the trophic role of crayfish to be evaluated within the stream invertebrate community and compared between stream systems subject to different environmental conditions.

Crayfish populations ingested similar amounts of leaf litter that contributed to their annual secondary production in native forest and pasture streams (mean = 3.9 and 2.9 g dw m^{-2} y^{-1}, respectively). Conversely, mean annual ingestion of invertebrates towards crayfish production was 1.3 g dw m^{-2} y^{-1} in native forest streams and 3.1 g dw m^{-2} y^{-1} in pasture streams. Although more leaf litter was eaten and incorporated into crayfish production in native forest streams, and more invertebrate food in pasture streams, there were no significant differences as crayfish production estimates were highly variable between sites.

Leaf litter inputs (vertical) in the streams in this study were < 200 g dw m^{-2} y^{-1} for pasture streams and 250 – 350 g dw m^{-2} y^{-1} for native forest streams (Dr M. Scarsbrook, NIWA, unpubl. data). Crayfish were estimated to have incorporated 1 – 8% of the vertical litter inputs in pasture streams into their production but only 0.7 – 2.6% in native forest streams. There is little information available on the annual ingestion of leaf matter by other New Zealand shredders. However, as population annual ingestion was calculated relative to crayfish secondary production, a comparison of *P. planifrons* annual production (0.8 - 3.4 g dw m^{-2} y^{-1}) with that of other stream shredders may indicate whether crayfish have a significant role in the transfer of energy from basal resources to higher trophic levels. Crayfish production was within the range of two leaf shredding caddisflies in Canterbury streams (0.35 - 7.5 g dw m^{-2} y^{-1}; Linklater & Winterbourn 1993), and similar to the facultative shredder *Olinga* sp. (1.2 g dw m^{-2} y^{-1}; Hopkins 1976) and the omnivore *Aoteopsyche colonica* (3.13 g dw m^{-2} y^{-1}; Scrimgeour 1991). In a study of open and shaded streams, Hopkins (1976) found that production of herbivores and detritivores ranged from 7.6 - 72.1 g dw m^{-2} y^{-1}. Crayfish incorporation of leaf litter into production is therefore likely to be less than that of the total leaf shredding population, although it is difficult to compare the relative importance of crayfish as shredders without site-specific information on annual ingestion of other stream invertebrate detritivores. In addition, obligate shredders are relatively rare in New Zealand streams (Winterbourn et al. 1981), so other invertebrates classed as detritivores are unlikely to obtain all of their production from leaf litter, and annual ingestion estimates therefore will not be as high as indicated by their production values. However, the stable isotope analyses

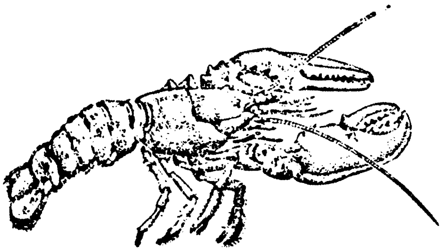
(Chapter 5) contradict the results of this study and indicate that energy from basal resources such as leaf litter does not pass into crayfish production and therefore, crayfish do not have a role in the conversion of energy from detritus to a form that can be utilised by higher trophic levels.

A major effect of crayfish consumption of leaf litter on the stream community may be the conversion of leaf litter into fine particulate organic matter (FPOM) that is potentially available as food to other stream invertebrates. Egestion of leaf detritus ranged from 0.9 – 4.8 g dw m^{-2} y^{-1} in pasture streams and 2.0 – 5.2 g dw m^{-2} y^{-1} in native forest streams. Processing of leaf litter into FPOM (as faeces) equated to 0.7 – 6.4 % of annual leaf litter inputs in pasture streams and 0.6 – 2.1 % in native forest streams. Most production of FPOM appeared to be from adult crayfish, particularly in native forest streams, due to high consumption but low assimilation efficiency (crayfish egested 80% of the leaf detritus consumed).

In two pasture streams surveyed by Hopkins (1976), total production of invertebrate predators ranged from 1.6 – 11.9 g dw m^{-2} y^{-1} in open stream sections and from 0.8 – 5.5 g dw m^{-2} y^{-1} in shaded sections. Total production of invertebrate predators in an Otago stream was 2.1 g AFDM m^{-2} y^{-1} (Huryn 1996). Crayfish may therefore make up a significant proportion of the invertebrate predator community, particularly when annual production is expressed per lineal metre of stream (3.1 (native forest) and 2.7 g dw m^{-1} y^{-1} (pasture); Chapter 3). Snails (*Potamopyrgus antipodarum*), leptophlebiid mayflies and chironomids are the main prey items of crayfish (Chapter 5). Based on the relative proportions of snails, mayflies and chironomids in crayfish gut contents (Chapter 5) and the annual ingestion of invertebrates in native forest and pasture streams (this study), crayfish were estimated to have incorporated between 0.3 and 0.5 g dw m^{-2} y^{-1} of each taxon into their production in native forest streams and between 0.3 – 0.9 g dw m^{-2} y^{-1} in pasture streams. Hopkins (1976) obtained production estimates in small streams for snails (*P. antipodarum*) of 5 g dw m^{-2} y^{-1} in shaded sections and 21 g dw m^{-2} y^{-1} in open sections, mayflies (*Deleatidium* sp.) of c. 2.5 g dw m^{-2} y^{-1} in both open and shaded sections, and Chironomidae of c. 0.9 g dw m^{-2} y^{-1} in open sections only. If we compare the annual ingestion of crayfish from these streams with the production estimates of Hopkins (1976), a small percentage of the production of snails in unshaded stream sections would be incorporated into crayfish production, but two-thirds of the estimated amount of chironomid production would pass into crayfish production. Conclusions on the trophic pathways of energy from predation in native forest and pasture streams are only speculative without accompanying production values of their dominant prey species in these streams. However, densities of snails and chironomids were low in native forest streams and incorporation of 0.4 and 0.3 g dw m^{-2} y^{-1}, respectively, into crayfish production may be a substantial proportion of their production in these streams and indicate potentially important pathways of energy.

The amounts and types of food ingested by crayfish changed in response to deforestation; more invertebrates were consumed in pasture streams and more leaf detritus in native forest streams. Ironically, this study has shown that the trophic role of crayfish as predators may be more important in native forest streams where densities of invertebrates are lower than in pasture streams and the role of crayfish as shredders may be more important in pasture streams with lower leaf litter inputs.

The trophic analyses appeared to produce an anomaly in native forest streams where invertebrate foods were the trophic basis of production, but high amounts of leaf detritus were also consumed. By looking at the effect of age on the trophic basis of crayfish production it appeared that leaf detritus provided energy to adult crayfish in native forest streams but was insufficient to provide for the growth of juvenile crayfish. Most *P. planifrons* production comes from the juvenile cohorts which dominate crayfish numbers (Chapter 3), and their predation may account for the importance of invertebrates to production observed for the population as a whole. Most of the processing of leaf litter into FPOM was performed by adult crayfish, but they may need to consume large amounts of leaf detritus to gain energy, causing the higher ingestion rates observed in native forest streams. Therefore, separating the juvenile and adult components of the population was important to understanding the role of crayfish within native forest streams. However, the effect of environmental change through deforestation and conversion to pastoral land use was a greater influence on the trophic basis of crayfish production than age, as both adult and juvenile crayfish in pasture streams capitalised on the abundant invertebrate resources. Flexible feeding strategies have allowed crayfish populations in these hill-country pasture streams to maintain similar annual production to those in native forest streams despite deforestation. Therefore, the role of crayfish as omnivores may have a stabilising effect on food webs through their ability to switch food sources in response to land use disturbance.



Chapter 8

Summary:

Land use effects on the population dynamics and role of crayfish

Population dynamics in native forest and pasture streams

Deforestation and conversion to pastoral land use has affected the water quality, physical habitat and biotic communities of New Zealand streams (Hicks & McCaughan 1997, Quinn et al. 1997, Harding et al. 1999). Crayfish in the Waikato hill-country streams studied here appear to have adapted to these changes by altering the way in which they utilise shelter and obtain energy from the environment. Thus, although crayfish densities were greater in native forest streams, due primarily to greater juvenile recruitment, annual production was not significantly different, suggesting that the overall success of the crayfish populations was similar in both land uses.

Crayfish in pasture streams exhibited much greater growth leading to a shorter life cycle and earlier reproductive maturity (after 1 year as opposed to 2 years in native forest streams). The greatest mortality for juvenile cohorts occurred during winter and mortality was greater in pasture streams than native forest streams. However, due to faster growth rates, crayfish in pasture streams did not have to experience two winter periods before reproducing. Therefore, despite greater densities in native forest streams, the faster reproductive cycle of crayfish in pasture streams may have contributed to the similarity in production estimates between land uses. In contrast, Hollows (1998) found little difference in growth rates of *P. zealandicus* in Otago pastoral and native forest streams where water temperatures were similar. Temperature appeared to be the primary factor influencing the earlier hatching and higher moult frequency (from becoming free-living earlier in summer) of juvenile *P. planifrons* in the Waikato pasture stream sites. Food source may also have been a significant factor. The diet of crayfish in pasture streams contained a higher volume of invertebrates than in native forest streams where leaf detritus dominated stomach contents (Chapter 5). Invertebrate food was shown to increase the moult increment and decrease the length of the intermoult period compared to conditioned leaf litter, which did not promote growth and was not assimilated into body tissue (Chapter 6). Warmer water temperatures in this experiment decreased the length of the intermoult period, but had no effect on the size of moult increment. In the pasture streams of this study, crayfish moult frequency and increment were greater than in native forest streams suggesting that factors such as diet, in addition to temperature, were important for growth.

Habitats of crayfish in native forest streams were primarily tree roots, bank undercuts, accumulations of woody debris and pools. The removal of riparian trees (particularly their roots) may undermine the stability of under cut banks (Hanchet 1990), and reduce the amount of woody debris entering streams and the number of pools formed by woody debris (Quinn et al. 1997). However, deforestation and ongoing pastoral management has led to increased abundance of macrophytes (Winterbourn 1995), which have provided alternative cover habitat for crayfish in pasture streams. These along with cobble substrates and terrestrial vegetation growing within the stream were important habitats for crayfish in pasture streams. Macrophytes are structurally complex and may provide good protection from predation (Jordan et al. 1996a,b), as crayfish have been able to coexist with eel predators in these streams. However, crayfish in pasture streams were not as resistant to a major flood disturbance as in native forest streams, suggesting that the available habitats in pasture streams do not provide stable refugia. Furthermore, the rate of recovery of a crayfish population in one pasture stream following the flood was very slow indicating that *P. planifrons* does not exhibit resilience traits, such as rapid recolonisation or body form adaptations to increased flow, and is dependent on stable refugia to persist during disturbances (Townsend et al. 1997).

Under normal flow regimes, streams within pastoral catchments support similar levels of crayfish production to native forest streams. Flood events in pasture streams may dramatically affect population densities because of a lack of stable habitat, but the significance of such events to the overall distribution of crayfish is difficult to determine on the basis of a one in 20 year flood. Nevertheless, this study has demonstrated one potential mechanism by which crayfish populations may be adversely affected by land use change.

What's best for crayfish in New Zealand streams?

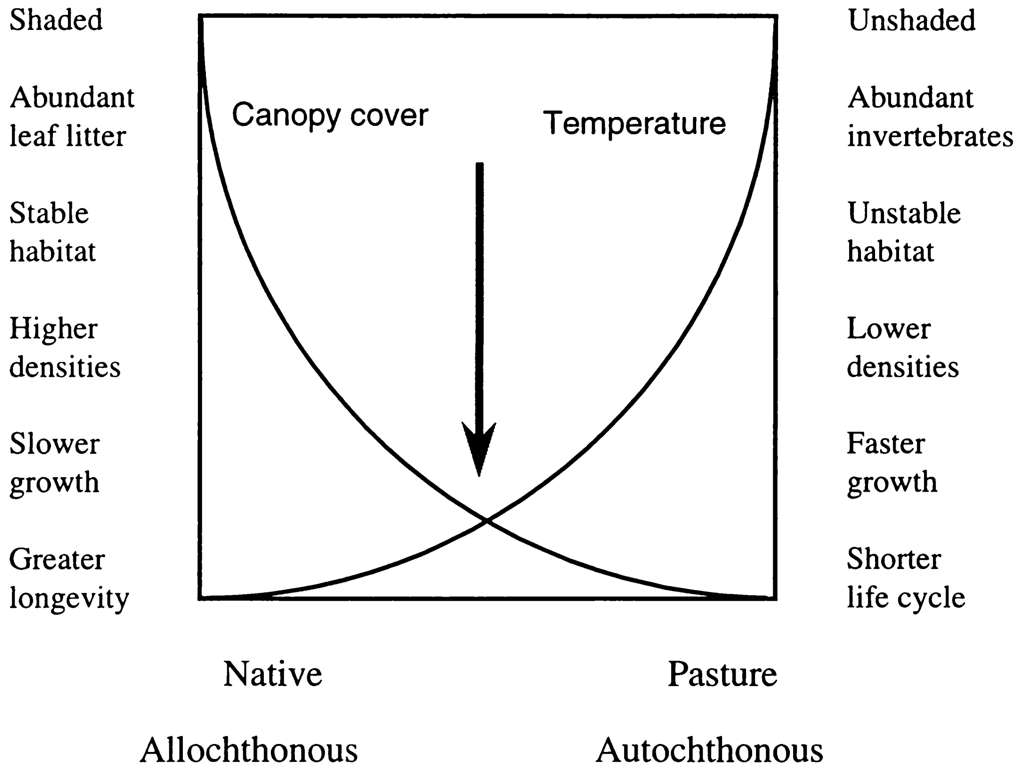


Figure 8.1. A summary of features of the crayfish populations in native forest and pasture hill-country streams in the Waikato region. The arrow represents a possible "best scenario" where intermediate conditions promote best growth and survival for crayfish populations.

Crayfish grew faster and achieved greater sizes in pasture streams due to warmer water temperatures and the higher abundance of invertebrate foods. However, in native forest streams, crayfish lived longer and produced more juveniles resulting in higher densities. Furthermore, the available habitats in native forest streams such as tree roots and undercut banks were more stable than those in pasture streams and provided refugia for crayfish during a major flood. Therefore, the best growth and survival of crayfish may be achieved in environmental conditions intermediate between those present in native forest and pasture streams (Fig. 8.1.), where warm temperatures, high densities of invertebrate food sources, and stable habitat prevail. Jones (1981a) found that experimental populations of *P. planifrons* became stressed above 20°C, and that best growth was achieved at constant temperatures of 19°C. The planting of riparian buffer zones has been recommended as a means to restore degraded pasture streams (Collier et al. 1995). Riparian buffer zones may provide some of the intermediate conditions that are likely to benefit crayfish populations. Riparian trees provide protection from extreme temperatures and provide stable refugia that are of fundamental importance to crayfish survival during large-scale flood disturbance.

The role of crayfish in native forest and pasture streams

Crayfish were identified as top invertebrate predators in these hill-country streams despite omnivorous feeding habits that allowed crayfish to exploit a variety of food resources. Crayfish populations in native forest streams had greater volumes of leaf detritus in their guts than in pasture streams, but stable carbon and nitrogen isotope analyses identified aquatic invertebrates as the major energy source contributing to tissue production for crayfish in both native forest and pasture hill-country streams. Snails, mayflies and chironomids were the most important taxa in crayfish diets particularly in native forest streams, but by acting largely as a predator of a wider range of invertebrate taxa in pasture streams, crayfish were able to take advantage of both allochthonous and autochthonous energy pathways.

Although allochthonous detritus dominated *P. zealandicus* stomach contents in Otago streams, stable isotope analysis showed that they were top predators (Hollows 1998). In contrast to *P. planifrons*, Hollows (1998) found that *P. zealandicus* consumed more detritus in pastoral streams than in native forest streams, although he also found that the most important invertebrate taxa to crayfish were snails, mayflies and chironomids. As omnivores, crayfish may have dual functional roles as both predators and processors of organic matter, and through production of FPOM they may make leaf matter available to a wider range of invertebrates (e.g. collectors) in stream ecosystems.

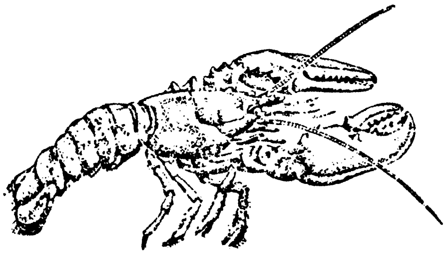
The functional importance of crayfish to the stream community may differ between land uses as crayfish food choice appears to be closely related to the abundance of local food resources. Crayfish annual production estimates (Chapter 3) and volumes of food sources consumed (Chapter 5) were combined with bioenergetic efficiencies in Chapter 7 to determine the trophic basis of crayfish production and to quantify the amounts of different foods ingested and egested annually that contribute to their production. As indicated by stable isotope analysis, invertebrates were the trophic basis of crayfish production in both native forest and pasture streams. The amounts and types of foods ingested by crayfish changed in response to deforestation; more invertebrates were consumed in pasture streams and more leaf detritus in native forest streams.

Juvenile crayfish were shown to have higher rates of assimilation of detrital food and higher ingestion rates per gram of body mass of all food types than adult (reproductively mature; ≥ 20 mm OCL) crayfish. Most of the annual production of crayfish populations in both native forest and pasture streams came from juveniles, due to their high growth rate and the low numbers of adult crayfish. Juveniles in pasture streams gained more of their production from consuming invertebrates than in native forest streams, which may have contributed to their faster growth rates. Age affected the role of crayfish in native forest streams where adult crayfish processed more leaf litter into FPOM and juveniles were more carnivorous. However, in pasture streams, the roles of juvenile and adult crayfish were similar, as there was no difference in the amount of invertebrates or leaf detritus ingested or egested. Large crayfish in pasture streams were able to take advantage of the abundant invertebrate resources, but in native forest streams their diet was largely detritus either as a consequence of habitat selection or reduced availability of invertebrates. The role of crayfish as predators or processors of leaf detritus may change according to their growth requirements, but more importantly, according to environmental influences on local food resources.

Omnivores as community "stabilisers"

The most important role of crayfish in these streams may not be solely as a predator or processor of organic matter, but rather as an omnivore. Direct effects of crayfish predation have been demonstrated for snail species (Hanson et al. 1990, Lodge et al. 1994) but crayfish often have complicating indirect effects that disrupt classical trophic cascade models (Nystrom et al. 1996). As an example of a classical trophic cascade, crayfish may prey on snails, which in turn consume algae, and increased densities of crayfish would result in lower snail populations and a corresponding increase in algal biomass. Omnivorous crayfish can interrupt this trophic cascade in two ways. Firstly they may consume algae directly (e.g. Creed 1994) and a change in crayfish densities may affect both snails and algae, or secondly, they may consume a wide range of basal resources as well as primary and secondary consumers, and have little direct effect on any resource. In addition, crayfish may affect the physical environment of streams through bioturbation, which may have indirect positive effects on other stream invertebrates (Parkyn et al. 1997, Whitmore 1997).

The importance of omnivory has not been widely investigated (Diehl 1993), possibly because of a belief that omnivory in food webs is relatively rare (Pimm 1982). Many New Zealand stream invertebrates can be described as feeding generalists (Winterbourn 1995) and omnivory was reported to be relatively common in food webs of Otago streams (Jaarsma et al. 1998). Omnivores increase the connectance and therefore the stability of food webs, which is potentially most important when stream communities are faced with disturbance. Pringle & Hamazaki (1997) demonstrated that omnivorous fishes influenced the stability of algal assemblages during flood disturbance by maintaining the dominance of an alga resistant to scouring. Crayfish in the hill-country streams of this study have maintained their populations despite the disturbance of significant land use change, largely through omnivory. Flexibility in feeding has allowed crayfish to survive in pasture streams where deforestation has greatly decreased leaf litter inputs. Crayfish consumed substantial amounts of stream invertebrates and leaf litter in these streams, and consequently they act as both predators and processors of organic matter, and have an additional trophic role as a food source for eel predators (Hicks 1997). The role of omnivory in food web dynamics is complex, and the influence of omnivores such as crayfish in maintaining the stability of stream food webs may be of greater significance to community structure than their direct effects on the stream community.



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