Growth and population dynamics of crayfish *Paranephrops planifrons* in streams within native forest and pastoral land uses

STEPHANIE M. PARKYN[1,2]

KEVIN J. COLLIER[1]

BRENDAN J. HICKS[2]

[1]National Institute of Water and Atmospheric
 Research Limited
 P.O. Box 11 115
 Hamilton, New Zealand
 email: s.parkyn@niwa.co.nz

[2]Centre for Biodiversity and Ecology Research
 Department of Biological Sciences
 University of Waikato
 Private Bag 3105
 Hamilton, New Zealand

Abstract   Population dynamics of crayfish (*Paranephrops planifrons* White) in streams draining native forest and pastoral catchments, Waikato, New Zealand, were investigated from September 1996 to July 1998. Crayfish densities were generally greater in native forest streams because of high recruitment over summer, but varied greatly between streams in both land uses. Peak densities in summer were 9 crayfish m^{-2} in native forest and 6 crayfish m^{-2} in pasture streams, but peak biomass in summer was much greater in pasture 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 reached reproductive size at c. 20 mm orbit-carapace length (OCL) after their first year in pasture streams, but after 2 years in native forest streams. Annual degree days >10°C appeared to explain the differences in the timing of life cycles. Estimates of annual crayfish production (range = 0.8–3.4 g dry weight m^{-2} $year^{-1}$) were similar in both land uses, and P/B ratios were between 0.95 and 1.2. 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

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 (Quinn et al. 1997; Harding et al. 1999; Quinn 2000). 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 fish diversity has declined (Hanchet 1990; Hicks & McCaughan 1997).

New Zealand has two endemic species of freshwater crayfish, *Paranephrops planifrons* (White) and *P. zealandicus* (Parastacidae). *P. planifrons* is found in the North Island and in the north and west of the South Island and *P. zealandicus* in the southeast of the South Island and in Stewart Island (Chapman & Lewis 1976). Hopkins (1967a,b) studied growth and breeding in *P. planifrons* from pastoral streams, and Jones (1981) studied the growth rates of *Paranephrops* spp. in relation to temperature, but no studies have investigated the difference in crayfish life histories between native

forest and pasture streams. Crayfish are often missed by conventional invertebrate fauna sampling techniques. Environmental factors can affect growth rates and also the losses to predation, non-predatory mortality, or emigration through changes in habitat or predator populations. 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.

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) describe 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

Population density and biomass

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, Waikato, New Zealand (see Parkyn et al. 2001 for site location and description) were monitored on four seasonal sampling dates per year from September 1996 to July 1998. The stream widths, depths, and velocities were measured on two occasions (Table 1) and water

temperature was monitored continuously using Onset temperature loggers in each stream from September 1996 to March 1998. Mean, maximum, and minimum temperatures for each month were averaged over the three sites in each land-use type (Fig. 1).

Four sampling reaches (6–8 m long) were chosen using a stratified random method at each site. Estimates of crayfish abundance were determined from the removal method (Armour et al. 1983) by electro-fishing as this is considered the most effective method of removing crayfish from heavy cover (Rabeni et al. 1997). 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 area (m^2) and by length (linear metre) in each reach, and density estimates for each stream were the mean of the four reaches.

Orbit-carapace length (OCL) of each crayfish 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). 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.

Relationships between OCL and dry weight (0.0001 g DW) were developed before 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: $DW = 0.0001 \, OCL^{3.26}$; $DW = 0.0001 \, OCL^{3.24}$; $DW = 0.0001 \, OCL^{3.13}$, 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

Table 1 Mean channel widths, water widths, velocity, and depths measured in the Waikato region, New Zealand, September 1996 and March 1997 at the time of crayfish (*Paranephrops planifrons*) sampling.

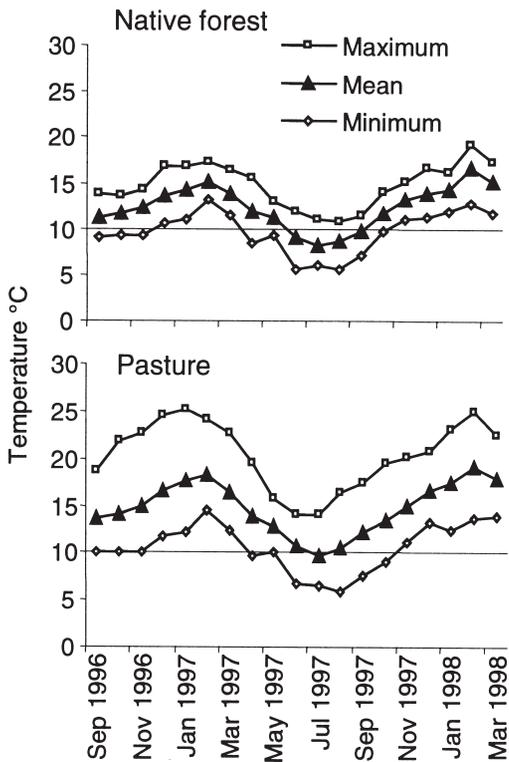| Site	Channel widths (m)	Water widths (m)	Water velocity (m s^{-1})	Water depth (cm)
PW3	1.2	0.9	0.20	10
PW2	1.6	1.4	0.24	16
PW5	2.2	2.0	0.23	23
NKL	1.9	1.6	0.17	14
NF	4.1	2.9	0.17	17
NW5	3.9	3.2	0.16	17

Fig. 1 Monthly maximum, minimum, and mean temperatures (mean of three native forest and three pasture stream sites) in the Waikato region, New Zealand, from September 1996 to March 1998. Line at 10°C represents the threshold for mean temperatures below which growth may not occur.

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.

OCL lengths were converted to dry weights (g DW) for each crayfish using the equations above to determine biomass, mean cohort weight, and production at 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.

Growth of mark-recapture crayfish

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 *P. zealandicus* (Hollows 1998), and was tested in this study before use in the field. 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.

Crayfish were individually identifiable once marked using a total of 255 tag combinations (Hollows 1998). Over the course of the 2-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 that had low crayfish densities, to add to the numbers of marked individuals in each stream.

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 were averaged over the four reaches on each date. The annual density and weight (W) of each cohort was taken as the mean of the five sampling dates. Cohort 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:

$$P = GB$$

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 over all age classes (Rabeni et al. 1995).
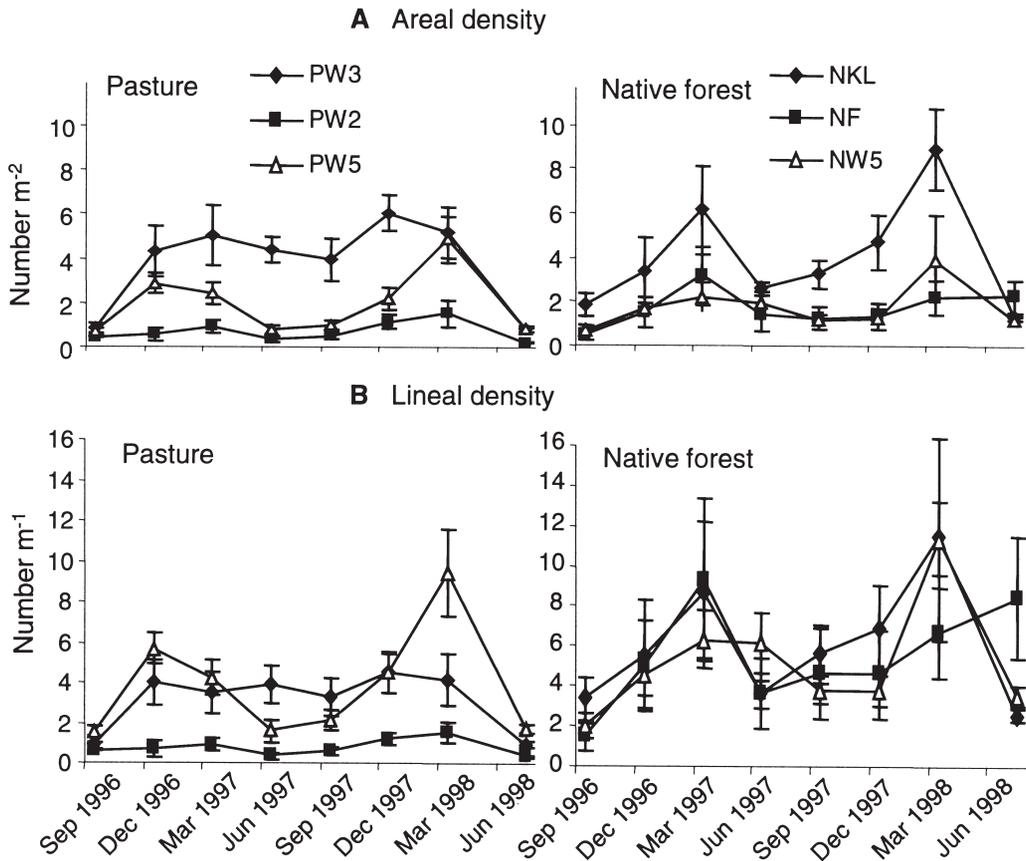
Fig. 2 Mean (±1 SE; *n* = 4) density of crayfish *Paranephrops planifrons* from three pasture and three native forest sites in the Waikato region, New Zealand, between September 1996 and July 1998. **A**, Number m^{-2}; **B**, number per linear metre.

Statistical analysis

Log-transformed densities and biomass of crayfish per m^2 and per stream linear metre 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 3 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 in the regression lines of annual growth increments against initial carapace length were compared between land uses 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 field observations. Differences in the regressions of moult increment with OCL were tested between land uses

with ANCOVA as above. Annual production estimates were compared for differences between land use with a *t*-test.

RESULTS

Population density and biomass

Crayfish abundance varied greatly between dates and between stream sites from September 1996 to July 1998 (Fig. 2A). Mean densities ranged from <1 to 6 crayfish m^{-2} in pasture streams and from <1 to 9 crayfish m^{-2} in native forest streams. Population numbers generally peaked in late summer 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, as a result of variable availability
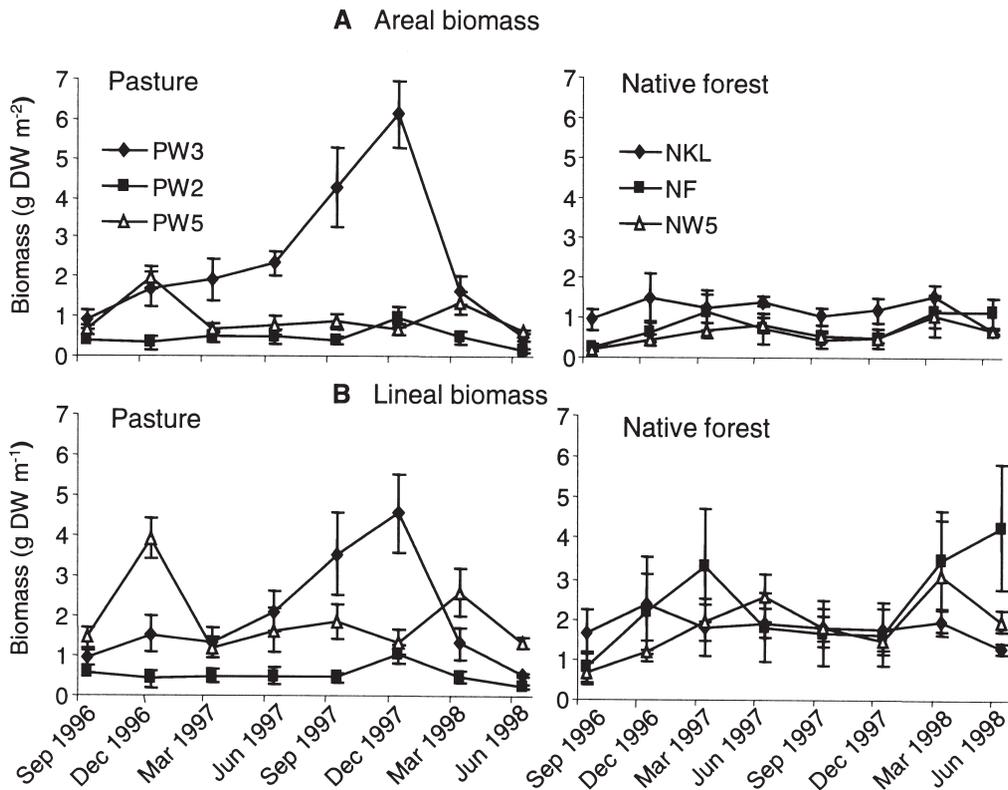
A Areal biomass

B Lineal biomass

Fig. 3 Mean (±1 SE; $n = 4$) biomass (g DW) of crayfish *Paranephrops planifrons* from three pasture and three native forest sites in the Waikato region, New Zealand, between September 1996 and July 1998. **A**, Biomass m^{-2}; **B**, biomass per linear metre.

of habitats that crayfish occupy within and between sample reaches.

Over all sampling dates combined, log-transformed densities of crayfish from native forest streams were higher than from pasture streams ($P < 0.05$), with sites nested into land use. There was no significant interaction between land use and sampling date, indicating that the pattern was consistent over time. The pasture site PW2 had consistently low numbers throughout the study period.

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, and therefore the area sampled was greater, although crayfish were not usually present in the middle of these streams where there were few cover habitats. Hicks (unpubl. data)

also found that *P. planifrons* abundance was related to the amount of edge habitat. When densities were expressed per linear metre to account for this difference (Fig. 2B), peak densities in pasture streams were highest at the largest stream (PW5; 9 crayfish m^{-1} in March 1998) and the variation between sites was less. Numbers of crayfish per linear metre of native forest stream were higher than in pasture streams ($P < 0.001$) and there was no interaction between land use and date. Densities per linear metre remained high at the smallest site (NKL; 11 crayfish m^{-1} in March) and this site supported the highest densities regardless of the manner in which data were expressed.

Biomass (g DW) of crayfish populations in pasture streams was significantly higher than native forest streams when expressed by area ($P < 0.001$; Fig 3A) 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

linear metre, crayfish in native forest streams had significantly higher biomass than those in pasture streams ($P < 0.001$) over all dates and with sites nested into land use. Expressing biomass per linear metre in native forest streams distinguished the summer peaks in juvenile numbers that were not evident when biomass was expressed by area. These 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 population densities (m^{-1}) contributed to the higher linear biomass over all dates. In pasture streams, a combination of high numbers and high growth (see below) over summer dramatically increased peak biomass estimates. Mean (± 1 SE) crayfish weights were similar between sites within each land use and were greater in pasture (0.7 g DW $\pm$ 0.03) than native forest (0.4 g DW $\pm$ 0.02) streams (*t*-test, $P < 0.01$).

Size frequency

Three size classes were identified as cohorts in pasture streams compared with four size classes in native forest streams (Fig. 4). Crayfish >26 mm OCL were determined to be >4 years old in native forest streams and crayfish >30 mm OCL were >3 years old in pasture streams, but numbers were too low to reliably identify year classes above that age. The largest crayfish found in the pasture streams was 37 mm OCL, 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) and was estimated to be 7 years old based on reproduction and growth data. The young-of-the-year (YOY) cohort (Fig 4; open bars) entered the population in pasture streams between September and December 1996, earlier than in native forest streams, and their growth was much faster, although 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. Mortality for the first year cohort in pasture streams was 39% between March 1997 and September 1997, whereas in native forest streams mortality was 18% over 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 (Fig. 4).

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). Mating appeared to occur in autumn (March–June) and females carried their eggs through winter. Juveniles were released generally between September and December in pasture streams and between December and March in native forest streams.

Females up to 3 years old were identified in pasture streams but females 5 years or older were identified only in native forest streams, based on the size range of each cohort in March. 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 a similar reproductive size after 2 years.

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. 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. 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 with 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.

Three year classes in pasture streams and five year classes in native forest streams were identified by following the growth of individually marked crayfish that were recaptured more than 3 times during September 1996–July 1998 (Fig. 5). 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 after >4 years in native forest streams. Numbers of large crayfish caught were low and variation in growth was high causing apparent declines in mean size between some sampling

Fig. 4 Size-frequency plots for crayfish *Paranephrops planifrons* populations in native forest and pasture streams in the Waikato region, New Zealand (three sites pooled). Open bars represent the 0–1 year cohort that entered the population between September and December 1996. (OCL = orbit-carapace length.)
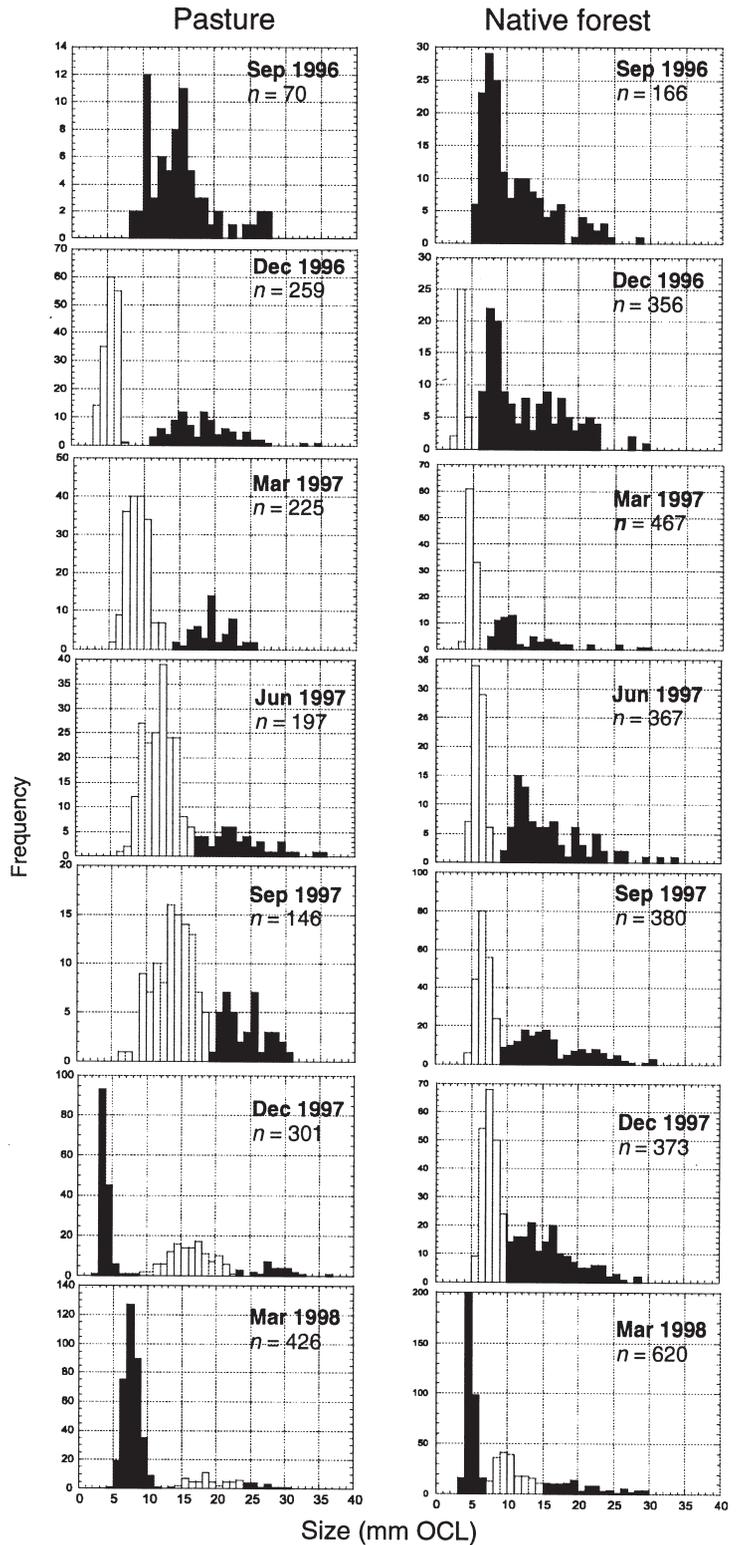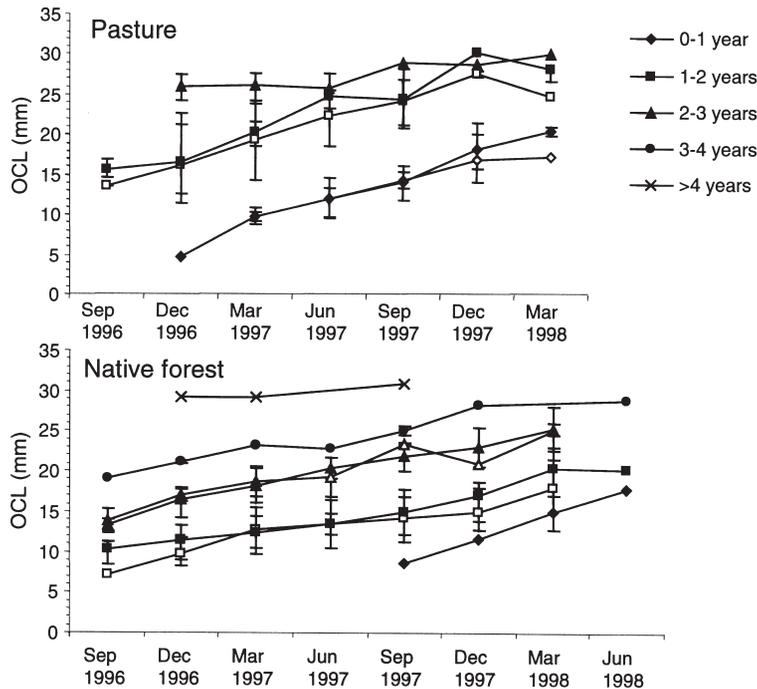
Fig. 5 Mean growth (in length) of year classes identified from individually marked crayfish (*Paranephrops planifrons*) that were captured 3 or more times from September 1996 to July 1998 in native forest and pasture streams in the Waikato region, New Zealand. (Error bars = range of sizes; open symbols = females, closed symbols = males, for the two year classes with sufficient numbers to enable comparisons, otherwise both sexes combined; OCL = orbit-carapace length.)

periods. This artefact of small sample size should not be interpreted as a decline in growth rates (Fig. 5).

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. 5). 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 comparisons between sexes.

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 6A). Variation in growth was high, particularly in small-sized crayfish. Annual growth declined with the size of crayfish because the frequency of moulting reduced with age.

Crustacean growth is a function of both size increase at moult (moult increment) and the moult frequency. To separate these components of growth from field mark-recapture data, plots of the growth increments against pre-moult OCL (mm) were compared with a regression equation of moult increments observed in the field over a range of crayfish sizes (Fig. 6B). There was considerable variation in the size of single moult increments, although increments increased with crayfish size, and at a constant rate between land uses. The regression equation produced for crayfish in native forest streams was: growth increment = 0.76 + 0.074(pre-moult OCL) ($R^2 = 0.23$); and for pasture streams: growth increment = 0.94 + 0.079 (pre-moult OCL) ($R^2 = 0.29$). Comparisons between land-use regressions of 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; $F = 8.84$, $P < 0.01$).

Moult frequency also appeared to be greater in pasture streams, particularly with small crayfish
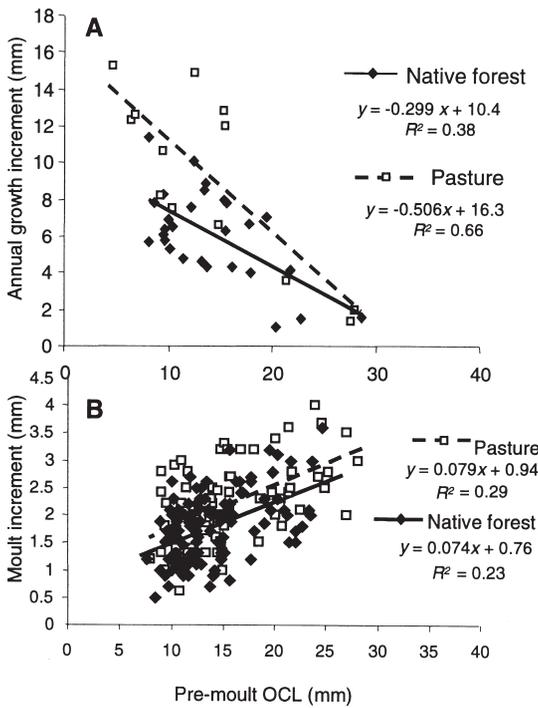
Fig. 6 **A**, Annual growth increment; and **B**, size of moult increment, plotted against pre-moult length (orbit-carapace length, OCL) for crayfish (*Paranephrops planifrons*) recaptured after a 12-month period between September 1996 and July 1998 from three native forest and three pasture streams in the Waikato region, New Zealand.

(<15 mm OCL) that may have moulted up to 2 times in native forest streams and up to 3 times in pasture streams within any 3-month period. The difference in annual growth increments between native forest and pasture stream crayfish (Fig. 6A) may therefore be from both the greater size of moult increment in pasture streams and the higher moult frequency of small-sized crayfish.

Cohort growth and production

Growth in crayfish from both native forest streams and pasture streams was exponential for the first 2 years and became linear in the third year at 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 forest streams primarily because of greater initial growth rates in the first year of growth for pasture stream crayfish (Table 2). Annual growth rate was

much higher for pasture stream crayfish in the first year allowing them to attain weights 13 times greater than native forest stream crayfish (0.9 and 0.07 g DW, respectively) at the end of the first year. Growth rates declined for both native forest and pasture crayfish in subsequent years as the number of moults decreased.

Crayfish annual production ranged from 0.8–3.4 g DW m^{-2} year^{-1} in pasture streams and from 0.8–1.6 g DW m^{-2} year^{-1} in native forest streams, but was not significantly different between land uses (Table 3). Site PW2 had very low production because of consistently low density throughout the study. The smallest streams in both native forest (NKL) and

Table 2 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 not present).

	Natural log of relative growth rate (*G*)	
Cohort	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	–

Table 3 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 (m^{-2}) and per lineal (m^{-1}) metre of streambed sampled. (DW = dry weight.)

Site	Biomass (g DW)		Production (g DW year^{-1})		
	m^{-2}	m^{-1}	m^{-2}	m^{-1}	P/B
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

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. When expressed per linear metre of streambed sampled, crayfish production at all native sites was similar (3.0–3.2 g DW m^{-1} year^{-1}), but production remained high in the smallest pasture stream (4.0 g DW m^{-1} year^{-1}). There was no significant difference in mean annual production per linear metre between land uses. Crayfish biomass (g DW m^{-2}) in native forest streams was half that in pasture streams, although when expressed per linear metre, the biomass estimates were almost equal. Turnover (P/B) ratios were near one (0.95–1.2) for crayfish in both native forest and pasture streams, but were lower for crayfish in most pasture stream sites due to high biomass.

DISCUSSION

Life history

Land-use change affected the timing of juvenile crayfish recruitment and the length of time before adults reached reproductive size (Fig. 7). Recruitment of juvenile (0–1 year class) crayfish in pasture streams (monthly average water temperature from June to September = 14–16°C) occurred c. 2 months earlier than in cooler native forest streams (10–12°C). Juveniles that enter the population in spring or early summer are likely to grow larger in their first year than those who 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–2 years, depending on temperature, based on growth studies in aquaria (Jones 1981). Crayfish in the pasture streams of this study reached a size where they would be reproductively mature after 18 months, much earlier than in native forest streams, and earlier than many other crayfish species (cf. 3 years for *Pacifastacus leniusculus* in the United States (Lewis 1997) and in Britain (Guan & Wiles 1999); and 6–7 years for *P. zealandicus* in southern New Zealand (Whitmore & Huryn 1999). Free-living juveniles that entered the population between September and December in warm pasture streams grew to between 7 and 22 mm OCL in 1 year; those that reach c. 20 mm OCL (17–24 mm OCL) by the following autumn would be reproductively mature. In cooler native forest streams, most juveniles became independent between December and March and took 2

years to reach a similar reproductively mature size to those in pasture streams.

As a consequence of faster growth, crayfish in pasture streams reached maximum ages faster (3–4 years; c. 35 mm OCL) than in native forest streams where the maximum age of similar-sized crayfish would be 4–5 years. 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 monthly water temperatures were below 10°C (believed to be a threshold for crayfish growth; Whitmore & Huryn 1999) from June to August. Annual degree days (sum of daily mean temperatures) for a native forest and a pasture stream were 4281 and 5069, respectively. Annual degree days above 10°C (an indication of degree days available for growth) were 3422 (native forest stream) and 4698 (pasture stream). Growth halts completely in winter for *P. zealandicus* in Otago streams where the mean daily temperatures only rise above 10°C for c. 60 days of the year (annual degree days = 2600, annual degree days above 10°C = c. 660; Whitmore & Huryn 1999). The largest *P. zealandicus* found by Whitmore & Huryn (1999) was estimated to be >25 years old (85 mm carapace length).

Degree days >10°C appear to be a useful measure to explain differences in longevity and life history. Crayfish in the Waikato pasture streams have experienced c. 18800 degree days to reach a maximum age of 4 years. Based on degree days >10°C, crayfish in native forest streams would reach maximum age at 5.5 years, and *P. zealandicus* in Otago streams would attain a maximum age of c. 28 years, which compares well with estimates by Whitmore & Huryn (1999). Similarly, degree days >10°C to reach reproductive maturity for pasture stream crayfish were 7200 over 18 months, which equates to 2 years to reach maturity in native forest streams.

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 than in lentic environments. Populations of *Austropotamobius pallipes* in large lakes in Britain grew more slowly than those found in rivers because the larger waterbody took longer to reach maximum summer temperatures and never attained temperatures equivalent to the river (Lowery 1988). It is likely that *P. planifrons* spend much of their time at depths within lakes where temperatures would be cooler and more constant
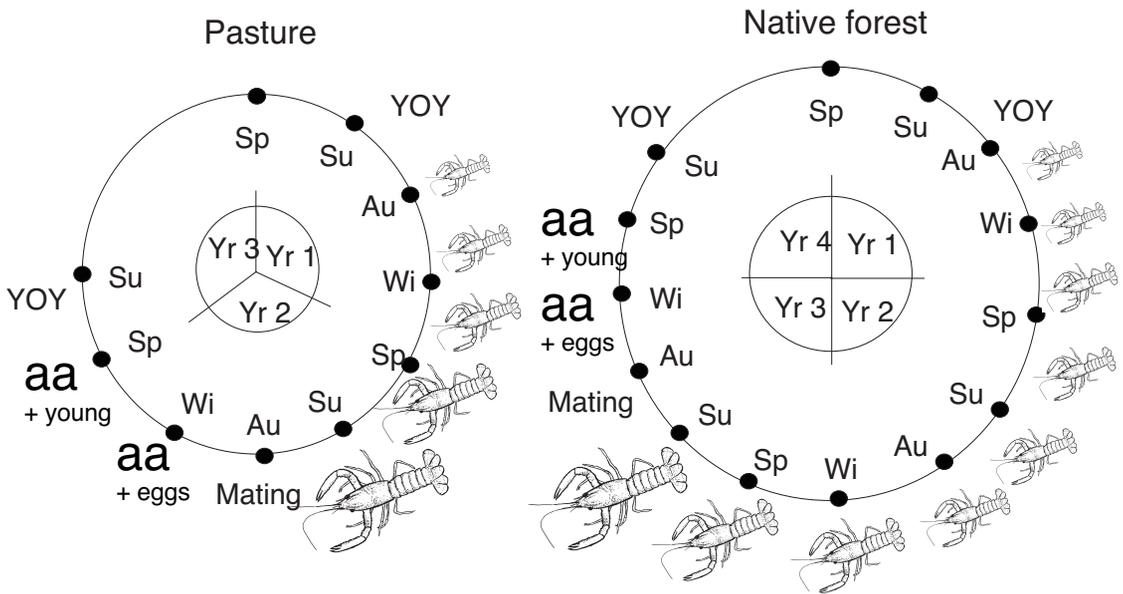
Fig. 7 Diagrammatic representation of the reproductive cycle of crayfish *Paranephrops planifrons* in native forest and pasture streams in the Waikato region, New Zealand. (YOY = young-of-the-year; aa = females.)

than streams. Therefore, assessment of degree days >10°C may be a useful technique to explain the differences in growth between stream and lake populations of crayfish.

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 c. 20–30 eggs on 17 mm OCL females of *P. planifrons*, compared with up to 150 eggs on 30 mm OCL females. The longer life of crayfish in native forest streams combined with the greater fecundity of large females suggests greater juvenile recruitment in natural systems and that conversion to pastoral land use may reduce recruitment of juveniles and contribute to lower population density.

Compared with 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 and the abundance and biomass of eels is greater in pasture than in native forest streams (Hicks & McCaughan 1997). Crayfish are likely to be most susceptible to predation when small and during moulting when their carapaces are soft. The

greater moult frequency of juveniles in pasture streams than in native forest streams may leave them more vulnerable to predation. Floods may also contribute to mortality during winter, particularly in pasture streams, as the habitat is less stable than in native forest (Parkyn & Collier unpubl. data). Although there was greater mortality during winter in pasture streams, the faster growth of these crayfish means that they did not have to experience two periods of high mortality (winter) before reproducing, potentially enabling them to achieve similar annual production as crayfish in native forest streams.

Land-use influences on growth

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 1997; Whitmore & Huryn 1999). In the present study, temperature has been shown to affect longevity and growth rates of crayfish. Jones (1981) followed the growth of *P. planifrons* in heated (18–21°C) and unheated (10–21°C) aquaria for 2 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 (Ackerfors 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 from 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 with 12 mm OCL for crayfish in native forest streams. Variation in moult frequency was particularly high for juvenile crayfish, contributing to the variation in annual growth increment. Growth rates of adult crayfish were similar in native forest and pasture streams, and adults are likely to be less affected by land use than juvenile crayfish, as they moult only once or twice per year regardless of water temperature.

Laboratory growth experiments with *P. planifrons* fed invertebrate or leaf detritus and kept in warm or cool temperatures approximating those in pasture and native forest streams, showed that temperature affects moult frequency, but diet may affect both moult frequency and moult increment (Parkyn & Collier 2002). Similarly, Verhoef et al. (1998a) reported that warm temperatures increased moult frequency, but decreased 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. Parkyn et al. (2001) found that crayfish in pasture streams consumed more aquatic invertebrate prey, whereas crayfish in native forest streams consumed a greater proportion of the abundant leaf detritus. The higher consumption of invertebrates by crayfish from pasture streams may have contributed to increased growth rates, particularly through increases in moult increment, in conjunction with warmer water temperatures that increase the moult frequency of crayfish in pasture streams.

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 water 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 our hill-country streams.

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 variations in food availability or population density (Turvey & Merrick 1997). Temperature is unlikely to cause variation in moult increments in our study streams, as it is unlikely to 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) appear to be the most likely factors affecting variability in 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 streams. Expressing densities per linear 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 because of higher recruitment over summer. However, during winter the population densities were similar to those 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 period of stable winter flows, although differences in the proportion of females breeding from year to year may also be a factor.

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 from warmer stream temperatures, or consuming more invertebrate food, or a combination of these factors. Once again, expressing biomass per linear metre provided a better representation of the peaks of recruitment in native forest streams, as the centre of streams are largely under-utilised by crayfish and are thus excluded from 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} year^{-1}) despite production of *O. luteus* attributed 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 this study was largely from 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 of *P. planifrons* was expressed per linear 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 by far 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, because of limited 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 linear 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} year^{-1}) in these streams was lower than that of the other New Zealand crayfish species *P. zealandicus* (2–11 g ash free dry mass (AFDM) m^{-2} year^{-1}, approximately equivalent to 3–16.5 g DW m^{-2} year^{-1}) in a cool temperate Otago stream (Whitmore & Huryn 1999). The high annual production of *P. zealandicus* was attributed 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) from higher growth rates, and within the range found for most other crayfish species (0.5–1.5; Momot 1995).

Summary of land-use effects

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, possibly from greater longevity of crayfish in native forest streams and higher recruitment of YOY, or greater winter mortality of juveniles in pasture streams. Water temperature seems to be a major factor contributing to the higher growth rates and consequently shorter life cycle of crayfish in pasture streams. The mechanism of faster growth in pasture streams was primarily the increase in moult frequency with warmer stream temperatures, although differences in diet between land uses may also be a factor.

REFERENCES

Abrahamsson, S. A. 1966: Dynamics of an isolated population of the crayfish, *Astacus astacus* Linné. *Oikos 17*: 96–107.

Ackerfors, H.; Castell, J. D.; Boston, L. D.; Räty, P.; Svensson, M. 1992: Standard experimental diets for crustacean nutrition research. II. Growth and survival of juvenile crayfish *Astacus astacus* (Linné) fed diets containing various amounts of protein, carbohydrate and lipid. *Aquaculture 104*: 341–356.

Armour, C. L.; Burnham, K. P.; Platts, W. S. 1983: Field methods and statistical analyses for monitoring small salmonid streams. United States Fish and Wildlife Service. FWS/OBS-83/33. 200 p.

Benke, A. 1984: Secondary production of aquatic invertebrates. *In*: Resh, V. H.; Rosenberg, D. M. *ed*. The ecology of aquatic insects. New York, Praeger Publishers. Pp. 89–322.

Brown, P. B.; Wetzel, J. E.; Spacie, A. 1992: Evaluation of naturally-occurring organisms as food for juvenile crayfish *Procambarus clarkii*. *Journal of the World Aquaculture Society 23*: 211–216.

Chapman, A.; Lewis, M. H. 1976: An introduction to the freshwater Crustacea of New Zealand. Auckland, New Zealand, William Collins (NZ) Ltd. Pp. 188–195.

Devcich, A. A. 1979: An ecological study of *Paranephrops planifrons* (White) (Decapoda: Parastacidae) in Lake Rotoiti, North Island, New Zealand. Unpublished PhD thesis, University of Waikato, Hamilton, New Zealand. 247 p.

Figler, M. H.; Cheverton, H. M.; Blank, G. S. 1999: Shelter competition in juvenile red swamp crayfish (*Procambarus clarkii*): the influences of sex differences, relative size and prior residence. *Aquaculture 178*: 63–75.

Flint, R. W. 1975: Growth in a population of the crayfish *Pacifastacus leniusculus* from a subalpine lacustrine environment. *Journal of the Fisheries Research Board Canada 32*: 2433–2440.

Guan, R. Z.; Wiles, P. R. 1999: Growth and reproduction of the introduced crayfish *Pacifastacus leniusculus* in a British lowland river. *Fisheries Research 42*: 245–259.

Hanchet, S. 1990: Effect of land use on the distribution and abundance of native fish in tributaries of the Waikato River in the Hakarimata Range, North Island, New Zealand. *New Zealand Journal of Marine and Freshwater Research 24*: 159–171.

Harding, J. S.; Young, R. G.; Hayes, J. W.; Shearer, K. A.; Stark, J. D. 1999: Changes in agricultural intensity and river health along a river continuum. *Freshwater Biology 42*: 345–357.

Hicks, B. J.; McCaughan, H. M. C. 1997: Land use, associated eel production, and abundance of fish and crayfish in streams in Waikato, New Zealand. *New Zealand Journal of Marine and Freshwater Research 31*: 635–650.

Hollows, J. W. 1998: Effects of land use on the diet and growth of freshwater crayfish *Paranephrops zealandicus* in some New Zealand streams. Unpublished MSc thesis, University of Otago, Dunedin, New Zealand.

Hopkins, C. L. 1966: Growth in the freshwater crayfish, *Paranephrops planifrons* White. *New Zealand Journal of Science 9(1)*: 50–56.

Hopkins, C. L. 1967a: Breeding in the freshwater crayfish *Paranephrops planifrons* White. *New Zealand Journal of Marine and Freshwater Research 1*: 51–58.

Hopkins, C. L. 1967b: Growth in a population of the freshwater crayfish *Paranephrops planifrons* White. *New Zealand Journal of Marine and Freshwater Research 1*: 464–474.

Hopkins, C. L. 1976: Estimate of biological production in some stream invertebrates. *New Zealand Journal of Marine and Freshwater Research 10*: 629–640.

Jansma, F. 1995: Past and present distribution of the crayfish (*Paranephrops zealandicus*) in Eastern Otago, New Zealand, and its relationship with land use. Unpublished Wildlife Management Report 72, University of Otago, Dunedin.

Jones, J. B. 1981: Growth of two species of freshwater crayfish (*Paranephrops* spp.) in New Zealand. *New Zealand Journal of Marine and Freshwater Research 15*: 15–20.

Jones, P. D.; Momot, W. T. 1983: The bioenergetics of *Orconectes virilis* in two pothole lakes. *Freshwater Crayfish 5*: 192–209.

Kawai, T.; Hamano, T.; Matsuura, S. 1997: Survival and growth of the Japanese crayfish *Cambaroides japonicus* in a small stream in Hokkaido. *Bulletin of Marine Science 61*: 147–157.

Lewis, S. D. 1997: Life history, population dynamics, and management of signal crayfish in Lake Billy Chinook, Oregon. Unpublished MSc thesis, Oregon State University. 98 p.

Lowery, R. S. 1988: Growth, moulting and reproduction. *In*: Holdich, D. M.; Lowery, R. S. *ed*. Freshwater crayfish biology, management and exploitation. London, Croom Helm Timber Press. Pp. 83–113.

McClain, W. R.; Neill, W. H.; Gatlin III, D. M. 1992: Nutrient profiles of green and decomposed rice-forages and their utilization by juvenile crayfish (*Procambarus clarkii*). *Aquaculture 101*: 251–265.

Momot, W. T. 1995: Redefining the role of crayfish in aquatic ecosystems. *Reviews in Fisheries Science 3*: 33–63.

Morgan, R. I. G.; Paveley, D. S. 1996: Management and ecological note: a simple batch mark for fish studies using injected elastomer. *Aquaculture Research 27*: 631–633.

Morrissy, N. M.; Bird, C.; Cassells, G. 1995: Density-dependent growth of cultured marron, *Cherax tenuimanus* (Smith 1912). *Freshwater Crayfish 10*: 560–568.

Musgrove, R. J. B.; Geddes, M. C. 1995: Tissue accumulation and the moult cycle in juveniles of the Australian freshwater crayfish *Cherax destructor*. *Freshwater Biology 34*: 541–558.

Oliveira, J.; Fabião, A. 1998: Growth responses of juvenile red swamp crayfish, *Procambarus clarkii* Girard, to several diets under controlled conditions. *Aquaculture Research 29*: 123–129.

Parkyn, S. M.; Collier, K. J.; Hicks, B. J. 2001: New Zealand stream crayfish: functional omnivores but trophic predators? *Freshwater Biology 46*: 641–652.

Parkyn, S. M.; Collier, K. J. 2002: Differentiating the effects of diet and temperature on juvenile crayfish (*Paranephrops planifrons*) growth: leaf detritus versus invertebrate food sources at two diurnally varying temperatures. *Freshwater Crayfish 13*: 371–382.

Quinn, J. M. 2000: Effects of pastoral development. *In*: Collier, K. J.; Winterbourn, M. J. *ed*. New Zealand stream invertebrates: ecology and implications for management. Christchurch, New Zealand Limnological Society. Pp. 208–229.

Quinn, J. M.; Cooper, A. B.; Davies-Colley, R. J.; Rutherford, J. C.; Williamson, R. B. 1997: Land use effects on habitat, water quality, periphyton and benthic invertebrates in Waikato, New Zealand, hill-country streams. *New Zealand Journal of Marine and Freshwater Research 31*: 579–597.

Quinn, J. M.; Collier, K. J.; Thorrold, B. 1999: Incorporating stream health into New Zealand hill-land farm management. *In*: Craig, J. L.; Mitchell, N.; Saunders, D. S. *ed*. Nature conservation 5: conservation in production environments: managing the matrix. Surrey Beatty & Sons. Pp. 278–289.

Rabeni, C. F.; Collier, K. J.; Parkyn; S. M.; Hicks, B. J. 1997: Evaluating methods of sampling stream crayfish. *New Zealand Journal of Marine and Freshwater Research 31*: 693–700.

Rabeni, C. F.; Gossett, M.; McClendon, D. D. 1995: Contribution of crayfish to benthic invertebrate production and trophic ecology of an Ozark stream. *Freshwater Crayfish 10*: 163–173.

Roell, M. J.; Orth, D. J. 1992: Production of three crayfish populations in the New River of West Virginia, USA. *Hydrobiologia 228*: 185–194.

Scott, D.; White, J. W.; Rhodes, D. S.; Koomen, A. 1994: Invertebrate fauna of three streams in relation to land use in Southland, New Zealand. *New Zealand Journal of Marine and Freshwater Research 28*: 277–290.

Turvey, P.; Merrick, J. R. 1997: Moult increments and frequency in the freshwater crayfish, *Euastacus spinifer* (Decapoda: Parastacidae), from the Sydney region, Australia. *Proceedings of the Linnean Society of New South Wales 118*: 187–204.

Verhoef, G. D.; Austin, C. M.; Jones, P. L.; Stagnitti, F. 1998a: Effect of temperature on molt increment and intermolt period of a juvenile Australian freshwater crayfish, *Cherax destructor*. *Journal of Crustacean Biology 18*: 673–679.

Verhoef, G. D.; Jones, P. L.; Austin, C. M. 1998b: A comparison of natural and artificial diets for juveniles of the Australian freshwater crayfish *Cherax destructor*. *Journal of the World Aquaculture Society 29*: 243–248.

Whitmore, N. 1997: Population ecology of the freshwater crayfish *Paranephrops zealandicus* and its effect on the community structure of a lowland bush stream. Unpublished MSc thesis, University of Otago, Dunedin, New Zealand.

Whitmore, N.; Huryn, A. D. 1999: Life history and production of *Paranephrops zealandicus* in a forest stream, with comments about the sustainable harvest of a freshwater crayfish. *Freshwater Biology 42*: 467–478.