

# New Zealand stream crayfish: functional omnivores but trophic predators?

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## SUMMARY

1. The feeding ecology of the crayfish *Paranephrops planifrons* in streams draining catchments in native forest and pastoral land was investigated using analyses of both stomach contents and stable isotopes of carbon and nitrogen. We aimed to (1) identify the energy sources of crayfish, (2) determine whether these were affected by ontogeny or land use change, and (3) assess the functional and trophic roles of crayfish in New Zealand hill-country streams.
2. In native forest streams, crayfish stomach contents were dominated volumetrically by leaf detritus (>60%), but in pasture streams aquatic invertebrates constituted more than 40% of stomach volumes and leaf detritus <30%. Stable isotope analyses revealed that crayfish from both native forest and pasture streams incorporated energy from aquatic invertebrates into their body tissue but did not appear to utilize detritus for growth. Therefore, deforestation had little impact on crayfish energy sources.
3. In native forest streams, adult crayfish ( $\geq 20$  mm orbit-carapace length (OCL)) consumed greater amounts of leaf detritus than juvenile crayfish, but a corresponding change in stable isotope signatures was not detected. Ontogenetic shifts in diet were not consistent between land use suggesting that change in local habitat and food resources, as a result of land use change, affect crayfish food choice more than factors related solely to age or size.
4. Crayfish appear to occupy the trophic position of a predator, but by functioning as omnivores, they have dual roles as both predators and processors of organic matter. The use of gut content analysis in conjunction with stable isotope analyses revealed that the functional and trophic roles of *P. planifrons* differed, with implications for the interpretation of diet studies and understanding of the role of omnivores in food webs.

*Keywords:* energy sources, functional role, land use, omnivory, ontogenetic, stable isotopes, trophic role

## Introduction

Crayfish may utilize resources from several trophic levels in aquatic food webs, although detritus and vegetation have been assumed to be the major food sources of many crayfish species (Lorman & Magnuson, 1978; Goddard, 1988; Whitmore, 1997). Therefore,

the primary trophic role of crayfish was thought to be in converting detritus, periphyton and macrophytes into body tissue that then becomes readily available to higher trophic levels (Lorman & Magnuson, 1978; Momot, Gowing & Jones, 1978).

Increasing recognition of the importance of animal food to crayfish nutrition (McClain, Neill & Gatlin, 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

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stream systems (Huryn & Wallace, 1987; Rabeni, Gossett & McClendon, 1995; Whitmore, 1997), and Momot (1995) argues that crayfish could not achieve dominance of invertebrate biomass without a substantial contribution of invertebrates to their diet. It has long been recognized 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 in trophic position have not been fully investigated.

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 substantially 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 & Cooper, 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.

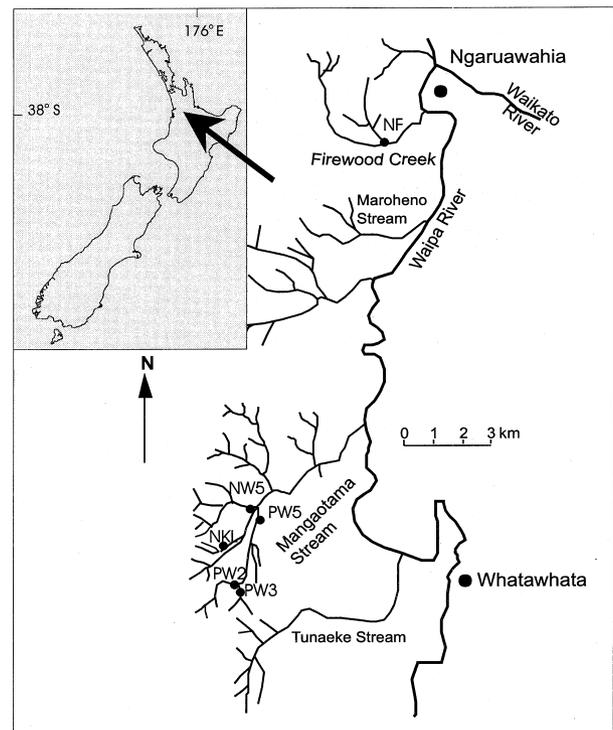
*Paranephrops planifrons* White (Parastacidae) is commonly found in streams and lakes of the North Island, New Zealand. Little is known about the diet of *P. planifrons*, although it is assumed to be predominantly detritivorous (Chapman & Lewis, 1976; Devcich, 1979). A potentially major impact of deforestation could therefore be 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 we aimed to: (1) identify the energy sources of crayfish, (2) determine whether these were affected by ontogeny or land use change, and (3) assess the functional and trophic roles of crayfish in New Zealand 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.

## Methods

### Study sites

Six streams were selected for study. These are in the Hakarimata Ranges, west of Hamilton in the North Island of New Zealand (Fig. 1, Table 1). Three of the sites (PW2, PW3 and PW5) drain catchments entirely in pasture and three (NW5, NF and NKL) drain catchments in native forest. The native and pasture streams chosen were matched approximately by catchment size (0.5–3.2 km<sup>2</sup>) and the site elevations and slopes did not differ significantly (Table 1). Leaf litter inputs in these native forest streams were much greater than in the pastoral streams (Dr M. Scarsbrook, NIWA, unpublished data), and macrophytes and periphyton were seasonally abundant in pasture



**Fig. 1** Location of sites on the Mangaoatama Stream system at Whatawhata and at Firewood Creek, Waikato, New Zealand (native forest sites = NKL, NW5, NF; pasture sites = PW3, PW2, PW5).

**Table 1** Site characteristics from the three native forest and three pasture stream sites. Characteristics marked with (\*) were measured in November 1992 or 1994 (Boulton *et al.*, 1997; Quinn *et al.*, 1997; Davies-Colley & Quinn, 1998). All other characteristics were means of four seasonal samples between December 1995 and September 1996 (Dr J. Quinn, NIWA, unpublished data). Land use differences are indicated by *P*-values (Mann–Whitney *U*, Wilkinson, 1997). DIFN = Diffuse non-interceptance

	Pasture			Native			<i>P</i>
	PW3	PW2	PW5	NKL	NF	NW5	
Site elevation (m a.s.l.)*	100	90	60	120	40	70	NS
Catchment area (km <sup>2</sup> )*	0.488	0.948	2.59	0.525	2.01	3.2	NS
Channel slope (m m <sup>-1</sup> )*	0.035	0.032	0.018	0.039	0.008	0.01	NS
Light (DIFN)*	0.45	0.465	0.323	0.008	0.02	0.056	<0.05
Nov. low flows (L s <sup>-1</sup> )*	7	16	36	10	32	48	NS
CPOM (g dw m <sup>-2</sup> )	6.17	4.5	5.06	6.46	14.02	3.54	NS
MPOM (g dw m <sup>-2</sup> )	2.55	3.17	1.2	1.73	1.23	0.83	NS
Periphyton (g afdw m <sup>-2</sup> )	4.0	14.8	3.6	1.6	0.9	1.1	<0.05
Chl <i>a</i> (mg m <sup>-2</sup> )	35.5	94.7	21.9	1.1	1.3	3.7	<0.05
Invertebrate density (0.4 m <sup>-2</sup> )	1113	1476.4	1446.7	318.1	438.2	816.3	<0.05
Invertebrate taxa richness (0.4 m <sup>2</sup> sample)	34.9	30.7	36.6	30.9	33.3	35.4	NS

streams. Invertebrate densities were much greater in pasture than in native forest streams. Although invertebrate taxa richness was similar between the land uses, community composition was altered so that species that utilize autochthonous energy sources predominated in pasture streams (Quinn *et al.*, 1997).

#### Sample collection and preparation

Twenty crayfish of both sexes, ranging in size from 5 to 32 mm orbit-carapace length (OCL, measured from the eye socket to the mid-dorsal posterior edge of the carapace; after Hopkins, 1967) were sampled from each of six study 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. 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 described below. Crayfish that had moulted recently before capture were excluded from analysis of stomach contents as they generally had empty stomachs, but their muscle tissue was included in stable isotope analysis.

#### Gut content analysis

Percentage volume of each food type was assessed visually through a binocular microscope. Particulate

organic matter (*c.* >0.5 mm CPOM) was identified as leaf detritus, grass, woody detritus, fern detritus, macrophytes and moss, filamentous green algae (FGA), terrestrial invertebrates, or aquatic invertebrates. Invertebrates were identified to the lowest practicable level using the keys of Winterbourn & Gregson (1989) and Winterbourn (1973), and whole individuals were counted.

#### Abundance of stream invertebrates

Stream invertebrates were sampled at each of the six streams in each season, 2–4 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<sup>2</sup> 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 & Gregson (1989).

#### Stable isotope analysis

##### Crayfish

Crayfish abdomen muscle was dried at 50 °C for 24 h, then ground in a mortar and pestle. Any visible parasites were removed from the flesh prior to drying to avoid contamination. A small sub-sample (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, New Zealand). The precision was  $\pm 0.17\%$  for  $\delta^{13}\text{C}$  and  $\pm 0.09\%$  for  $\delta^{15}\text{N}$ .

#### *Potential food sources*

Samples of aquatic invertebrates were collected by disturbing the substrate upstream of a kick net at each site at the time of crayfish sampling. Filamentous green algae and epilithon were collected by brushing streambed stones with a scrubbing brush in pasture sites and scraping stone surfaces with a knife in native forest sites. Samples were frozen on return to the laboratory until the results of crayfish gut and stable isotope analyses were known.

The two dominant invertebrates found in crayfish gut contents, snails and leptophlebiid mayflies, were chosen for stable isotope analysis in both native and pasture streams. Only specimens that were collected in December 1996 were analysed in order 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. Mayfly (*Deleatidium* sp.) gut contents were removed, and the snails (*Potamopyrgus antipodarum*) were extracted from their shells to avoid contamination from non-dietary carbon (Hicks, 1997). Each sample consisted of several individuals, and only one or two samples per stream were possible. Samples were dried at 50 °C for 24 h and ground in preparation for stable isotope analysis.

To characterize the autochthonous energy base of these streams further, five additional epilithon samples were collected in early September 1999 from run habitats at each site. Stone surfaces of between three to six large gravels or small cobbles (Wolman, 1954) were rubbed free of sediment and invertebrates and then 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- $\mu\text{m}$ -mesh sieve to remove silt and small invertebrates, and left to settle and evaporate and in a drying oven at 70 °C for 48 h.

Small sub-samples (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  $^{13}\text{C}$  and 0.3‰ for  $^{15}\text{N}$  (University of Waikato, Hamilton, New Zealand).

#### *Statistical analysis*

Percentage frequency of occurrence, and percentage volume of food items in crayfish diets were tested for differences between land uses using ANOVA in SYSTAT 7.0 after arcsine square root transformation followed by 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 forest and pasture stream crayfish gut contents were tested for differences between seasonal sampling dates with ANOVA as above. Differences in the proportions of taxa in crayfish diet and in the proportions of taxa from benthic samples within native forest and pasture streams were also tested with ANOVA after arcsine square root transformation. Differences in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of crayfish between seasons at each site were tested with ANOVA and Tukey's *post-hoc* test for differences between means.

## **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 terrestrial plant detritus (Table 2). The mean frequency of occurrence of total aquatic invertebrates ingested by crayfish was higher in pasture streams than native forest streams, but was not significantly different ( $P = 0.085$ , ANOVA). Leaf detritus occurred in more crayfish from native forest than pasture streams ( $P < 0.05$ , ANOVA) and fern leaf detritus was identified in over 20% of crayfish in native forest streams. Seeds and spores, woody detritus, and flesh of unknown origin also featured frequently in the diet (mean  $>c.$  10% in pasture and native forest streams), but FGA, 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 native forest stream crayfish ( $P < 0.01$ ).

Aquatic invertebrates featured more often in the diets of pasture stream crayfish than the two other

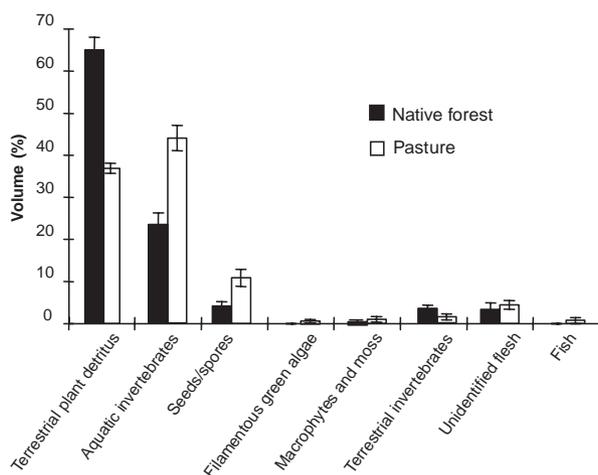
**Table 2** Mean ( $\pm 1$  SE) frequency of occurrence (percentage of crayfish) of food items in crayfish stomachs from three native forest and three pasture sites pooled over four seasonal sampling dates

	Frequency of occurrence	
	Native forest	Pasture
Leaf detritus	81.1 $\pm$ 5.5	65.9 $\pm$ 4.2
Aquatic invertebrates	68.3 $\pm$ 4.2	81.8 $\pm$ 3.6
Seeds/spores	14.4 $\pm$ 2.4	35.7 $\pm$ 8.2
Woody detritus	24.9 $\pm$ 2.3	28.4 $\pm$ 1.9
Fern detritus	22.3 $\pm$ 4.9	1.0 $\pm$ 0.5
Terrestrial invertebrates	10.6 $\pm$ 3.4	3.4 $\pm$ 1.8
Crayfish exoskeleton	8.4 $\pm$ 4.5	5.7 $\pm$ 1.3
Unidentified flesh	9.0 $\pm$ 3.1	10.4 $\pm$ 2.8
Macrophyte detritus	0	1.8 $\pm$ 0.5
FGA	0	1.3 $\pm$ 0.7
Fish	0	2.0 $\pm$ 2.0
Moss	2.5 $\pm$ 1.3	0.9 $\pm$ 0.9

frequently occurring (>30%) food items, leaf detritus ( $P < 0.05$ ) and seeds ( $P < 0.0001$ ). However, there was no difference in the frequency of aquatic invertebrates and leaf detritus in the diets of crayfish from native forest 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. 2), also showed that aquatic invertebrates and detritus were the dominant food items. Volumes of the main food

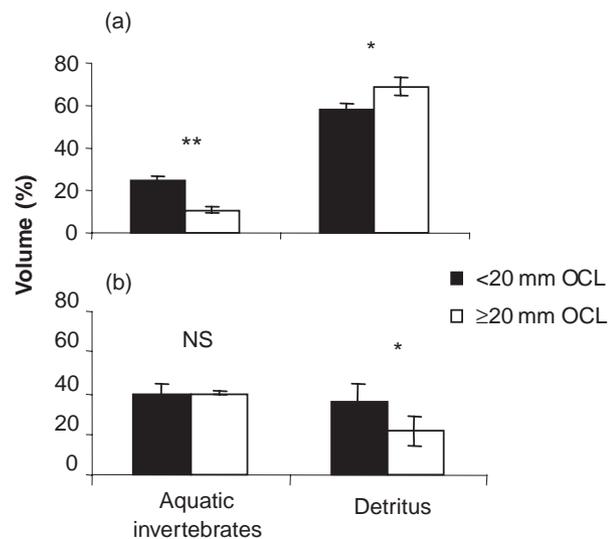


**Fig. 2** Mean ( $\pm 1$  SE) percentage volume of food items found in *P. planifrons* stomach contents from three native forest and three pasture sites averaged over four seasonal sampling dates.

groups in crayfish diets varied little with season and so were averaged over the four sampling periods. Crayfish consumed more plant detritus (all types combined but largely leaf detritus) in native forest streams than in pasture streams ( $P < 0.01$ ), and the amount of total detritus consumed by crayfish in forest streams was significantly higher than the amount of aquatic invertebrates ( $P < 0.0001$ ). Conversely, crayfish in pasture streams consumed more aquatic invertebrates than in native forest streams ( $P < 0.01$ ), but there was no difference between the volume of invertebrates and detritus for crayfish in pasture streams.

#### Effect of size

A marked difference in consumption of leaf detritus or aquatic invertebrates was detected in crayfish larger than 20 mm OCL after 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;  $\geq 20$  mm OCL) crayfish (Parkyn, 2000). Adult crayfish in native forest streams consumed more detritus than juvenile crayfish did ( $P < 0.05$ , Fig. 3a), who consumed more aquatic invertebrates ( $P < 0.01$ ). However, in pasture streams there was no significant



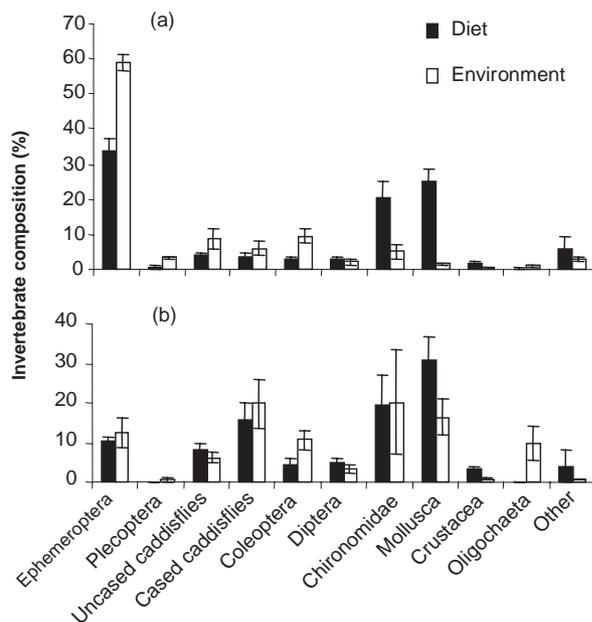
**Fig. 3** Mean ( $\pm 1$  SE) percentage volume of aquatic invertebrates and leaf detritus consumed by two size classes of native forest (a) and pasture (b) stream crayfish; <20 mm OCL ( $n = 195$  (a), 200 (b)) and  $\geq 20$  mm OCL ( $n = 54$  (a), 36 (b)). Asterisks indicate significant differences between size classes (\* $P < 0.05$ , \*\* $P < 0.01$ , NS = not significant).

difference between the amounts of aquatic invertebrates eaten by each size class, and there was significantly less detritus eaten by adult crayfish than juveniles ( $P < 0.05$ , Fig. 3b).

#### Composition of invertebrate diet

Ephemeroptera, Chironomidae, gastropod molluscs and Trichoptera (in particular cased caddisflies) were the most frequently occurring invertebrate groups of 70 taxa consumed by crayfish in both native forest and pasture streams. The relative importance of these taxa differed between land uses. In the forest streams, Ephemeroptera (mainly leptophlebiid mayflies such as *Zephlebia* sp. and *Deleatidium* sp.) occurred in 55% of crayfish whereas in pasture streams gastropod molluscs (almost exclusively *P. antipodarum*) occurred in 48% of crayfish.

The percentage of invertebrate groups consumed by crayfish largely reflected the percentage of those groups in the environment (Figs. 4a,b). For instance, in native forest streams, mayflies (Ephemeroptera) were the most abundant invertebrate taxon in the invertebrate community ( $P < 0.001$ ), and there was a high percentage of mayflies in the diet of crayfish.



**Fig. 4** Mean ( $\pm 1$  SE) percentage of each taxa group counted 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.

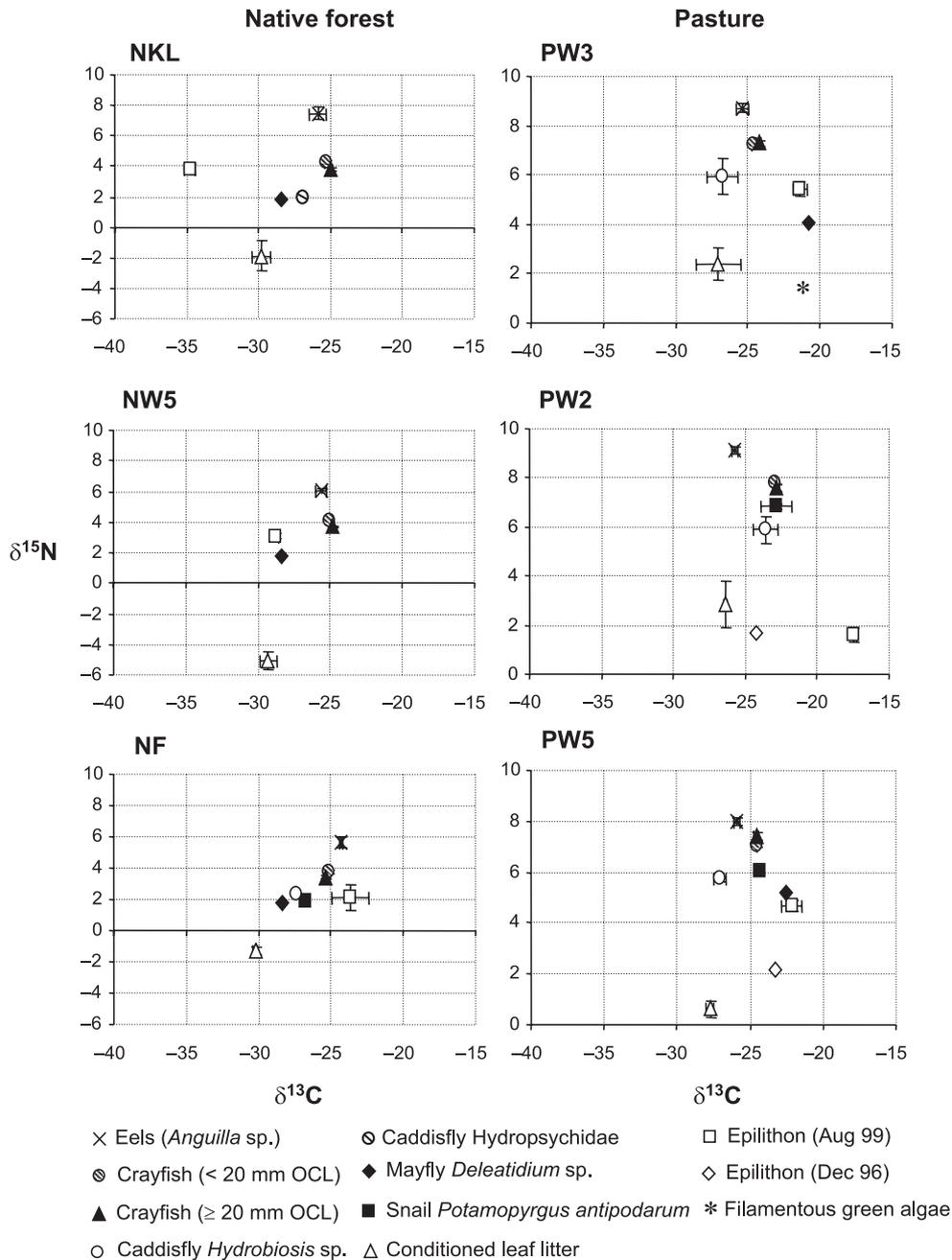
However, the percentage of chironomids and gastropod snails consumed by crayfish in native forest streams appeared to be greater than that in the environment. Crayfish consumption of invertebrate groups in pasture streams reflected the abundance of a wide range of invertebrate groups in the environment. 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.

#### 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). Crayfish were enriched in both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  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.

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

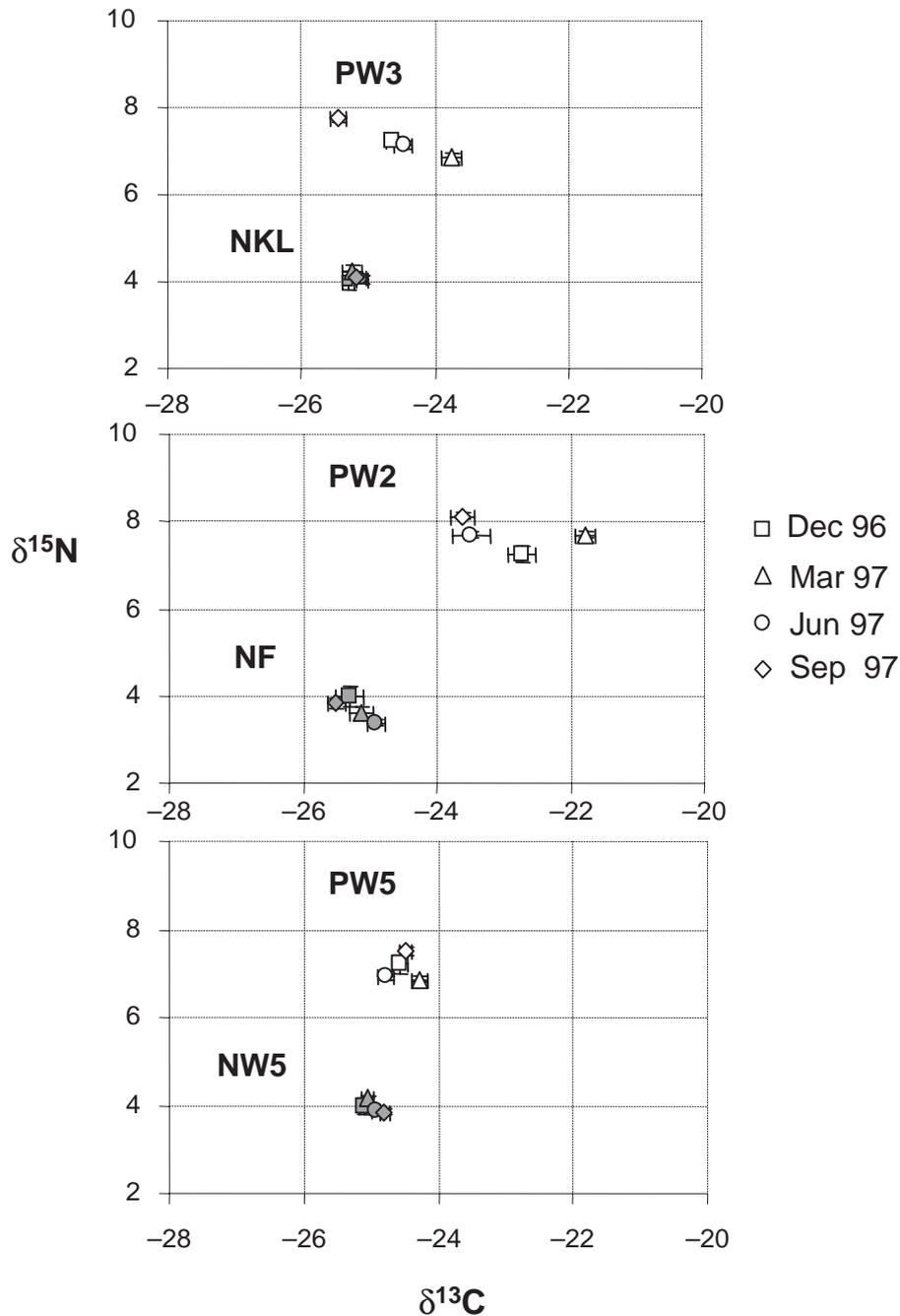
The differences between the  $\delta^{13}\text{C}$  signatures of juvenile ( $< 20$  mm OCL) and adult ( $\geq 20$  mm OCL) crayfish in native forest or pasture streams were very small indicating that there were no substantial changes in the energy source utilized for growth associated



**Fig. 5** Mean ( $\pm 1$  SE) stable isotope signatures ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) of two crayfish size classes (from four seasonal sampling dates in 1996/97) and those of a predator (eels) and potential food sources for each study site. Epilithon was sampled in December 1996 and August 1999; mayflies, snails and FGA were sampled in December 1996; leaf litter, caddisfly larvae and eels were sampled by Hicks (1997) in January 1993 and 1994.

with age. The  $\delta^{15}\text{N}$  signature of adult native stream crayfish was slightly lower than that of juvenile crayfish, although the decrease in  $\delta^{15}\text{N}$  was not consistent with a change in trophic level.

Temporal changes in the  $\delta^{13}\text{C}$  signature of crayfish were most pronounced in the small pasture streams PW2 and PW3 (Fig. 6). PW2 and PW3 have greater amounts of light reaching the water surface and more



**Fig. 6** Temporal differences in the mean ( $\pm 1$  SE)  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  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.

periphyton than the other pasture stream (PW5) and the native forest sites (Davies-Colley & Quinn, 1998; Dr J. Quinn, NIWA, unpublished data). Greatest enrichment occurred in March ( $P < 0.001$ ) and it is likely that this corresponds with changes in the algal carbon signatures (S. M. Parkyn, unpublished data).

Algal biomass is the greatest during summer in these streams and crayfish in the smaller pasture streams may therefore obtain most of their energy from an autochthonous pathway. Crayfish from site PW5 had less annual variation in their  $\delta^{13}\text{C}$  signatures than the smaller pasture streams. This may have been because

the crayfish in this stream are less reliant on autochthonous energy sources because of leaf litter inputs and shading from riparian trees. However,  $\delta^{15}\text{N}$  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 these study streams function as omnivores, acting as both predators and detritivores, but they occupy the trophic position of predators. The dominant food sources, by both volume and frequency of occurrence, were aquatic invertebrates and terrestrial leaf detritus in native forest and pasture streams. However, evidence from  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  data in this study showed that crayfish obtained most of their energy for growth from aquatic invertebrates, highlighting the importance of understanding resource assimilation as well as consumption when determining the trophic significance of aquatic species.

Deforestation did not impact on crayfish energy sources as might have been expected with the removal of most terrestrial leaf inputs. The energy base for crayfish in pasture streams was from allochthonous and autochthonous sources, and solely allochthonous in native forest streams, but the main pathway of this energy was through aquatic invertebrates regardless of land use. There is increasing evidence that the long-held belief that crayfish gain most of their nutritional needs from detritus and plant material has been overemphasized (Momot, 1995). Food choice (Ilheu & Bernardo, 1993) and growth experiments (Jones & Momot, 1983; McClain *et al.*, 1992; Oliveira & Fabião, 1998), with a range of crayfish species fed on natural foods clearly show a preference for animal over detrital food. Parkyn (2000) used stable carbon isotopes to show that juvenile *P. planifrons* were unable to assimilate conditioned leaf litter into their body tissue during growth experiments.

Detritus is a major component of the diets of many crayfish species (e.g. Turvey & Merrick, 1997; Whitley & Rabeni, 1997) and also of *P. zealandicus* in southern New Zealand (Whitmore, 1997; Hollows, 1998). Detritus made up a substantial part of

*P. planifrons* diet, particularly in native forest streams, and although it appears to contribute little or no energy towards growth, it presumably provides energy for respiration and maintenance. Consuming leaf detritus requires little energetic expenditure and may be a safer mode of obtaining energy while avoiding predation. Detritus may also be a source of non-protein nutrients or carotenoids unavailable to crayfish from animal foods, but much of the nutritional value of detritus for shredding invertebrates is thought to be derived from the microbial flora (fungi and bacteria) colonizing 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; McClain *et al.*, 1992).

### *Ontogenetic shifts in diet*

Many crayfish species exhibit an ontogenetic shift in diet, whereby juvenile crayfish feed predominantly on aquatic invertebrates, and adults feed mainly on detritus (Goddard, 1988; France, 1996; Guan & Wiles, 1998). This shift has been explained both in terms of increased need for protein for growth by juvenile crayfish (Momot, 1995) and inability of larger crayfish to catch fast moving invertebrate prey (Abrahamsson, 1966). Crayfish from native forest streams exhibited this ontogenetic shift in diet according to gut content analysis. However, stable isotope analyses did not show any difference in nutritional pathways in different sized crayfish.

France (1996) found that  $\delta^{13}\text{C}$  values for *Orconectes virilis* in oligotrophic Canadian lakes decreased from  $-18$  to  $-27\text{‰}$  with increasing size, which was attributed to a change from eating algal particles to leaf detritus. Similarly, Branstrator *et al.* (2000) found increasing  $\delta^{15}\text{N}$  values, and therefore changes in trophic position, for omnivorous opossum shrimp (*Mysis relicta*) with increasing age. Aquatic invertebrates remained the major source of energy for tissue production in adult *P. planifrons* in these native forest streams, despite their high consumption of leaf detritus. The ontogenetic shift in diet, detected from gut analyses, could be an indication that lower volumes of invertebrates were able to satisfy the energetic requirements for adult 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 size

where crayfish began to reproduce (Parkyn, 2000). However, this ontogenetic shift in diet did not occur in crayfish from pasture streams, where invertebrates were more abundant, and where habitat and the types of leaf litter available differed. This suggests that large crayfish do not have difficulty catching invertebrates (see also Ilheu & Bernardo, 1993) and that adults do not necessarily reduce their consumption of invertebrates when their energetic requirements for growth decrease.

Choice of food sources by *P. planifrons* may depend on a range of factors interacting with crayfish age including food accessibility and palatability, habitat choice, and possible predator avoidance tactics. Apparent ontogenetic shifts in diet were not consistent across land use, suggesting that changes to the local habitat and food resources affect crayfish food choice more than factors related to physiological age and size.

#### *Potential roles for omnivorous crayfish*

Omnivores can have complex roles in stream communities as they utilize resources from more than one trophic level, including basal resources. Ontogenetic shifts in diet can complicate the role of omnivores further by altering the way in which resources are utilized by the population according to age. This study has shown that understanding the process of energy flow and material transfer between trophic levels is complicated further still if omnivores utilize resources from several trophic levels but only assimilate material from one trophic level. Although crayfish eat detritus, this material is not incorporated into their body tissue. Therefore omnivores, such as crayfish, may have a trophic role that differs from their functional roles. Crayfish function as omnivores by processing leaf detritus and preying on other invertebrates, but from an energetic standpoint they are primarily acting as predators.

A major functional role of crayfish may be in the breakdown of leaves into FPOM that can be utilized by other stream invertebrates. This detritus may often be tough, woody material that would be difficult for most invertebrates to digest (Turvey & Merrick, 1997). Crayfish detritivorous feeding habits 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.

The degree of leaf breakdown facilitated by crayfish, and the potential contribution of FPOM to other invertebrates, is yet to be measured in New Zealand streams. Parkyn, Rabeni & Collier (1997) demonstrated that *P. planifrons* significantly increased leaf breakdown of a soft-leaved native species, in artificial stream channels. Whitmore (1997) found detritus to be the major component of *P. zealandicus* diet but did not find a significant decline in CPOM in instream enclosures with *P. zealandicus*, relative to controls without crayfish. Huryn & Wallace (1987) studied the litter processing ability of *Cambarus* sp. (Cambaridae) and found it to process 4–6% of the annual litter input in a North American mountain stream and concluded that crayfish litter processing may be particularly important after autumn leaf fall.

Perhaps more importantly than their role in leaf litter processing on benthic communities, crayfish may have a significant effect as major predators in stream ecosystems. This role has been overlooked in contemporary studies (Momot, 1995). *Paranephrops planifrons* relies on invertebrate food as an energy source in both native forest and pasture streams suggesting that they are significant predators. Crayfish in these streams tended to prey on the invertebrate taxa that were commonly available, although crayfish could possibly exert predation pressure on snail populations in native forest streams where they were an important component of crayfish diet but occurred in low numbers. Direct effects of crayfish predation on snail populations have been demonstrated with many crayfish species (Hanson, Chambers & Prepas, 1990; Lodge *et al.*, 1994; Nyström, Brönmark & Granéli, 1996), and crayfish have been shown to have significant effects on both the behaviour and morphology of snails (Crowl & Covich, 1990; Alexander & Covich, 1991).

Although the relative importance of the functional roles of crayfish may change with age and land use, stable isotope analysis suggests that the trophic role remains the same. Our findings suggest that determination of the role of omnivores such as the crayfish *P. planifrons* by discrete trophic levels is inadequate to determine their direct and indirect effects on community dynamics. Furthermore, while omnivores may be assigned to several functional feeding groups based on feeding modes or gut content analysis, these do not necessarily reflect resource assimilation, and may misrepresent the flow of energy in stream food webs.

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## References

- Abrahamsson S.A. (1966) Dynamics of an isolated population of the crayfish, *Astacus astacus* Linne. *Oikos*, **17**, 96–107.
- Alexander J.E. & Covich A.P. (1991) Predator avoidance by the freshwater snail *Physella virgata* in response to the crayfish *Procambarus simulans*. *Oecologia*, **87**, 435–442.
- Boulton A.J., Scarsbrook M.R., Quinn J.M. & Burrell G.P. (1997) Land-use effects on the hyporheic ecology of five small streams near Hamilton, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, **31**, 609–622.
- Branstrator D.K., Cabana G., Mazumder A. & Rasmussen J.B. (2000) Measuring life-history omnivory in the opossum shrimp, *Mysis relicta*, with stable nitrogen isotopes. *Limnology and Oceanography*, **45**, 463–467.
- Chapman M.A. & Lewis M.H. (1976) *An Introduction to the Freshwater Crustacea of New Zealand*. William Collins (NZ) Ltd, Auckland, New Zealand, pp. 188–195.
- Crowl T.A. & Covich A.P. (1990) Predator-induced life-history shifts in a freshwater snail. *Science*, **247**, 949–951.
- Davies-Colley R.J. & Quinn J.M. (1998) Stream lighting in five regions of North Island, New Zealand: control by channel size and riparian vegetation. *New Zealand Journal of Marine and Freshwater Research*, **32**, 591–605.
- 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.
- France R.L. (1996) Ontogenetic shift in crayfish  $\delta^{13}\text{C}$  as a measure of land–water ecotonal coupling. *Oecologia*, **107**, 239–242.
- Goddard J.S. (1988) Food and feeding. In: *Freshwater Crayfish Biology, Management & Exploitation* (Eds D.M. Holdich & R.S. Lowery), pp. 145–166. Croom-Helm Timber Press, London.
- Guan R.Z. & Wiles P.R. (1998) Feeding ecology of the signal crayfish *Pacifastacus leniusculus* in a British lowland river. *Aquaculture*, **169**, 177–193.
- 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.
- Hanson J.M., Chambers P.A. & Prepas E.E. (1990) Selective foraging by the crayfish *Orconectes virilis* and its impact on the macroinvertebrates. *Freshwater Biology*, **24**, 69–80.
- Hicks B.J. (1997) Food webs in forest and pasture streams in the Waikato region, New Zealand: a study based on analyses of stable isotopes of carbon and nitrogen, and fish gut contents. *New Zealand Journal of Marine and Freshwater Research*, **31**, 651–664.
- 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. (1967) Growth rate in a population of the freshwater crayfish, *Paranephrops planifrons* White. *New Zealand Journal of Marine and Freshwater Research*, **1**, 464–474.
- Huner J.V. (1998) Just how important is detritus as crayfish food? *IAA Newsletter*, **19**, 10.
- Huryn A.D. & Wallace J.B. (1987) Production and litter processing by crayfish in an Appalachian mountain stream. *Freshwater Biology*, **18**, 277–286.
- Ilheu M. & Bernardo J.M. (1993) Experimental evaluation of food preference of red swamp crayfish, *Procambarus clarkii*: vegetal versus animal. *Freshwater Crayfish*, **9**, 359–364.
- Jones P.D. & Momot W.T. (1983) The bioenergetics of *Orconectes virilis* in two pothole lakes. *Freshwater Crayfish*, **5**, 192–209.
- Lodge D.M., Kershner M.W., Aloï J.E. & Covich A.P. (1994) Effects of an omnivorous crayfish (*Orconectes rusticus*) on a freshwater littoral food web. *Ecology*, **75**, 1265–1281.
- Lorman J.G. & Magnuson J.J. (1978) The role of crayfishes in aquatic ecosystems. *Fisheries*, **3**, 8–10.

- 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.
- Momot W.T., Gowing H. & Jones P.D. (1978) The dynamics of crayfish and their role in ecosystems. *American Midland Naturalist*, **99**, 10–35.
- Nyström P., Brönmark C. & Granéli W. (1996) Patterns in benthic food webs: a role for omnivorous crayfish? *Freshwater Biology*, **36**, 631–646.
- 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. (2000) Effects of native forest and pastoral land use on the population dynamics and trophic role of the New Zealand freshwater crayfish *Paranephrops planifrons* (Parastacidae). Unpublished PhD Thesis, University of Waikato, New Zealand.
- Parkyn S.M., Rabeni C.F. & Collier K.J. (1997) Effects of crayfish (*Paranephrops planifrons*: Parastacidae) on in-stream processes and benthic faunas: a density manipulation experiment. *New Zealand Journal of Marine and Freshwater Research*, **31**, 685–692.
- Pullar L. & McLeod M. (1992) *Facts New Zealand*. Department of Statistics and Eaphne Brasell Associates Press, Wellington, New Zealand.
- Quinn J.M. & Cooper A.B. (1997) Land–water interactions at Whatawhata, New Zealand: introduction and synthesis. *New Zealand Journal of Marine and Freshwater Research*, **31**, 569–577.
- 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**, 579–598.
- 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.
- 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) Diet and feeding in the freshwater crayfish, *Euastacus spinifer* (Decapoda: Parastacidae), from the Sydney region, Australia. *Proceedings of the Linnean Society of New South Wales*, **118**, 175–185.
- Whitledge G.W. & Rabeni C.F. (1997) Energy sources and ecological role of crayfishes in an Ozark stream: insights from stable isotopes and gut analysis. *Canadian Journal of Fisheries and Aquatic Sciences*, **54**, 2555–2562.
- 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.
- Wilkinson L. (1997) *Systat*® 7.0 for Windows: Statistics. SPSS Inc., Chicago, IL, USA.
- Winterbourn M.J. (1973) A guide to the freshwater Mollusca of New Zealand. *Tuatara*, **20**, 141–159.
- Winterbourn M.J. & Gregson K.L.D. (1989) Guide to the aquatic insects of New Zealand. *Bulletin of the Entomological Society of New Zealand*, **9**.
- Wolman M.G. (1954) A new method of sampling coarse river-bed. *Transactions of the American Geophysical Union*, **35**, 951–956.

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