

Ecology and distribution of the freshwater crayfish *Paranephrops* *zealandicus* in Otago

Implications for conservation

SCIENCE FOR CONSERVATION 148

Nathan Whitmore, Alexander D. Huryn, Chris J. Arbuckle,
and Femke Jansma

Published by
Department of Conservation
P.O. Box 10-420
Wellington, New Zealand

Science for Conservation presents the results of investigations by DOC staff, and by contracted science providers outside the Department of Conservation. Publications in this series are internally and externally peer reviewed.

Publication was approved by the Manager, Science & Research Unit, Science Technology and Information Services, Department of Conservation, Wellington.

© May 2000, Department of Conservation

ISSN 1173-2946

ISBN 0-478-21952-0

Cataloguing-in-Publication data

Ecology and distribution of the freshwater crayfish *Paranephrops zealandicus* in Otago : implications for conservation / Nathan Whitmore ... [et al.]. Wellington, N.Z. : Dept. of Conservation, 2000.

1 v. ; 30 cm. (Science for conservation, 1173-2946 ; 148)

Includes bibliographical references.

ISBN 0478219520

1. *Paranephrops zealandicus*—Ecology—New Zealand—Otago Region. 2. Crayfish—Ecology—New Zealand—Otago Region. I. Whitmore, Nathan, 1971- Series: Science for conservation (Wellington, N.Z.) ; 148.

CONTENTS

| | |
|--|----|
| Abstract | 5 |
| <hr/> | |
| 1. Introduction | 6 |
| <hr/> | |
| 2. Distribution of koura within the Taieri River catchment | 6 |
| <hr/> | |
| 2.1 Study area | 6 |
| 2.2 Methods | 8 |
| 2.2.1 Koura distribution | 8 |
| 2.2.2 Habitat variables associated with koura presence/absence | 9 |
| 2.2.3 Relationship between land-use and crayfish distribution | 9 |
| 2.2.4 Results | 9 |
| 2.3 Fine spatial-resolution analysis of habitat variables and koura distribution | 11 |
| 2.3.1 Riparian habitat variables | 11 |
| 2.3.2 In-stream habitat variables | 12 |
| 2.3.3 Coarse spatial-resolution analysis of land cover and koura distribution | 12 |
| 2.4 Discussion | 13 |
| 2.4.1 Riparian and in-stream habitat variables | 14 |
| <hr/> | |
| 3. Koura ecology | 16 |
| <hr/> | |
| 3.1 Life history, longevity and production | 16 |
| 3.1.1 Method | 16 |
| 3.1.2 Results | 17 |
| 3.1.3 Discussion | 21 |
| 3.2 Effects of koura on stream community structure | 23 |
| 3.2.1 Method | 23 |
| 3.2.2 Timetable | 24 |
| 3.2.3 Macroinvertebrate and CPOM sampling | 25 |
| 3.2.4 Analysis | 25 |
| 3.2.5 Results | 26 |
| 3.2.6 Discussion | 29 |
| 3.3 Predatory capabilities | 31 |
| 3.3.1 Method of stomach content analysis | 31 |
| 3.3.2 Results | 33 |
| 3.3.3 Discussion | 35 |
| <hr/> | |
| 4. Conclusions and recommendations | 37 |
| <hr/> | |
| 5. Acknowledgements | 39 |
| <hr/> | |
| 6. References | 39 |
| <hr/> | |

Ecology and distribution of the freshwater crayfish *Paranephrops zealandicus* in Otago

Implications for conservation

N. Whitmore¹, A.D. Huryn², C.J. Arbuckle^{1*}, and F. Jansma¹

¹Department of Zoology, University of Otago, PO Box 56, Dunedin, New Zealand. (*Author for correspondence) Emails: nathan.whitmore@toroa.otago.ac.nz and chris.arbuckle@stonebow.otago.ac.nz

²Department of Biological Sciences, 5722 Deering Hall, University of Maine, Orono, Maine 04469-5722, U.S.A. Email: huryn@maine.maine.edu

ABSTRACT

The distribution of the crayfish *Paranephrops zealandicus* (koura) in the Taieri River catchment, Otago, New Zealand, was analysed with respect to land use and drainage history. Koura are widely distributed in the lower Taieri catchment, but sporadic in the upper catchment and uncommon on inland plains. Their macrodistribution is correlated with major spatial discontinuities caused by events in the evolution of the drainage system; effects of land-use are vague. A strong positive relationship exists with the extent of native vegetation within the riparian zone. Life history, production and longevity were assessed for a population of koura in Powder Creek, a stream within a regenerating coniferous-broadleaf forest. Koura biomass (4–33g AFDW m⁻²) and production (2–11g AFDW m⁻²yr⁻¹) was high. Production depended upon biomass rather than growth rate. Relative to other crayfish species individual koura were slow-growing and long-lived. Enclosure experiments in Powder Creek examined koura influence on invertebrates. Changes in the structure of the stream community occurred where koura were present. Enclosures without koura accumulated silt; bioturbation from foraging and movement appeared to be the main cause. Stomach contents of koura were analysed to determine their predatory capabilities. *Deleatidium*, *Aoteapsyche*, and chironomid larvae were the most common prey. The incidence of these species in the koura gut likely reflects the high abundance of these prey in koura streams. *P. zealandicus* showed an ontogenetic shift in diet, with smaller specimens consuming a lower proportion of plant tissues. Within the Taieri catchment *P. zealandicus* is a superb generalist, capable of surviving in a variety of natural and modified habitats, but limited in macrodistribution by historic drainage patterns.

Keywords: freshwater crayfish, koura, land use, ecology, *Paranephrops zealandicus*, Taieri River, New Zealand

© May 2000, Department of Conservation. This paper may be cited as: Whitmore, N.; Huryn, A.D.; Arbuckle, C.J.; Jansma, F. 2000. Ecology and distribution of the freshwater crayfish *Paranephrops zealandicus* in Otago. *Science for conservation* 148. 42 p.

1. Introduction

New Zealand has two recognised species of freshwater crayfish, *Paranephrops zealandicus* and *P. planifrons* (Parastacidae), both of which are endemic (Hopkins 1970). These species are allopatric: *P. zealandicus* is restricted to Stewart Island and the south-eastern side of the South Island, while *P. planifrons* inhabits the North Island, Marlborough and northern half of the west coast of the South Island (Hopkins 1970). These crayfish are commonly known in New Zealand as koura.

The plight of native crayfish in New Zealand is currently a conservation issue. Studies outside New Zealand have shown that crayfish often have a major role in freshwater communities, as consumers and habitat modifiers (Langlois 1935; Flint & Goldman 1975; Momot 1995). The importance of *Paranephrops* in New Zealand freshwater communities, however, remained unstudied. Anecdotal information suggests a general decline in the abundance and distribution of the freshwater crayfish *Paranephrops zealandicus* over the last century (Jansma 1995). The practice of harvesting of wild stocks for the seeding of aquaculture ventures, and the possibility of direct commercial harvest have fuelled concerns for the sustainability of targeted populations.

These concerns provided the impetus for this study, in which we sought to establish ecological and distributional baselines for crayfish in the Otago area. Specifically we interpreted new and archived data concerning the distribution of *P. zealandicus* in the Taieri River catchment, and examined the population and community ecology of crayfish in a lowland Otago bush stream.

2. Distribution of koura within the Taieri River catchment

2.1 STUDY AREA

The Taieri River catchment (Figure 1) is in the southeast of the South Island of New Zealand. The 5702 km² drainage basin is dissected by parallel mountain ranges and extensive intermontane plains. Bedrock is primarily schist with localised regions of basalt. The Taieri River rises in the Lammerlaw and Lammermoor ranges at 1150 m and flows 318 km before reaching the Pacific Ocean (Otago Catchment Board 1983). Over much of this distance, the river is deeply entrenched and constrained by gorges. However, constrained reaches are regularly punctuated by alluvial plains through which the river meanders to form extensive scroll plains. The Taieri River receives eight tributaries with catchments >100 km²: Loganburn and the Kye Burn (upper reaches), Sutton, Nenthorn, Deep and Lee Stream (mid-reaches), and Silver Stream and the Waipori River (lower reaches), (Otago Catchment Board 1983).

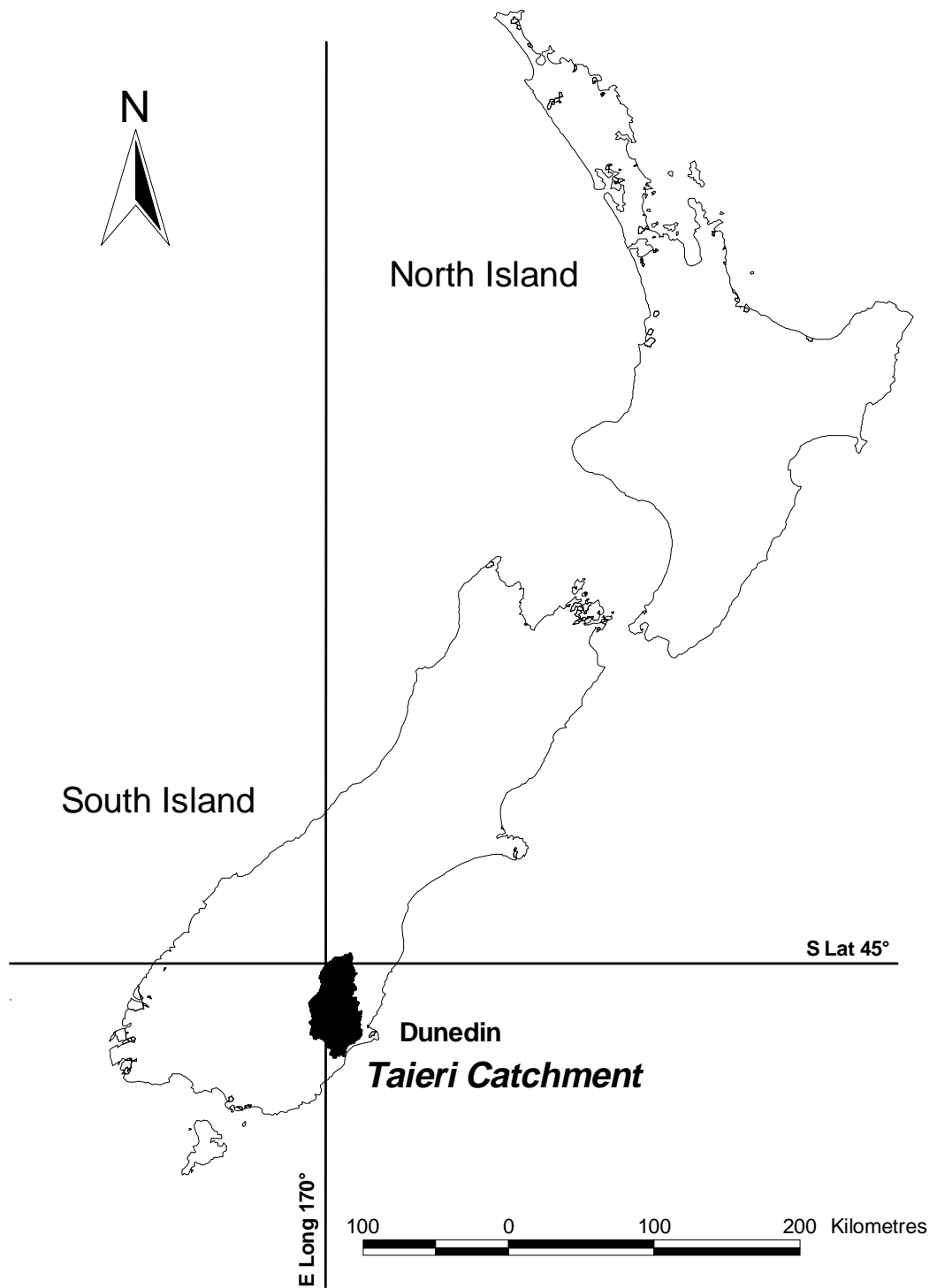


Figure 1. New Zealand, showing the location of the Taieri River catchment.

It is believed that at the time of initial human colonisation (about 1200 years ago), the Taieri River catchment was forested toward the coast, while the inland plains and mountains to the west were covered by open woodland up to the climatic tree line. Shortly before European colonisation, forest was restricted to the coastal region, while tussock grasslands or low shrubland and scrub dominated the interior (McGlone 1983). Extensive areas of marshes occurred on

the coastal and interior plains, and bogs were widespread on the mountain tablelands. Major changes following European colonisation (commencing about 1850) include the conversion of indigenous vegetation to improved pasture by burning and grazing (sheep, cattle), followed more recently by aerial over sowing and top dressing. Irrigation by water extracted from the Taieri River and its tributaries has enabled clover, lucerne, exotic pasture grasses and crops to be grown in the low rainfall drought-prone regions of the Maniototo Plain and Strath Taieri. Beginning in the latter half of the 19th century, mining activities have also had important and widespread effects on the Taieri River landscape (Otago Catchment Board 1983).

At present, most regions of tussock grasslands throughout the drier interior of the catchment have been influenced to some extent by burning and grazing. Of the eight major catchments (areas >100 km²), vegetation cover of the Loganburn and the upper Kye Burn is primarily tall tussock grassland. Much of the lower Kye Burn, and the Sutton, Nenthorn, Deep and Lee Stream catchments have been converted to improved pasture. The Silver Stream and Waipori catchments are mosaics of remnant indigenous forest, exotic production forests, improved pasture, and intensive cropping. The conversion of tussock grassland to improved pasture to altitudes c.700 m is still ongoing. Areas devoted to exotic forest are rapidly increasing in the lower catchment and are replacing grasslands in many areas. Indigenous forest is now limited to relict stands in isolated areas of the catchment. Isolated communities of native shrubs and herbs are widespread in rugged areas.

2.2 METHODS

2.2.1 Koura distribution

Archived records of koura distribution within the Taieri River region were obtained from the following sources: National Institute for Water and Atmospheric Research (NIWA), Department of Conservation, Dunedin (M. Nielson), Otago Fish and Game Council (M. Wright), Department of Zoology, University of Otago (C. Arbuckle and D. Scott). Although the dates of these combined archived data range from 1963 to 1995, the majority were recorded after 1989.

From 10 March to 8 June 1995, selected streams throughout the Taieri River region were surveyed for crayfish. A total of 81 streams were surveyed using the following technique: The stream at each designated site (usually a map reference from archived records) was inspected for presence of koura by turning over rocks and other cover, by sweeping under overhanging banks and among macrophytes with handnets, and by searching for other signs of crayfish (exoskeletons, gastroliths). If no koura were found during the initial search, the site was electro-fished. Each site was photographed (Taieri and Southern Rivers Programme Archive) and its position recorded by a Global Positioning System (Trimble Scoutmaster GPS).

2.2.2 Habitat variables associated with koura presence/absence

During the 1995 survey, the following habitat variables were recorded at 5 m stream reaches at each survey location: proportional cover of silt, coarse mineral substrata and bedrock, riparian vegetation assemblage, land use in the catchment at large (intensive grazing/extensive grazing/no grazing), and the presence/absence of brown trout (*Salmo trutta* L.) and long finned eels (*Anguilla dieffenbachii* Gray). The riparian vegetation assemblage consisted of six categories according to dominant vegetation type: (1) exotic grasses; (2) willow and exotic grasses; (3) willow and exotic shrubs; (4) native tussock grasses; (5) native shrubs; (6) native forest. Brown trout and eels were selected as variables because they are predators of koura (Shave et al. 1994) and because anecdotes have linked trout to an apparent decline in koura (Thompson 1922; McDowall 1990).

2.2.3 Relationship between land-use and crayfish distribution

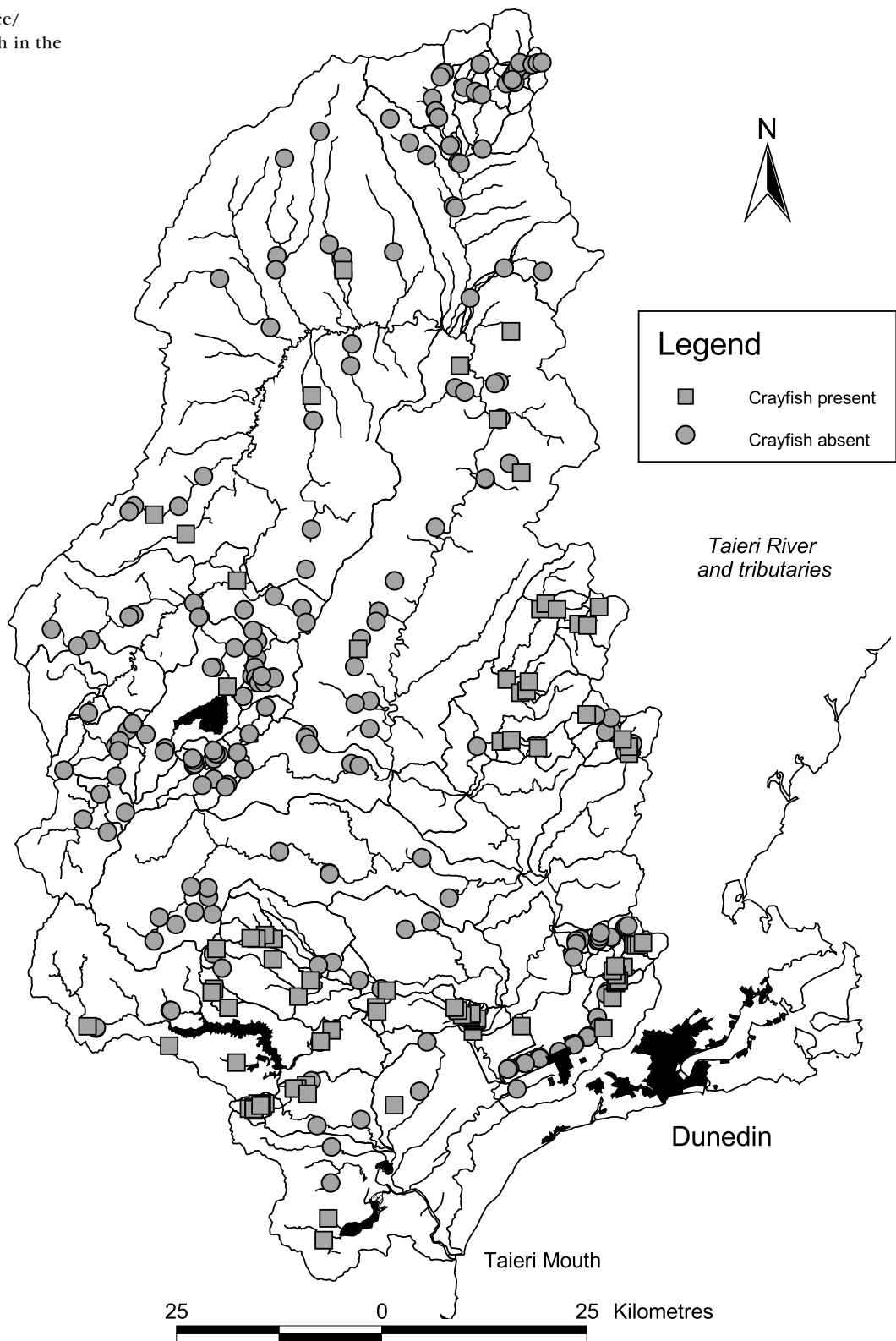
Because distributional data from different sources of archived koura records were variable with regard to how data were recorded (e.g. presence/absence, abundance, size-structure), koura presence/absence was selected as the most consistent dependant variable for analysis. The analysis of the relationship between land-use and crayfish distribution was conducted at two spatial scales:

1. A finer spatial-resolution analysis was performed using the habitat data recorded during the 1995 survey. The relationship of koura presence/absence to all habitat variables was screened for significance with Chi-square analysis. G-tests (Sokal & Rohlf 1981) determined which categories within a variable were most strongly associated with koura distribution. Following the initial screening for significance, logistic regression was used to determine combinations of significant variables that explained the most variation in koura presence/absence among survey sites.
2. A coarse spatial-resolution analysis was performed based on the land-use classification derived from the remote sensing data. Maps of present-day vegetation cover were made using a hybrid of classified satellite imagery (*Satellite Pour l'Observation de la Terra*, SPOT) and other topographic geographic information system (GIS) databases, these were combined with a GIS database of recent koura distribution (1989-1996). The dominant vegetation class within a defined proximity (100 m) to the site was calculated from an overlay of the presence/absence site coverage and the vegetation coverage database. Hierarchical vegetation classes (n = 30) were further collapsed into five ground cover and vegetation associations for Chi square analysis (NF = native forest, IF = introduced forest, IP = introduced pasture, NG = native grassland and BG = barren ground) (Arbuckle 1999).

2.2.4 Results

The most populations of koura in the Taieri River catchment occur in the lower catchment, below the confluence of the Taieri River and Sutton Stream (Figure 2). In this region, koura are widely distributed throughout the headwaters of each of the major tributaries (Nenthorn, Three O'Clock, Silver, and Lee Streams, Traquair Burn, and the Waipori River), with the notable exception of Deep Stream. In contrast, koura are sporadically distributed in the upper catchment.

Figure 2. Presence/absence of crayfish in the Taieri catchment.



Isolated populations are recorded from the major inland plains: Serpentine Flats (1 population), Maniototo Plain (2 populations), and Strath Taieri (5, includes populations from Taieri Ridge). With the exception of populations in the Loganburn Reservoir (Rock & Pillar Range) and Totara Creek (Rough Ridge), koura are absent from Taieri tributaries in the mountain ranges (Lammerlaw, Lammermoor, Rock & Pillar, Kakanui and Hawkdun ranges, and Rough Ridge).

2.3 FINE SPATIAL-RESOLUTION ANALYSIS OF HABITAT VARIABLES AND KOURA DISTRIBUTION

2.3.1 Riparian habitat variables

Of all habitat variables documented during the 1995 survey, riparian vegetation was most strongly associated with koura presence/absence (Figure 3A, $\chi^2_5=23.15$, $p < 0.004$). The riparian vegetation types most often associated with the presence of koura are native tussock grasses, native shrub, and native forest. Koura presence was more likely in shrub and forest categories than in riparian areas dominated by exotic grasses, willows and exotic grasses and willows and exotic shrubs (G-test, $p < 0.05$). No significant differences were detected between the latter three riparian vegetation assemblages ($G=3.37$, $p > 0.1$). Native tussock grass was not significantly different from any other category. Koura distribution was also significantly related to land use (Figure 3B, $\chi^2_3=14.21$, $p < 0.003$), where upon extensive or mixed intensive/extensive grazing had a lower association with koura than sites with either intensive or no grazing (G-test, $p < 0.05$).

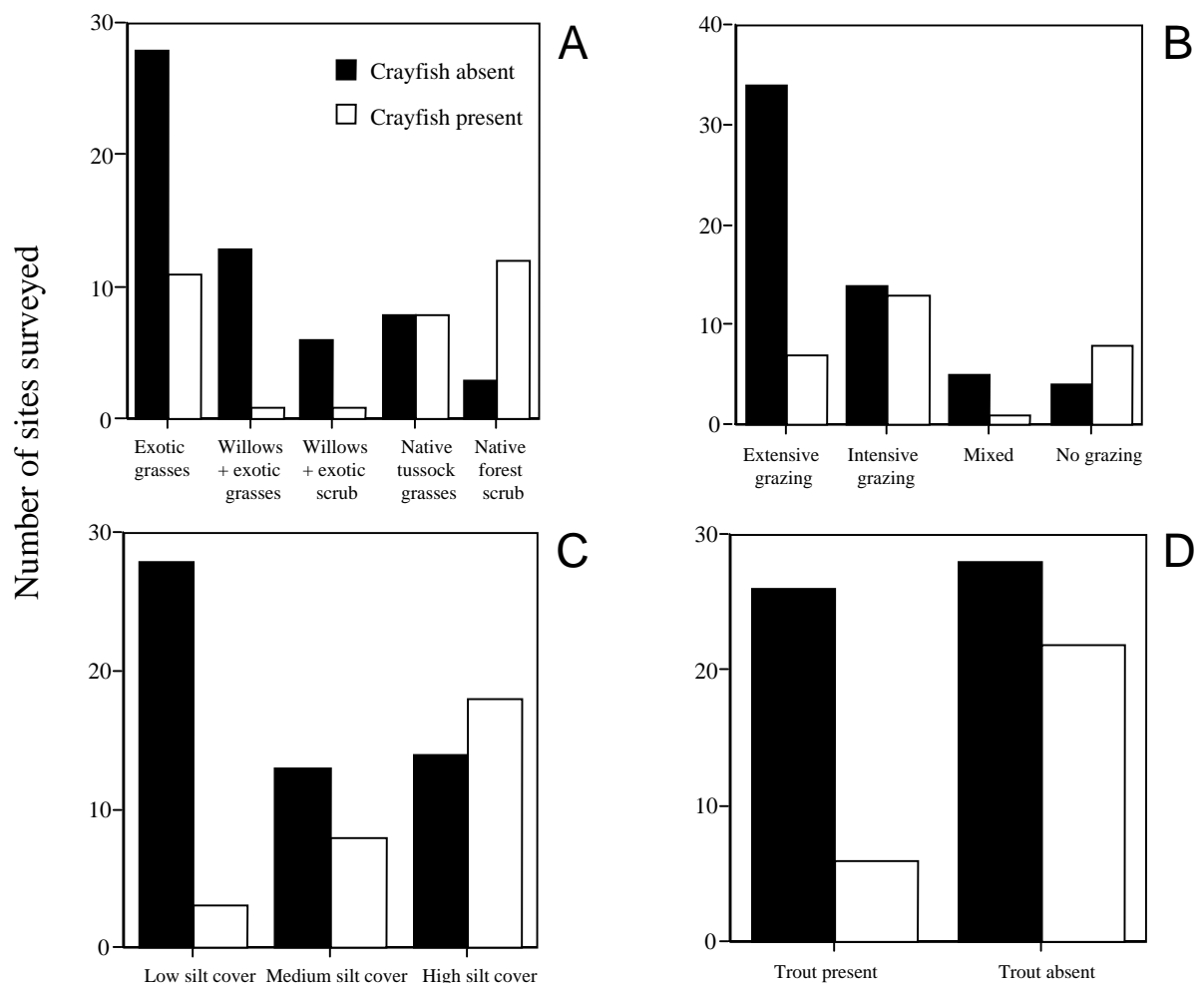


Figure 3. Crayfish presence/absence in relation to riparian variables: A, vegetation; B, land use and in-stream habitat variables; C, proportion of silt cover over the stream bed; D, trout (*Salmo trutta*) presence/absence.

2.3.2 In-stream habitat variables

The proportion of silt cover over the streambed varied significantly with respect to koura presence/absence (Figure 3C, $\chi^2_2 = 15.27$, $p < 0.0006$). High (80+) and medium (21-79%) levels of silt cover had a stronger association with koura presence than low (0-20%) levels of silt cover. Trout presence/absence also showed a significant relationship with koura distribution (Figure 3D, $\chi^2_1 = 5.53$, $p < 0.02$). Trout presence was negatively associated with koura presence. Eel distribution was apparently not related to koura presence/absence.

Logistic regression indicates that category of riparian vegetation combined with proportion of silt cover explained the greatest proportion of variation in koura presence/absence observed among the 1995 survey sites ($r^2 = 0.36$, $\chi^2_9 = 23.38$, $p < 0.006$). The proportion of overall variation explained by the logistic regression model was not improved by adding additional significant variables. It must be mentioned that many of the habitat variables are intercorrelated. For example, riparian vegetation and land use ($\chi^2_{15} = 54.76$, $p < 0.0001$), riparian vegetation and silt cover ($\chi^2_{10} = 20.47$, $p < 0.03$), silt cover and land use ($\chi^2_6 = 12.78$, $p < 0.05$), were all significantly correlated. Consequently, it is not clear what the underlying cause and effect of any apparent relationship might be.

2.3.3 Coarse spatial-resolution analysis of land cover and koura distribution

At a coarse scale koura presence/absence is strongly associated with vegetation (Figure 4, $\chi^2_5 = 50.04$, $p < 0.001$). Koura presence was significantly associated with riparian zones of native forest, scrub and grassland vegetation (G-test, $p < 0.05$). Koura absence was significantly associated with riparian zones of improved pasture, barren ground and introduced forest/scrub (G-test, $p < 0.05$).

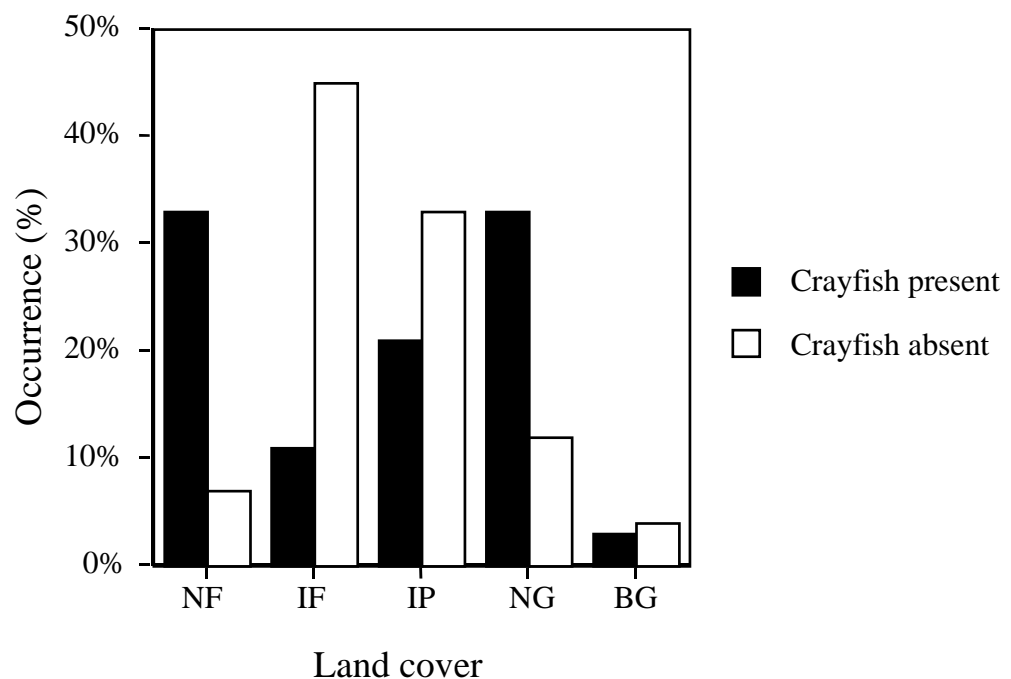


Figure 4. The percentage of crayfish absent/present in relation to land cover. NF = native forest; IF = introduced forest; IP = introduced pasture; NG = native grassland; BG = barren ground.

2.4 DISCUSSION

Factors determining the pre-European distribution of koura within the Taieri River catchment must be considered before attempting to describe potential land use effects that have occurred during the last 150 years. Although koura may have been introduced or extirpated from local areas by human activities, a starting point for determining the early Holocene distribution in the Taieri River can be established by assuming that the present day macrodistribution reflects the pre-human distribution, and that human-induced changes, if any, have been on a local scale contained within this macrodistribution.

In the Taieri River catchment, koura are widely distributed in the lower Taieri catchment, but are uncommon and occur in isolated populations in the upper catchment. Since comprehensive data concerning biogeography and habitat requirements for *Paranephrops* are lacking, reasons underlying this pattern must be speculative. Carpenter (1977) reported that the altitudinal range for *Paranephrops* is from sea level to c. 1500–2500 m, although documentation was not provided. *P. planifrons* has been reported from sub-alpine tarns and streams at c. 1300 m in the North Island and the western South Island (Fordham et al. 1979; McLellan 1979). *P. zealandicus* has been reported from 470 m in a Southland lake (Hopkins 1970; Fordham et al. 1979). In the Taieri River catchment, a population occurs at 800 m in the Loganburn Reservoir on the Rock & Pillar Range (A. Huryn pers. obs.). Although permanent streams range up to 1000 m or more, within the Taieri River catchment, it appears that altitude alone is not a major determinant of koura distribution in this region. (Note only 3% of catchment is above 1000 m, and 84% of catchment is below 300 m).

Koura are apparently uncommon in high-gradient mountain streams (Archey 1915; Hopkins 1970), with records from high altitudes referring to populations in lakes and tarns, or low-gradient streams with silt substrata (Hopkins 1970; Fordham et al. 1979; McLellan 1979). They are also apparently absent from streams with avulsive channels and / or mobile bed loads (Archey 1915), although they may be abundant in physically stable tributaries of such rivers. Lotic habitats commonly reported for *Paranephrops* are low gradient streams with gravel and silt-beds and banks of cohesive sediments that drain catchments with vegetation ranging from native forest to exotic pasture grasses (Archey 1915; Hopkins 1970).

The presence of numerous high gradient streams throughout the mountainous regions of the Taieri River catchment may explain the absence of koura in areas of the upper catchment; however, there are also numerous streams that are apparently suitable, yet lack koura. The region encompassed by the present-day Taieri River catchment has a relatively small proportion of avulsive and braided streams (e.g. the Kye Burn and its tributaries provides the only clear example); however, this is a relatively new phenomenon from a geological perspective. Other reasons for the lack of koura in the upper Taieri might include water abstraction for irrigation and mining activities (cf. Otago Catchment Board 1983).

2.4.1 Riparian and in-stream habitat variables

Within the Taieri River catchment, presence of koura is most often associated with low-gradient streams without trout, with silt-covered beds, and with riparian zones with predominantly native vegetation. An apparent negative association between presence of trout and koura has been reported for many years (Thompson 1922), and has been attributed to predation (McDowall 1990). Although correlative, the 1995 survey in the Taieri River catchment provides further support for this conclusion. The lack of any relationship between koura and eel presence/absence may provide indirect support for the conclusions of Shave et al. (1994), who provided evidence indicating that koura are able to detect the presence of eels, but unable to detect the presence of trout using chemical cues. Because of this predator detection system, koura should be better able to coexist with eels than trout.

The association between the presence of koura and silt and is usually assumed to be a function of habitat selection since koura are active burrowers (Archev 1915; Hopkins 1970). Alternatively, the association with high silt cover may be a function of koura feeding activity. Crayfish may produce large amounts of fine particulate material by feeding on coarse detritus (Huryñ & Wallace 1987), and the presence of silt may be a function of crayfish presence and activity rather than a prerequisite to habitat selection. Regardless, the proportion of silt cover was also correlated with riparian vegetation and land use furthermore obscuring the underlying processes between koura distribution and in-stream variables.

Although the relationship between type of riparian vegetation and koura presence/absence is relatively strong, it is apparent that land use in the catchment at large is only vaguely linked to koura distribution. For example, sites categorised by extensive grazing had a lower association with presence of koura than sites with intensive or no grazing. Some streams draining catchments that are subject to intensive grazing and pasture development have abundant populations of koura (e.g. selected streams in the Lee Stream and Waipori River catchments); however, these streams also have riparian zones that are invested with native vegetation (tussock, shrubs). Such is often the case in the Taieri River region as catchments that are intensively grazed usually have pasture limited to hilltops while the rugged gullies and wetlands are largely left in native vegetation.

Catchments that are extensively grazed are usually located throughout the interior high-country. Since the high-country has only isolated populations of koura the negative relationship between koura presence and extensive grazing may be more of a function of drainage evolution rather than a direct effect of land use on koura distribution. This is emphasised by the lack of association between koura presence/absence and riparian zones of native tussock grass compared to either exotic (negative association) or native shrubs and trees (positive association). Unlike other riparian vegetation assemblages, riparian zones consisting of native tussock grasses are widespread throughout the Taieri River catchment. These zones are found along both high-gradient streams of the interior ranges (extensive grazing) where koura occur in isolated populations, and the low-gradient streams of the coastal lowlands (intensive grazing) where koura are widespread. It should be noted that koura are generally absent or uncommon on the plains, regardless of position within the catchment at large.

It is not clear why koura are so often associated with streams with riparian zones of native vegetation. Populations of koura may be protected from effects of intensive agricultural land changes by riparian buffer zones regardless of land use in the catchment at large. It is also possible that exotic riparian zones may indicate a history of disturbance to the stream channel with long-term effects on koura populations. For example, removal of riparian vegetation is often associated with changes in channel form, discharge, sedimentation, thermal regimes, and inputs of pesticides and fertilisers to the stream channel (Collier 1992), all of which may be detrimental to crayfish populations (Horwitz 1990; Merrick 1993). Crayfish with very local distributions have been eradicated by single major alterations to their habitat (Wells et al. 1983). Once eradicated by disturbance, recolonisation may be an extremely slow process depending upon proximity to refugia and geological activity (e.g. active transverse faulting systems; Main 1989). For example, koura have yet to recolonise a wide region east of Lake Taupo from which they were apparently eradicated following widespread devastation by a volcanic eruption about 1800 years ago (McDowall 1995). Taieri River tributaries with margins invested with high proportions of native vegetation may simply have morphologies that are suitable for koura while providing poor conditions for pasture development for intensive grazing near the stream channel.

Finally, on a larger time scale, factors influencing the pre-European distribution of koura also have to be considered before attempting to advise of any potential land management effects that have occurred over the past 150 years. Since the Miocene, the Taieri River drainage has undergone several major changes in response to basin subsidence and range uplift. About 10 million years ago, the headwaters of the proto-Taieri River were in the vicinity of Sutton Stream. The upper reaches of the present day Taieri River were isolated from the lower catchment by a low divide. It appears that these geological changes have had a major influence on the distribution of native fish, and potentially koura, throughout the Taieri drainage. To complicate matters, climate changes may have had a consequent effect on koura distribution by altering native vegetation patterns. The Taieri is thought to have had a substantial cover of podocarp forest/scrub (about 2400 years ago) but there are thought to have been major changes in the general climatic conditions leading to the drier Otago interior of today. In turn, there was continued modification of the vegetation cover by wild and anthropogenic fire. This altered the vegetation cover progressively over a period of 2000 years. The koura distribution present today may in fact be what is left of a more expansive distribution present at the time of complete native forest cover.

3. Koura ecology

3.1 LIFE HISTORY, LONGEVITY AND PRODUCTION

3.1.1 Method

Production and longevity were assessed for a population of koura in Powder Creek, a headwater stream draining a catchment of regenerating coniferous-broadleaf forest in eastern Otago. Three stream reaches were sampled (Figure 5). Each reach consisted of a single pool (20.9–42.6 m²) and a 20 m riffle. During the period January 1994 to June 1995 each pool and riffle was visited at 4–6 week intervals for the purpose of mark and recapture. Capture by handnetting of koura commenced 45 minutes after sunset. Each pool and riffle was cordoned off from the adjacent stream by nets. Koura were tagged by a method similar to that of Abrahamsson (1965), and released after two replicate measurements of carapace length (CL= tip of rostrum to posterior median margin of carapace) were taken. Koura smaller than 18 mm, in soft shell or with carapace wounds were not tagged, for fear of causing injury. Measurements of CL upon initial and subsequent captures allowed growth to be monitored. All koura caught were sexed and any peculiarities were noted (including disfigurements, ecdysial stage, estimated egg number, larval stage and colour). The growing season was estimated *a posteriori* from the incidence of soft integument amongst captured koura, and was defined as the months for which the mean frequency of soft integument exceeded 1%. To check for any distinct cohort structure size-frequency histograms were made for each mark and recapture event. Annual gain in carapace length (AGCL, mm) was chosen as the measurement of koura growth.

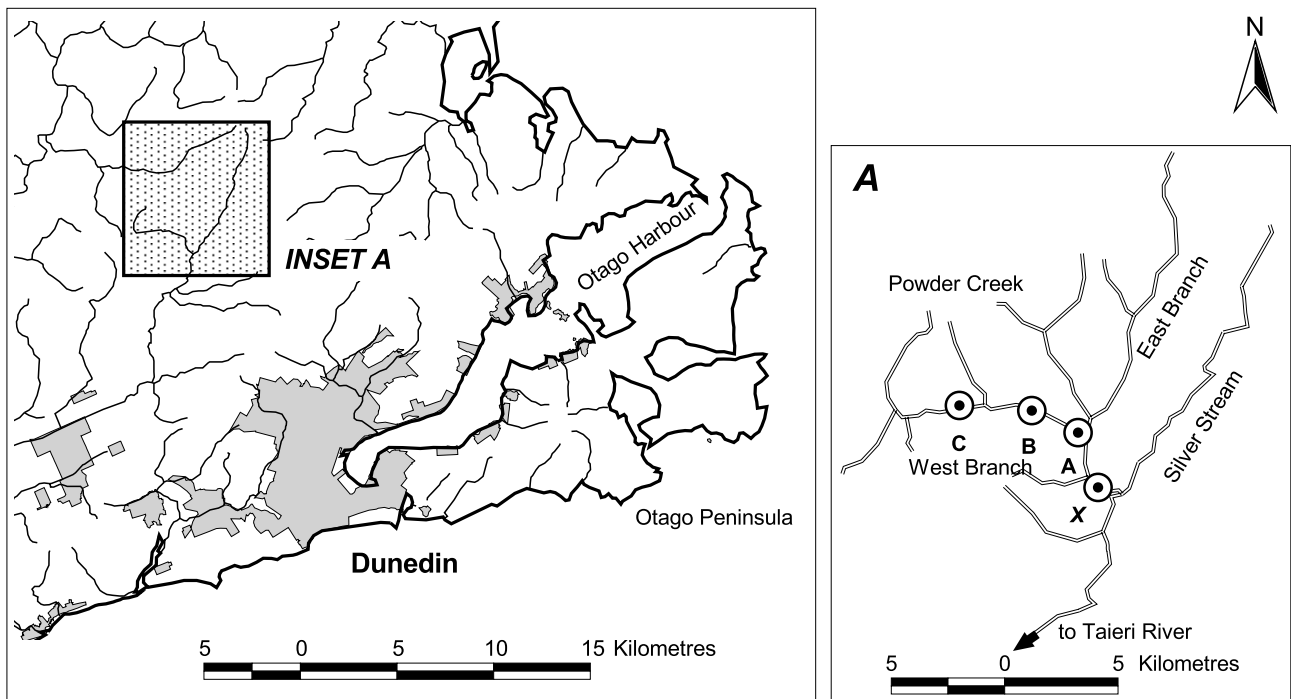


Figure 5. Location of Powder Creek study area. Inset A: Powder Creek, location of the three reaches (A, B, C) used for life history, longevity and production study and the experimental *in situ* enclosures (X).

Longevity was estimated with an iterative bootstrap model (Effron & Tibshirani 1993) based on annual growth increments. Annual gain in carapace length (AGCL, mm) provided the raw data required by the model. The longevity model was seeded at a CL of 20 mm which was assumed to represent one full-years growth from an egg.

Annual production was derived from size-specific growth rates and biomass structure of the population. Production (P) was estimated for each size class using the following equation:

$$P = G * \bar{B}$$

where G = annual instantaneous growth rate ($\text{mg mg}^{-1} \text{ AFDW m}^{-2} \text{ yr}^{-1}$) and \bar{B} = mean biomass (mg AFDW m^{-2}) (Huryñ 1987). Koura abundance was estimated using a depletion-removal method in pools, and quadrat sampling in riffles. To obtain estimates of individual mass, koura specimens were dried (60°C) for 48 hours, weighed to the nearest mg to obtain dry weight, ashed for 2.5 hours (550°C) and reweighed. Ash free dry weight (AFDW) was estimated as the difference between dry weight and ash weight. Measurements of live koura could then be converted to AFDW using a least-squares regression of log transformed AFDW (mg) against log CL (mm). Depletion-removal data from pools was analysed using Pop/Pro Statistical Software© (Kwak 1992) which uses a modified Zippin equation to provide estimates of minimum size classes, mean density and mean biomass density and their variances. Data from the riffles were separated into 10 mm CL classes.

Annual instantaneous growth rate G ($\text{mg mg}^{-1} \text{ AFDW yr}^{-1}$) was calculated as:

$$G = \frac{\ln(W_f + \sum W_e) - \ln(W_i)}{t}$$

where W_f is the final weight, W_e is the weight of shed exuviae and W_i is the initial weight, and t is one year (Pratten 1980). Measurement of CL was converted to mg AFDW using a length-weight regression. Growth was assumed to be exponential. Whole exuviae found during the study period were measured (CL) and dried (60°C) for 48 hours. Exuviae were then weighed to the nearest mg to obtain dry weight, ashed for 2.5 hours (550°C) and reweighed to obtain AFDW. Measurements of exuviae mass could then be converted to AFDW using a least squares regression of log transformed AFDW (mg) against log CL (mm). Log-transformed growth rates (G) were regressed against log-transformed CL to obtain equations to predict annual growth rate for koura size.

To account for variation observed among annual growth rates, a bootstrap analysis was performed on G by randomly re-sampling the data points with replacement. Production was estimated for each of the paired G and \bar{B} values, thereby giving estimates of production for each size class.

3.1.2 Results

Of 1447 koura tagged by cauterisation, increases in CL were recorded for 229 koura. The 1994-1995 growing season extended from 1 October to 31 March. Unlike other researchers using cauterization and puncture techniques, we were unable to determine the number of moults the koura had gone through by the appearance of the scar.

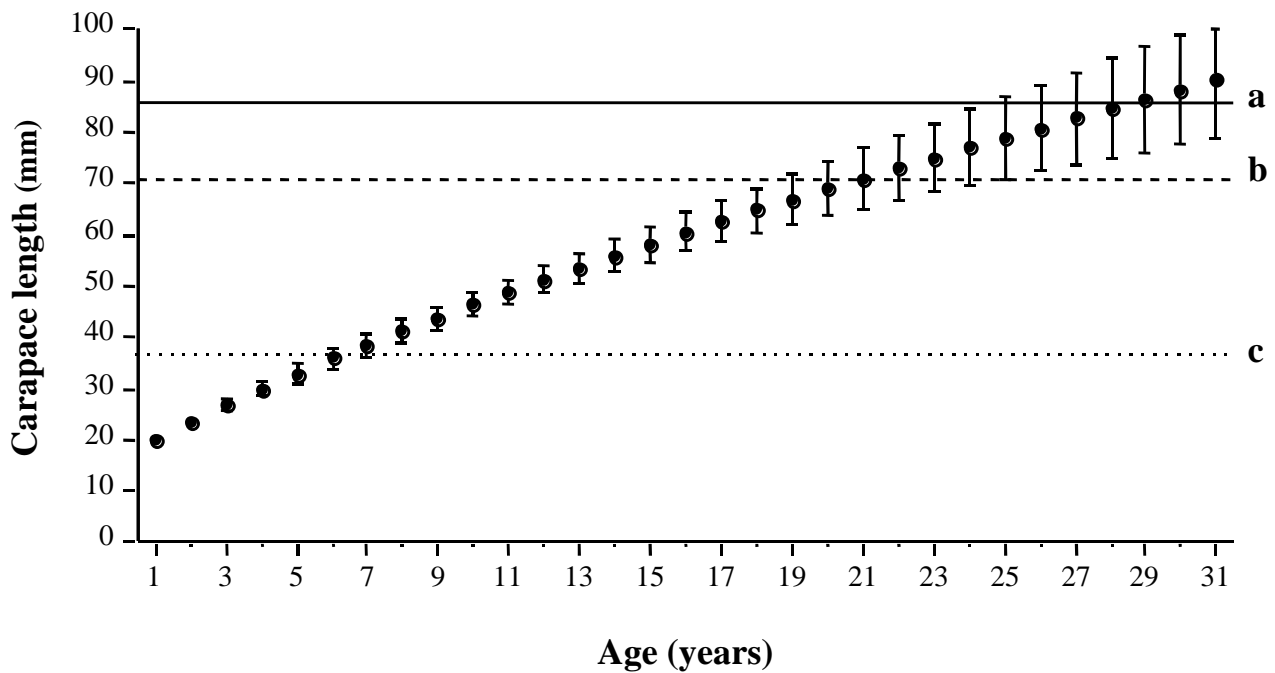


Figure 7. Estimates of crayfish age on basis of carapace length. Error bars represent \pm 95% confidence intervals generated by a bootstrap model; a = size of largest crayfish found in Powder Creek, b = size of crayfish used in generating bootstrap model, c = size of smallest berried female found in Powder Creek.

contribution of female egg and glair (the egg binding matrix) to overall production was assumed to be negligible.

Annual instantaneous growth was greatest for small koura and decreased with size. Koura density appeared to vary seasonally, with the highest densities being recorded in summer (Table 1). Mean biomass was no different in pools (range 9–33 g AFDW m^{-2}) than riffles (range 4–6 g AFDW m^{-2}) (two-tailed, two sample t-test $df = 2$; $p > 0.05$) (Figure 8). Mean production ranged from 3–11 g AFDW $m^{-2} yr^{-1}$ in pools to 2 g AFDW $m^{-2} yr^{-1}$ in riffles (Figure 8), but was not significantly different between the two sections (two-tailed, two sample t-test $df = 2$; $p > 0.05$). Turnover rates (P/B) were low in comparison with other crayfish species (Table 2). Consequently, high biomass rather than high rates of growth and/or population turnover were responsible for production. There was no

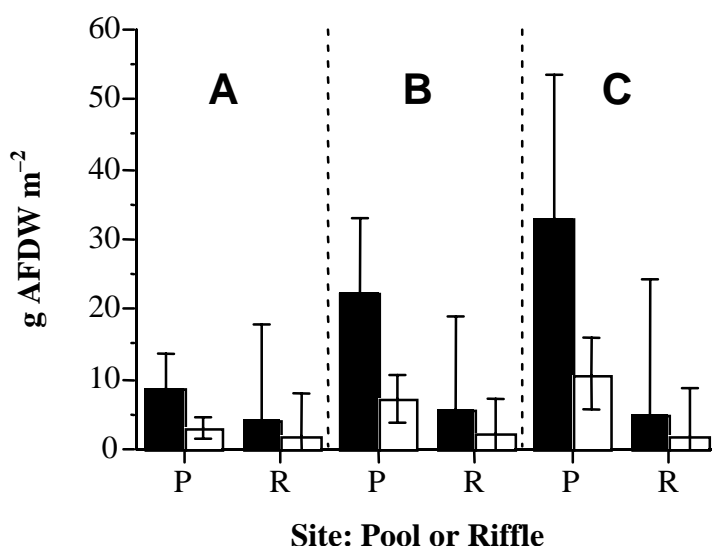
TABLE 1. SEASONAL CHANGES IN CRAYFISH DENSITY (CRAYFISH PER m^2).

| REACH | | SEASON | | |
|-------|--------|---------------|----------------|----------------|
| | | WINTER 1994 | SUMMER 1995 | WINTER 1995 |
| A | pool | * | 3.5 \pm 0.8 | NA |
| | riffle | 2.6 \pm 3.1 | 3.6 \pm 4.7 | 2.8 \pm 4.5 |
| B | pool | * | 10.0 \pm 1.9 | 5.0 \pm 1.2 |
| | riffle | 1.1 \pm 1.9 | 3.6 \pm 4.2 | 3.9 \pm 4.0 |
| C | pool | * | 12.3 \pm 1.6 | 10.9 \pm 1.1 |
| | riffle | 0.7 \pm 2.9 | 2.6 \pm 4.9 | 0.7 \pm 1.3 |

* Crayfish density was not estimated for pool sections in 1994. Error bars represent \pm 1 standard deviation.

NA Heavy treefall prevented the 1995 winter estimate for the pool section of reach A.

Figure 8. Biomass (black) and annual production (white) for crayfish in pool (P) and riffle (R) sections within the 3 study reaches (A, B, C) of Powder Creek. Error bars represent \pm 95% confidence intervals.



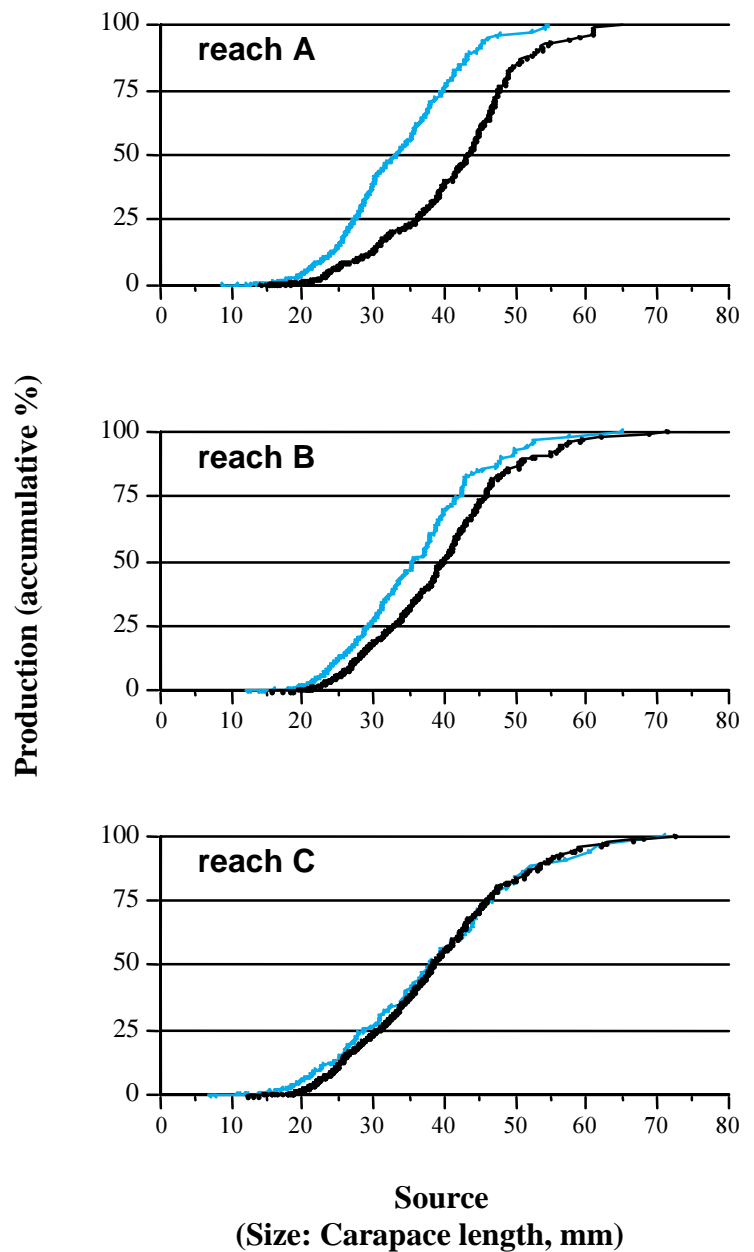
detectable difference between mean P/B in riffles (range 0.38-0.43) and pools (range 0.33-0.35) (two tailed, two sample t-test = -4.051; df = 2; p = 0.0559). Most production was generated from middle sized koura (30-50 mm CL) (Figure 9).

Large variances were associated with both the production and biomass estimates. Estimates of biomass were the major source of this variance, because koura were patchily distributed within the riffles, and pools were very hard to deplete (e.g. on one occasion we failed to deplete pool C despite having a total of 5 runs and amassing 161 koura in 140 minutes sampling effort). Since the sampling error in pools was dependent on the quality of the depletion runs (catchability), a large variance was associated with estimates of biomass from pools (Kwak 1992).

TABLE 2. COMPARISON OF P/B RATIOS BETWEEN CRAYFISH SPECIES OF TEMPERATE CLIMATES.

| SPECIES | ENVIRONMENT | P/B | AUTHOR |
|--|-------------------------|------------------|----------------------------|
| <i>Austropotamobius pallipes</i> | aqueduct | 0.32-0.44 | Brewis & Bowler (1983) |
| <i>Paranephrops zealandicus</i> | headwater stream | 0.33-0.43 | This study |
| <i>Cambarus bartoni</i> | headwater stream | 0.58 | Huryn & Wallace (1987) |
| <i>Cambarus bartoni</i> | 5-6th order river | 0.7 | Mitchell & Smock (1991) |
| <i>Astacus astacus</i> | lake | 0.78-0.82 | Cukerzis (1988) |
| <i>Orconectes virilus</i> | 4 lakes | 0.8-1.9 | Momot (1988) |
| <i>Orconectes virilus</i> | 5-6th order river | 1.1 | Mitchell & Smock (1991) |
| <i>Orconectes virilus</i> | 6th order river | 1.2 | Roell & Orth (1992) |
| <i>Cambarus sciotensis</i> | 6th order river | 1.5 | Roell & Orth (1992) |
| <i>Orconectes sanborni</i> | 6th order river | 1.9 | Roell & Orth (1992) |
| <i>Orconectes virilus</i> | lake | 2.33 | Momot (1967) |
| <i>Procambarus clarkii</i> | drainage channels | 5.03 | Anastácio & Marques (1995) |
| <i>Pacifastacus leniusculus</i> | headwater stream | 5.9 | Mason (1974) |

Figure 9. Predicted source of crayfish production in riffles (grey) and pools (black) for each study reach (A, B, C). The contribution of crayfish size to production is indicated by slope.



3.1.3 Discussion

Temperature is regarded as the primary environmental determinant of growth and development for crayfish (Lowery 1988; Merrick 1993; Lodge & Hill 1994). Momot (1984) noted that crayfish at high latitudes or altitudes in temperate regions usually live longer and mature later than those in warmer climates. Comparisons between the Powder Creek study and previous research on koura in New Zealand support these contentions. Water temperature appears to be the factor responsible for the life history characteristics of the Powder Creek koura population.

Powder Creek is constantly shaded as a result of the canopy cover and valley topography. This shading would appear to explain why it has a low stable temperature in comparison to many other streams in the Taieri catchment (e.g. mean daily temperature for Powder Creek ranged 10.1°C over 1994-95 while that of a grassland stream nearby ranged 17.5°C for the same period (A. Huryn unpub. data). Mean daily temperature of Powder Creek rises above 10°C for less

than 60 days each year, and peaks below 12°C (less than 2600 degree days per year). For 7 months of the year the temperature of Powder Creek is below the minimum threshold of 8–10°C required for reproduction and moulting in many cool water crayfish species (Lodge & Hill 1994).

Even though the koura of Powder Creek were long-lived and showed no obvious cohort structure, their density showed seasonal fluctuations. This would appear to be an artefact of seasonal changes in koura activity rather than actual population fluctuations. Quilter & Williams (1977) found that *P. zealandicus* was less active in winter months, and would spend much of this period in hibernacula and many specimens would remain completely inactive for several days in succession at temperatures of 5°C. Similarly, we found that diurnal activity in Powder Creek was common in summer, but was rare in the winter. Inactivity and increased cryptic behaviour during winter would explain the low biomass estimates recorded during this period. Furthermore, the summer increase in density could not be explained by recruitment of young, nor was there any evidence of higher mortality in winter (N. Whitmore pers. obs.).

Koura development in Powder Creek was extremely slow in comparison with other crayfish species (Lowery 1988) as well as other populations of *Paranephrops*. Hopkins (1967), for example, found that incubation of eggs and juveniles of *P. planifrons* in the Mangatere River (North Island) takes place between April and December and lasts for 25–26 weeks. Hopkins (1966) suggested the age for female sexual maturity for in this population was c. 2–3 years. In comparison, incubation of eggs by the Powder Creek population begins in December and January and lasts for at least minimum of 60 weeks, while the minimum predicted age for the smallest berried female (36 mm CL) was 6–7 years. These findings conflict with Hopkins' (1967) assertion that koura species which lay in spring or summer have shorter incubation periods, than those which lay in autumn.

Individual growth rates for koura recorded in Powder Creek were similar to those measured in Leith Stream, Dunedin. In both studies multiple moults were uncommon, and no moulting took place in winter. This similarity may be attributable to water temperature, as the temperature profile of Powder Creek was very similar to that of Leith Stream (mean maximum 12°C, minimum 3°C) (Jones 1981). While it appears that moulting can occur throughout the year for *P. planifrons* (Hopkins 1966) the koura of Powder Creek appear to be restricted to moulting over a discrete seasonal period (November to April).

Devcich (1979) estimated the age of a lake dwelling *P. planifrons* female of 70.9 mm CL to be 20 years. An equivalent sized koura of Powder Creek would be predicted to be a minimum of 19–25 years old. This similarity disputes the contention by Devcich (1979) that there is a large disparity in life span and growth rate between stream and lake-dwelling koura, typified by short life spans and small sizes in streams and long life spans and large sizes in lakes.

Mean production of the Powder Creek population (2–11 g AFDW m⁻² yr⁻¹) is amongst the highest recorded for stream-dwelling crayfish: compare with 0.2–8.8 g AFDW m⁻² yr⁻¹ (Mason 1974; Brewis & Bowler 1983; Huryn & Wallace 1987; Mitchell & Smock 1991; Roell & Orth 1992; Anastácio & Marques 1995). The trophic basis for this production in Powder Creek is unknown. Crayfish are able

to use any one, or combination of the food sources available in Powder Creek (Holdich & Reeve 1988; Musgrove 1988):

- Allochthonous detritus
- Microbial flora of detritus
- Aquatic animals especially macroinvertebrates
- Periphyton
- Suspended particles

There is no evidence that the koura population of Powder Creek could withstand harvesting. The P/B ratios alone, would suggest that a maximum annual harvest of 30–40% of standing stock may occur without deleterious effects. However, this ratio does not address the fact that Powder Creek population has low rates of reproductive success, slow recruitment, and slow development to sexual maturity. In the absence of any other information to the contrary these life history characteristics suggest any reduction in the number of sexually mature koura could further reduce the total reproductive success of this population and, in turn, initiate a population decline.

In all respects the individual rates of growth and reproductive success of koura in Powder Creek appear to be retarded. As such, the crayfish of this population rank amongst the longest lived and slowest growing ever recorded (cf. Lowery 1988). Water temperature is likely to be a major factor responsible for the life history characteristics of the Powder Creek koura population. Low temperatures will constrain koura metabolism, thereby slowing growth and reproductive rates and causing cohorts to overlap. Slow growth and reproductive rates result in low turnover rates, while overlapping cohorts result in high standing stocks.

3.2 EFFECTS OF KOURA ON STREAM COMMUNITY STRUCTURE

3.2.1 Method

The influence of koura on invertebrate community structure was assessed by *in situ* enclosure experiments in Powder Creek (see Figure 5). Two enclosure experiments were conducted. The first ran from mid spring to early summer (from 19 October 1994 to 8 December 1994), and the second ran from late summer through to late autumn (from 24 February 1995 to 29 April 1995). Each experiment was designed as a 4 treatment, 4 replicate, randomised block design, with 2-way ANOVA as the primary analysis. Treatments consisted of a control (no koura), and three different koura size classes, each of equal biomass. As the randomised block design was used to balance the heterogeneity of the environment the testing of block effects was not required (Sokal & Rohlf 1981).

The site for the enclosure experiment within Powder Creek was chosen on the basis of homogeneity of flow, depth and substrate. Sixteen koura enclosures were constructed from lengths of 300 mm diameter PVC culvert pipe with removable enclosure ends of 4 mm² stainless steel wire mesh and a shade cloth cover. Enclosures were attached to the substrate by steel fence posts.

TABLE 3. SUBSTRATA INSERTED INTO ENCLOSURES.

| SUBSTRATE TYPE | QUANTITY (L) | DIMENSIONS (min-max) |
|-----------------------------|--------------|---|
| gravel | 14 | <26.5 mm × 26.5 mm |
| pebble | 6 | >60 mm × 60 mm <90 mm × 90 mm |
| cobble | 1 | >90 mm × 90 mm <130 mm × 130 mm |
| cobble (long and narrow) | 1 | 180 mm < length <250 mm 60 mm < width <90 mm |

Substrata were obtained from the stream bank adjacent to the study site; substrata were dry at the time of selection and were sieved to the desired dimensions (Table 3). Gravel-size substrata were spread uniformly on the bottom of each enclosure. Four of the smallest-sized pebbles were laid at uniform distances apart, longitudinally down each enclosure. The remaining pebbles and cobbles were laid haphazardly.

An approximate measure of flow was obtained in each enclosure by timing how long fluorescein dye took to travel a distance of 1 m. The topography of the study site was then augmented to provide a consistent flow through all the enclosures. Koura used in the experiment were captured by hand from Powder Creek. Each of the three koura treatments were stocked at the same biomass density. The desired stocking rate was 4290 mg AFDW per enclosure (14.7 g AFDW m⁻²), which was less than half of the maximum mean biomass recorded in Powder Creek. The numerical density of koura in the four treatments was 6 small, 2 medium, 1 large, and zero koura per enclosure. The mean size of each individual required for each treatment was established from the following equation:

$$CL = \left(\frac{B}{0.0331n} \right)^{\frac{1}{3.108}}$$

Where B = desired biomass for each enclosure (mg AFDW m⁻² y⁻¹), n = number of koura in each treatment, CL = mean carapace length required (defined as the distance between the tip of rostrum to posterior median margin of carapace).

This equation gave treatment densities of six small (CL c. 24.8 mm), two medium (CL c. 35.3 mm) and one large koura per enclosure (CL c. 44.2 mm) (hereafter treatments are referred to as Control, Small, Medium, and Large). On the basis of the natural sex distribution of koura (N. Whitmore unpublished data) Small and Medium treatments were composed of a 1:1 (male:female) sex ratio, while Large treatments were represented by male individuals. Koura that were berried or in the process of moulting were not selected.

3.2.2 Timetable

After being filled with substrata, enclosures were left uncovered for two weeks, to allow colonisation by periphyton and aquatic organisms. At the end of this period, covers were attached, and each enclosure was seeded with 90 g wet weight of leaf litter. Leaf litter was collected from a pool upstream. Twelve additional samples of the leaf litter were returned to the laboratory to determine

the mean ash free dry weight (AFDW). Each sample was dried at 60°C for 48 hours, weighed to the nearest mg, then ashed at 550°C in a muffle furnace overnight and reweighed. The difference between the two weights yielded the AFDW. Throughout the experiments, enclosure ends and covers were cleared of debris every second day by hand.

3.2.3 Macroinvertebrate and CPOM sampling

At the conclusion of the experiment, covers were removed from each block of four enclosures in an upstream direction, and a drift net of 250 μm^2 mesh was attached to the downstream end of each enclosure. Rocks were removed by hand, and cleared of silt while still in the enclosure. The koura were collected, sexed and re-measured. The gravel substrata was then agitated by hand, causing invertebrates, silt and coarse particulate organic matter (CPOM) to be suspended into the water column, and carried by the current into the net. This procedure was repeated several times, until agitation did not cloud the water. Finally the downstream enclosure end was removed and scrubbed within the enclosure. The nets were removed, backwashed into a bucket of water that had been filtered through a 250 μm^2 mesh, and then poured through a 250 μm^2 sieve. The material collected was placed into a sealable container, and fixed with a 10% Formalin® solution stained with Rose Bengal.

In the laboratory samples were split into 8 samples using an automated subsampler (Waters 1969) from which a random subsample was selected. Invertebrates in the subsample were removed from CPOM under a 10-40 \times binocular microscope. Invertebrates were identified using taxonomic keys of Winterbourn (1973) and Winterbourn & Gregson (1989). Each taxa was assigned a functional feeding group. The body length of each specimen was measured to the nearest 0.5 mm and then converted to biomass (mg AFDW) using existing length-weight equations.

CPOM from each sample was sorted into 4 size classes using sieves: 0.25-0.5 mm^2 , 0.5-1 mm^2 , 1-4 mm^2 , and >4 mm^2 . Each CPOM size class was dried at 60°C for 48 hours, weighed to the nearest mg, then ashed at 550°C in a muffle furnace overnight, rewet and dried at 60°C and then reweighed to yield AFDW.

3.2.4 Analysis

Data were analysed by ANOVA. Dependent variables were:

- Numerical and biomass diversity of invertebrates (Simpson's Diversity index: Begon et al. 1988)
- Total number and biomass of invertebrates
- Numbers and biomass of each functional feeding group
- Total CPOM biomass
- Biomass of each CPOM size class.

Comparisons of means were unplanned (therefore nonorthogonal) and protected (applied only if the ANOVA *F* test was significant). The Bonferroni *post hoc* test (Velleman 1992), with an experiment wise error rate of 0.05, was used for unplanned multiple comparison procedures.

3.2.5 Results

Koura density

Koura of the necessary size could not always be located, consequently the less common, larger koura were often of a more variable size. The koura of one Large treatment escaped during Experiment 1, so the replicate was excluded from the analysis. After escape, enclosure lids were fastened more securely in Experiment 2. At the conclusion of Experiment 2, three koura were absent from the Small treatments. As at least two koura grew during this time it is possible that the missing koura were cannibalised during ecdysis. The disappearances in Experiment 2 did not cause major biomass changes in the treatments, and so were retained in the analysis.

Sedimentation of enclosures

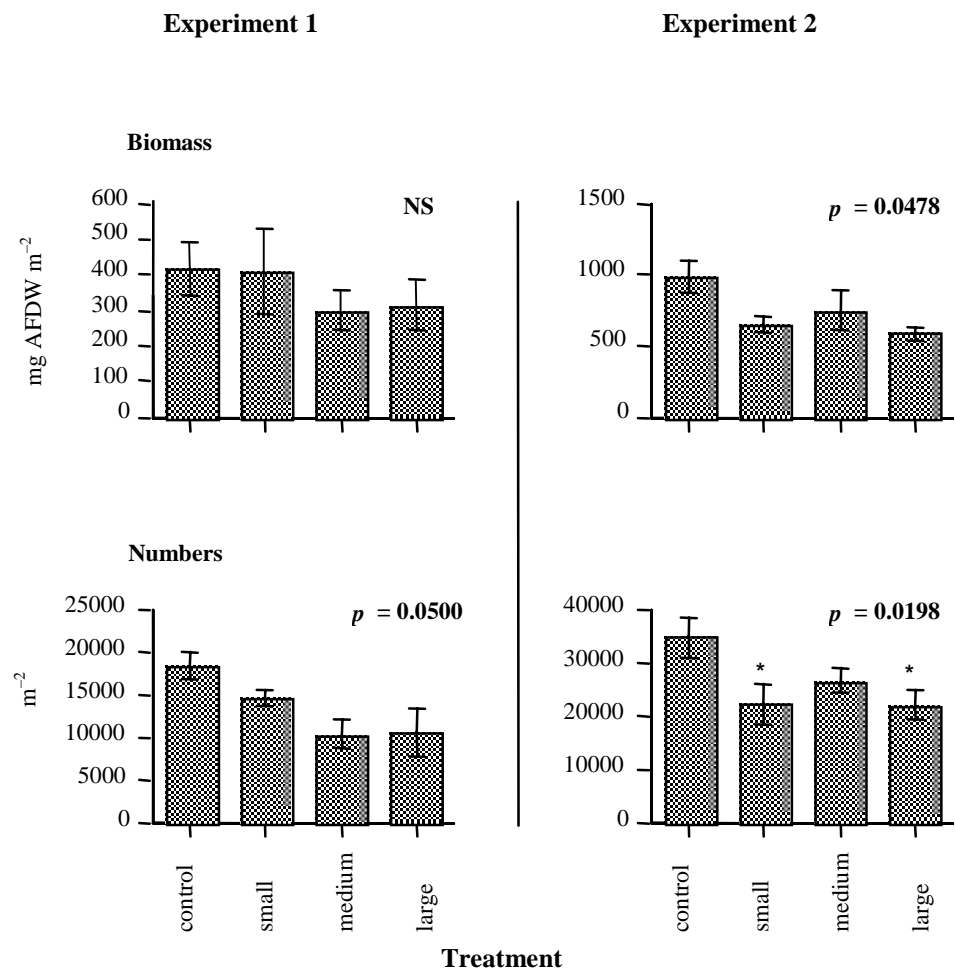
In both experiments the substrata of the control treatments were covered with a thick layer of silt, while the other treatment groups remained clear. The only non-control enclosure to show this characteristic was one large treatment of Experiment 1 from which the sole koura had escaped.

Macroinvertebrates in enclosures

Invertebrate diversity (Simpson's Diversity Index) did not differ among treatments for either experiment in terms of biomass or numerical abundance ($p > 0.05$). Both experiments shared a similar nucleus of taxa which dominated biomass. Chironomids were a major browser/collector-gatherer (BCG) component of both experiments. Between the two experiments there was a temporal shift amongst the dominant chironomid taxa within the BCG, from Orthoclaadiinae (Experiment 1) to Chironominae (Experiment 2). Oligochaetes, *Deleatidium* (Ephemeroptera), and Elimidae larvae (Coleoptera) were also major components of BCG biomass. In Experiment 2, ostracods and cyclopoid copepods were a small portion of the BCG biomass but a large component of BCG numbers. Both these taxa were negligible in Experiment 1. Tanypodinae were the most abundant predators in terms of both biomass and numbers. Where present, the shredder functional feeding group was dominated by *Austroperla*. Collector-filterers were generally poorly represented, and were entirely absent from Experiment 2.

Total invertebrate numbers differed among treatments for both experiments (Figure 10). Pairwise comparisons, however, failed to detect where the differences laid in Experiment 1 (Bonferroni *post hoc* test $p > 0.05$), however for Experiment 2, total invertebrate numbers were higher in the Control than the Small and Large koura treatments (Bonferroni *post hoc* test, Control-Small $p = 0.0388$, Control-Large $p = 0.0373$). Effects of treatment resulted in significant differences in total invertebrate biomass for Experiment 2 (F test $p < 0.05$). Pairwise comparisons, however, failed to indicate where specific differences occurred (Bonferroni *post hoc* tests; critical $p > 0.05$). Separation of invertebrate biomass by function feeding group did not reveal any differences for either experiment ($p > 0.05$). Analyses of predator, shredder, collector-filterer numbers revealed no differences between treatments for either experiment ($p > 0.05$) (Figure 11). Browser/collector gatherer numbers were negatively affected by the presence of koura (Figure 11). This trend was consistent for both experiments (Bonferroni *post hoc* test, Experiment 1; Control-Medium $p = 0.0250$,

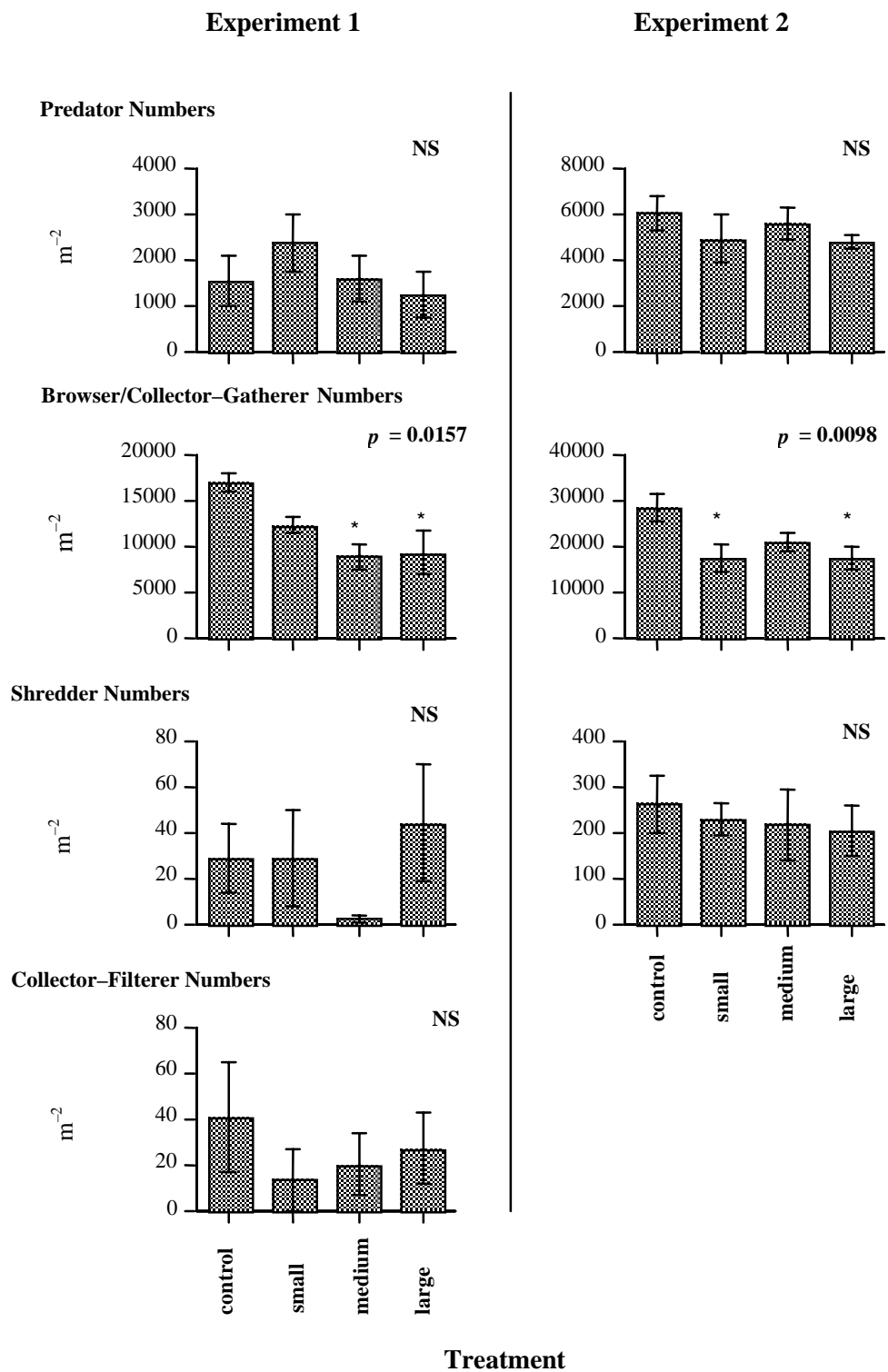
Figure 10. Total invertebrate biomass and numbers in each treatment. Results of 2 way ANOVA indicated for treatment: NS = not significant at $\alpha = 0.05$, significant results represented by p value. Significant treatment effects (Bonferroni *post hoc* test) against the control shown as: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.005$. Error bars represent ± 1 SE.



Control-Large $p = 0.0480$, Experiment 2; Control-Small $p = 0.0189$, Control-Large $p = 0.0194$).

ANOVAs were conducted *a posteriori* on the major numerical components of the browser/collector-gatherer group. Numerically the browser/collector-gatherer group was dominated by a single chironomid taxon, which appeared to control the general pattern (Bonferroni *post-hoc* test, Experiment 1, Orthocladiinae; Control-Small $p = 0.0374$, Control-Medium $p = 0.0266$, Control-Large $p = 0.0273$; Experiment 2, Chironominae; Control-Small $p = 0.0417$, Control-Large $p = 0.0429$) (Figure 12). Although oligochaetes contributed substantially to BCG numbers, they showed no differences due to treatment in either experiment ($p = 0.05$) (Figure 12). In Experiment 2 a large numerical component of the browser/collector-gatherer functional feeding group was made up of ostracods and cyclopoid copepods. Ostracods to a lesser extent reflected the generalised pattern (Bonferroni *post-hoc* test Control-Small $p = 0.0046$) (Figure 12), but cyclopoid copepods showed no pattern ($p > 0.05$). *Deleatidium* numbers followed an inverse pattern in Experiment 2, by being more prevalent in non control treatments than in controls (Bonferroni *post-hoc* test, Experiment 2; Control-Small $p = 0.0060$, Control-Medium $p = 0.0029$) (Figure 12).

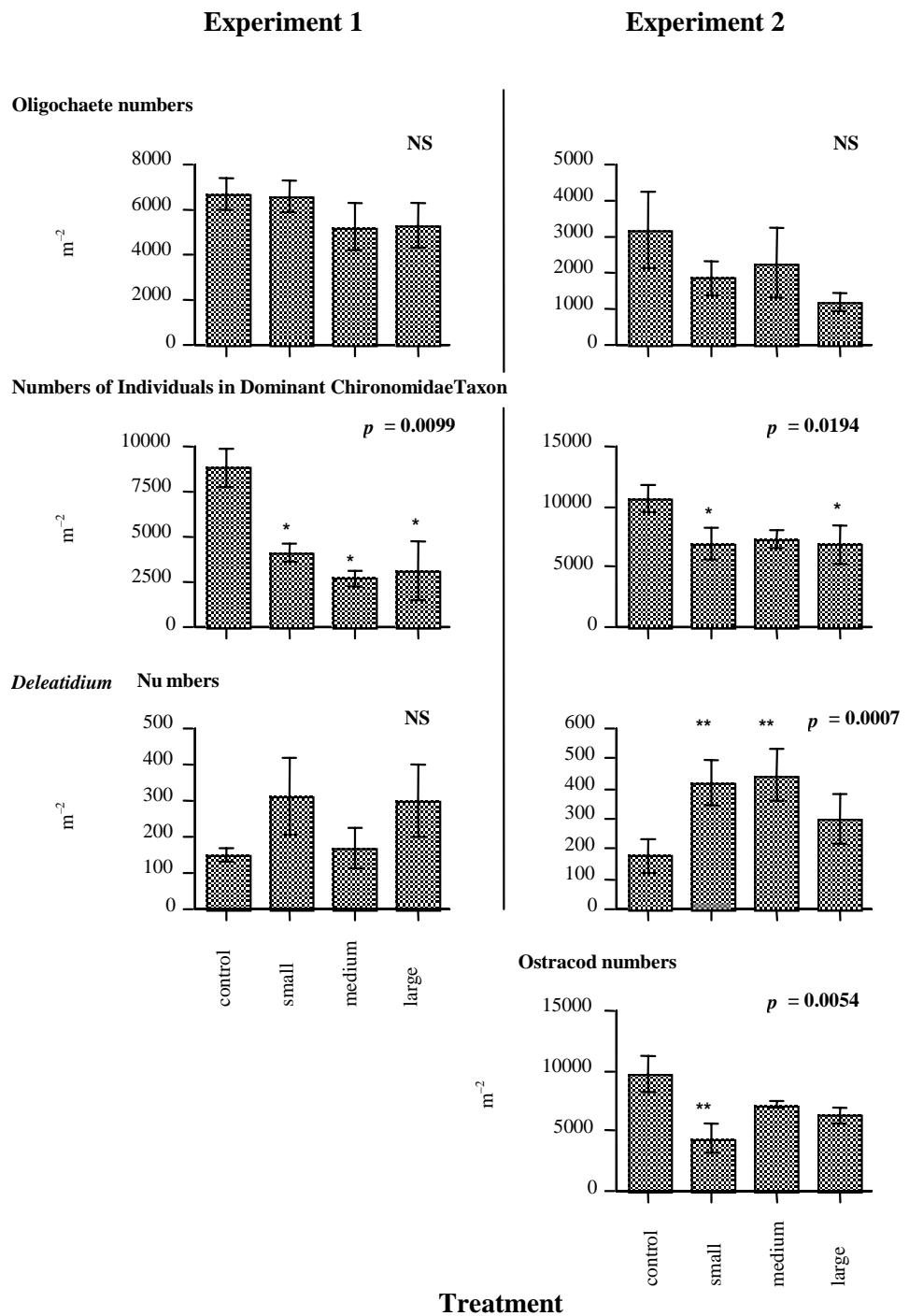
Figure 11. Numbers of each functional feeding group in each treatment. Results of 2 way ANOVA indicated for treatment: NS = not significant at $\alpha = 0.05$, significant results represented by p value. Significant treatment effects (Bonferroni *post hoc* test) against the control as: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.005$. Error bars represent ± 1 SE.



CPOM

In Experiment 1 and Experiment 2 the total amount of CPOM was not influenced by treatment ($p > 0.05$). The only CPOM component to be affected was the 0.25 mm²-0.5 mm² size class in Experiment 2, which was more plentiful in Medium treatments than Small treatments (Bonferroni *post hoc* test, $p = 0.0457$).

Figure 12. Major components of browser/collector-gatherer numbers in each treatment. Results of 2 way ANOVA indicated for treatment: NS = not significant at $\alpha = 0.05$, significant results represented by p value. Significant treatment effects (Bonferroni *post hoc* test) against the control shown as: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.005$. Error bars represent ± 1 SE.



3.2.6 Discussion

Although little is known regarding the general importance of bioturbation in streams, some studies have shown that organisms can be important in both sediment removal and stabilisation. Reductions in sediment cover have been observed as a result of fish (Power 1990; Flecker 1992) and atyid shrimp activity (Pringle et al. 1993; Pringle & Blake 1994); while accrual of, and stabilisation of sediment has been caused by retreat-building activities of benthic insects such as Chironomidae (Nilsen & Larimore 1973).

The results of this study show that *Paranephrops zealandicus* can influence stream environments through bioturbation. There are two mechanisms by which koura can accomplish this:

- Indirectly, by disturbance of the sediments as a result of body movements.
- Directly, by the removal of sediments via feeding (ingestion and egestion, or rejection) and burrow construction (ejection).

Sedimentation may have been exaggerated by the physical structure of the enclosures used for these experiments. Peckarsky and Penton (1990) found that reduced flow rates caused enclosures to function as detritus sinks and accumulate significantly more coarse detritus and fine sediments than surrounding substrata. Additionally, since the mesh size of the enclosures (4 mm²) restricted larger particles from saltating over enclosure substrata the possible scouring effect caused by the movement of these particles on the sediment was removed. Such conditions may well have exaggerated the importance of koura bioturbation. Furthermore, if enclosures were acting as coarse detritus sinks this interference may have masked the effects of leaf litter shredding by koura.

One of the disadvantages of enclosure/exclosure experiments is that in the event of a significant outcome, it is often hard to determine the mechanism responsible. It becomes even more difficult when the manipulated organism is an omnivore. We were not able to predict *a priori* the manner in which the stream community might be affected, nor whether the primary effect of koura would be via bioturbation, competition, predation, or by invoking behavioural changes in prey taxa.

Although the visual effect of bioturbation was striking, the actual impact of koura on the stream community was equivocal. The only effect common to both experiments was a decline in the number of browser/collector-gathers, in koura enclosures. This pattern was primarily caused by Orthocladinae and Chironominae abundance. In both experiments, these chironomids were far more abundant in control treatments than non-controls. However, the ephemeropteran *Deleatidium* showed the inverse of this pattern, being more common in treatments than controls.

It is not unexpected that the patterns in *Deleatidium* abundance appear to be related to the magnitude of bioturbation. In the studies of Ryder (1989) and Quinn et al. (1992) *Deleatidium* showed a consistent pattern of decline in density in relation to increasing sedimentation. Furthermore, *Deleatidium* has been shown to have a preference for unsilted substrata, and an inability to reject silt when feeding (Ryder 1989). However, Ryder (1989) also found that the abundance of chironomids in streams was also negatively related to silt. The decrease in the number of the chironomids in treatments with lower silt cover, shown in our experiments is contrary to the expectations of Ryder. Two possible explanations for this disparity are that koura inhibit chironomid abundance by disturbance (bioturbation) or active predation. Both of these factors would be of a greater magnitude to the chironomids, which are relatively sessile, than to the highly mobile *Deleatidium*. Corroborating evidence for the disturbance hypothesis comes from Harvey & Hill (1991) who found that snails reduced the accumulation of silt and the numbers of herbivorous invertebrates in enclosures, Harvey & Hill (1991) suggested that

snails reduced invertebrate numbers indirectly by bulldozing smaller taxa with low mobility, especially chironomids. Interestingly, Nilsen & Larimore (1973) found that chironomids may actually facilitate sedimentation, since the silken tubes of some taxa accumulate fine sediments.

The effects of *P. zealandicus* in these experiments closely parallel the community effects of other decapods inhabiting headwater streams. Pringle et al. (1993) found atyid shrimp foraging activities influenced benthic insect assemblages both directly and indirectly. Sessile invertebrates such as retreat-dwelling chironomid larvae were negatively affected by the constant foraging of atyid shrimp by direct removal and/or indirectly through depression of sediment resources. Conversely the abundance of the mobile grazer *Cloeodes maculipes* (Ephemeroptera: Baetidae) appeared to be facilitated by sediment removal by atyid shrimps. Similarly, Reed & Creed (1996) found that the crayfish *Cambarus bartoni* affected the size structure of chironomids (the dominant taxon) and leaf pack size. In all cases the decapods in these studies represent units of biomass many times greater than those of the benthic consumers.

Although control versus treatment differences were often marked in this study, differences between koura treatments were generally not supported. Consequently, the functional effects of an ontogenetic shift in niche appears to be obscure. Alternatively, trophic effects of ontogenetic shifts in diet or behaviour may have been masked by the magnitude of bioturbation.

Like other decapod species, the impact of *P. zealandicus* on the headwater community would appear to be a result of their physical effects as a consequence of their high community biomass, rather than energetic or trophic effects. The striking similarity between these findings and those of Pringle et al. (1993) suggest that bioturbation may be the main factor by which large benthic decapods influence their environment in headwater streams.

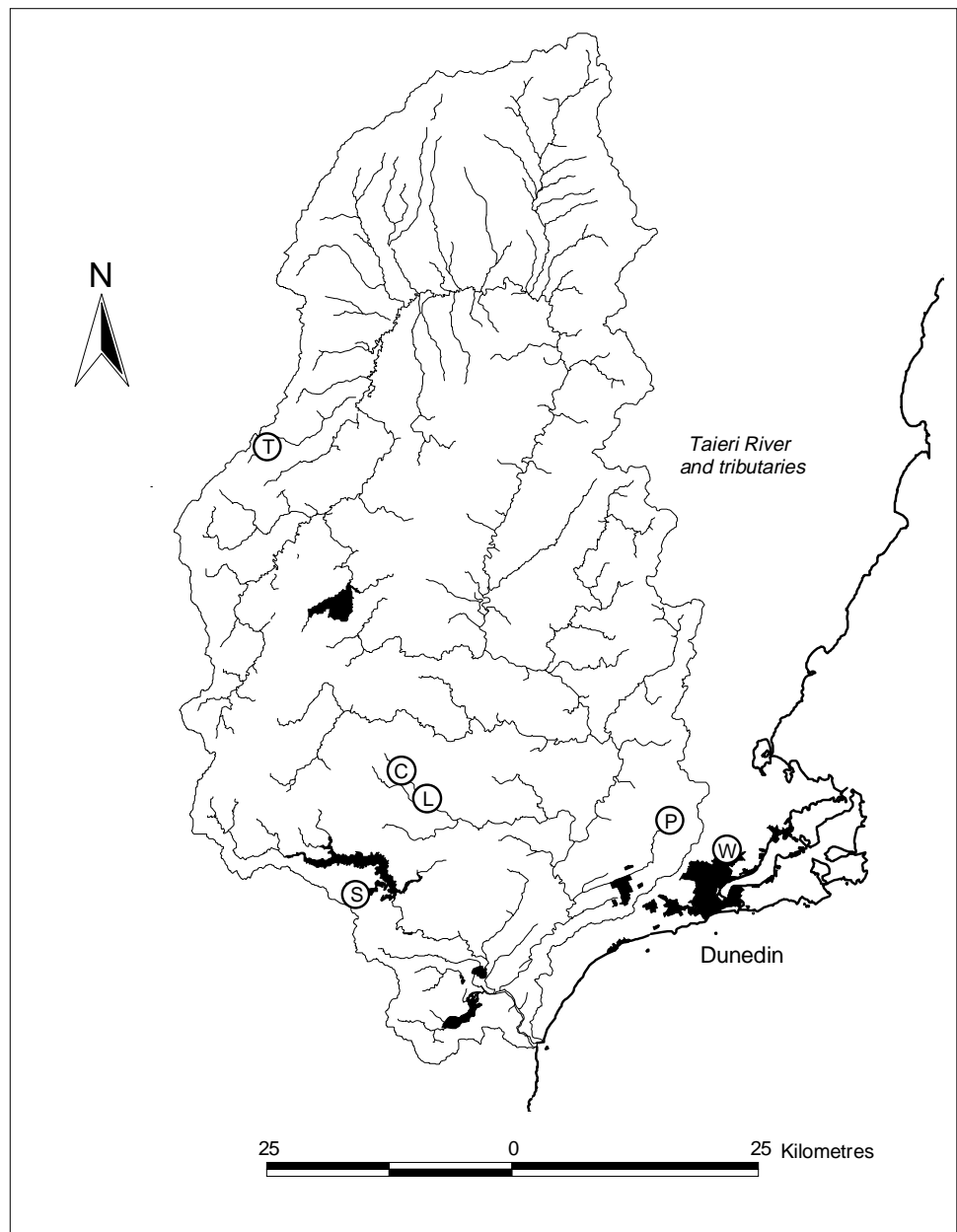
3.3 PREDATORY CAPABILITIES

3.3.1 Method of stomach content analysis

Koura were captured from six headwater streams in Otago, during 1993 and 1994, using a combination of electrofishing, net and hand capture techniques (Figure 13). Koura undergoing ecdysis were returned to the stream. Specimens were transported alive to the laboratory and then frozen. Specimens were later thawed, sexed and measured (CL). The pyloric and cardiac stomachs (proventriculus) were then dissected and the proventriculus was opened and flushed with water into a Petri dish. The stomach content was rinsed through a 250 µm sieve, backwashed and then preserved in 100% alcohol. The preserved stomach contents were examined under 10–40× binocular microscope. The articles in the stomach contents were grouped into eleven food categories (Table 4).

Aquatic invertebrates were identified to the following resolution: genus (Ephemeroptera, Plecoptera, Trichoptera, Megaloptera, Lepidoptera, Decapoda, Tubellaria), subfamily or family (Diptera, Coleoptera), order (Crustacea

Figure 13. Location map of crayfish sample sites in Otago.



| KEY: | STREAM | COLLECTION DATES | NO. OF SPECIMENS |
|------|------------------|---|---|
| C = | Canton Creek | 4.8.1994 6.5.1994 | (n = 6) (n = 26) |
| L = | Lee Stream | 24.8.1994 | (n = 6) |
| P = | Powder Creek | 18.11.1993 17.2.1994 15.3.1994 11.8.1994 | (n = 10) (n = 27) (n = 10) (n = 5) |
| S = | Shepherds Stream | 29.3.1994 4.8.1994 2.12.1994 | (n = 6) (n = 1) (n = 4) |
| T = | Totara Creek | 12.2.1994 30.5.1994 | (n = 16) (n = 20) |
| W = | Waters of Leith | 15 & 18.1.1994 11.7.1994 | (n = 20) (n = 3) |

TABLE 4. COMPONENTS OF CRAYFISH DIET.

| FOOD CATEGORY |
|--|
| 1. Aquatic invertebrates (whole or in part) |
| 2. Aquatic invertebrate exoskeletons (shed) |
| 3. Crayfish exoskeleton with tissue attached |
| 4. Crayfish exoskeleton |
| 5. Terrestrial invertebrates |
| 6. Terrestrial invertebrate exoskeleton |
| 7. Unidentifiable animal tissue (heavily masticated) |
| 8. Vascular plant (leaf fragments) |
| 9. Moss |
| 10. Terrestrial fungi and lichen |
| 11. Amorphous particulate matter |

other than Decapoda), class (Acari). Terrestrial invertebrates were identified to class. Single appendages of invertebrates in the absence of the body were considered as exoskeleton. Whole invertebrates with body lengths (BL) >2 mm were measured to the nearest 0.5 mm, while those with a BL <2 mm were estimated to the nearest 0.1 mm. Body lengths of invertebrates with at least 50% of their body remaining intact were estimated on the basis of probable total length. To determine whether prey size was related to the body size of koura, invertebrate body lengths were compared to CL by a least squares regression.

The proportional abundance of food in each category was estimated using a 100 point counting cell (1 mm² grid) and converted to a percentage of gut contents. ANOVA was used to assess whether ontogenetic changes occurred in koura diet. The proportional abundance of vascular plant fragments, animal tissue (excluding exoskeletons), and all other remains in the koura gut were considered dependent variables. Data from all sites and samples were pooled and separated into three koura size classes: small (<30 mm CL), medium (30–39.9 mm CL), and large (>40 mm CL). These size classes **represented** the factors in the ANOVA. An arcsine transformation was used to normalise the data (Sokal & Rohlf 1981).

3.3.2 Results

Of the 154 koura collected, 152 had some food items present in the stomach. Vascular plant material was the most ubiquitous item. Invertebrate exoskeletons, moss and unidentified animal tissue were also common. A wide range of aquatic invertebrates were consumed by koura (Table 5). Only 5 taxa, however, were represented by more than one specimen in a individual koura gut (Table 5). While koura exoskeletons were quite prevalent, there was only 1 definite case of cannibalism. In this case, 18 stage II, juvenile koura were removed from the stomach of a 68.4 mm CL male koura.

The maximum number of aquatic taxa found in any single koura gut was four. *Deleatidium* and *Aoteapsyche* made up 54% of the aquatic invertebrates found in koura guts. Aquatic invertebrate prey length increased positively with the size of the koura, but was not directly proportional to koura carapace length. Earthworms were the dominant terrestrial invertebrates found in the koura gut, and were the longest animals consumed by koura.

In terms of particle abundance, vascular plant material was the most common item found in koura stomachs. The stomachs of small koura <30 mm CL (n = 49) contained a lower percentage plant material than those of large koura >40 mm CL (n = 51) (Bonferroni *post hoc* test Small-Large $p = 0.0299$) but not a greater percentage of animal tissue ($p > 0.05$) (Figure 14). Medium sized koura 30-40 mm CL (n = 52) were no different from small or large koura in either respect ($p > 0.05$).

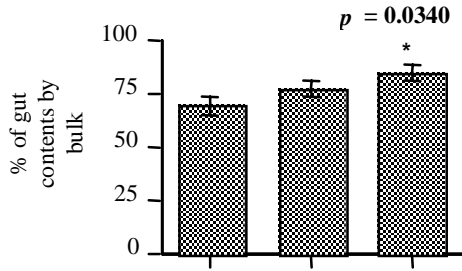
TABLE 5. DISTRIBUTION OF AQUATIC INVERTEBRATES CONSUMED BY CRAYFISH.

| CLASS | ORDER | FAMILY | TAXON | LOCA-TION* | MAX. NO. IN GUT | TOTAL NO. IN ALL GUTS |
|-----------------------|---------------|-------------------------|-----------------------|---------------|-----------------|-----------------------|
| Acari (Phylum) | | | Acari | 2, 3 | R | - |
| Crustacea | Amphipoda | | Amphipoda | 1 | 1 | 1 |
| | Decapoda | Parastacidae | <i>Paranepbrops</i> | 1 | 18 | 18 |
| | Ostracoda | | Ostracoda | 1 | 1 | 2 |
| Insecta | Coleoptera | Scirtidae | Scirtidae | 2 | 2 | 2 |
| | | Diptera | Chironomidae | Chironominae | 3 | 1 |
| | | Chironomidae | Diamesinae | 3 | 1 | 1 |
| | | Chironomidae | Orthoclaadiinae | 4 | 4 | 5 |
| | | Chironomidae | Tanypodinae | 2 | 1 | 1 |
| | | Empididae | Empididae | 1 | 1 | 1 |
| | | Simuliidae | <i>Austrosimulium</i> | 2, 5 | 1 | 1 |
| | | Tipulidae | Eriopterini | 1 | 1 | 1 |
| | Ephemeroptera | Leptophlebiidae | <i>Austroclima</i> | 4 | R | - |
| | | Leptophlebiidae | <i>Deleatidium</i> | 1, 3, 4, 5, 6 | 3 | 22 |
| | | Oligoneuriidae | <i>Coloburiscus</i> | 6 | 1 | 1 |
| | | Siphonuridae | <i>Nesameletus</i> | 2, 3 | 1 | 2 |
| | | Siphonuridae | <i>Oniscigaster</i> | 2 | R | - |
| | Plecoptera | Austroperlidae | <i>Austroperla</i> | 2 | 1 | 1 |
| | | Eustheniidae | <i>Stenoperla</i> | 1 | 1 | 1 |
| | | Gripopterygidae | <i>Zelandobius</i> | 3, 5 | R | - |
| | | Notoneumouridae | <i>Spaniocerca</i> | 6 | 1 | 1 |
| | Trichoptera | Conoesucidae | <i>Pycnocentria</i> | 2 | 1 | 1 |
| | | Hydrobiosidae | <i>Psilochorema</i> | 1, 2, 3 | 1 | 3 |
| | | Hydropsychidae | <i>Aoteapsyche</i> | 2, 3, 6 | 13 | 21 |
| Lepidoptera | Pyalidae | <i>Nymphula</i> | 2 | 1 | 1 | |
| Megaloptera | Corydalidae | <i>Archibabaultodes</i> | 1, 2 | 1 | 2 | |
| Mollusca | Prosobranchia | Hydrobiidae | <i>Potamopyrgus</i> | 1, 2, 3, 4, 5 | 1 | 5 |
| Tubellaria (Flatworm) | Rhabdocoela | | <i>Temnocephala</i> | 1 | R | - |

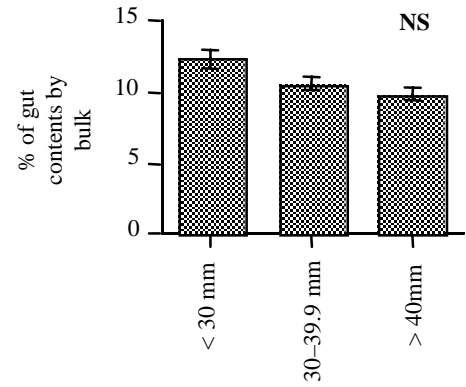
* 1 = Powder Creek, 2 = Totara Creek, 3 = Canton Creek, 4 = Water of Leith, 5 = Shepherd Stream, 6 = Lee Stream.

R = remains only (insufficient to produce a body length).

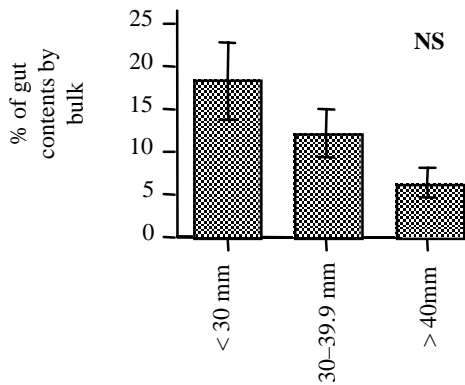
Vascular plant



Other



Animal tissue



Crayfish size class (carapace length)

Crayfish size class (carapace length)

Figure 14. The ontogenetic shift in crayfish diet. Results of one way ANOVAs are indicated; NS = non significant at $\alpha = 0.05$, significant results represented by p value. Significant treatment effects (Bonferroni *post hoc* test) against the control shown as: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.005$. Error bars represent ± 1 SE.

3.3.3 Discussion

P. zealandicus preys on a variety of aquatic invertebrates. The proportion of animal tissue in the in stomachs of stream dwelling *P. zealandicus* was comparable to that of *P. planifrons* inhabiting lakes (~10%) (Devcich 1979) *Deleatidium*, *Aoteapsyche*, chironomids and *Potamopyrgus* were the most common invertebrates found in the koura stomachs. The particularly high incidence of these taxa may be attributable to their availability. *Aoteapsyche*, chironomids and *Potamopyrgus* are sedentary, often common components of benthic stream communities. Consequently, these organisms are probably easily 'browsed' by koura. *Deleatidium*, although more mobile, is one of the most widely distributed and abundant aquatic invertebrates of New Zealand (Winterbourn et al. 1981). Its year round abundance and high standing stocks may ensure, its availability to koura. Whether koura are specifically targeting these organisms, or merely capitalising on the high of probability of encounters remains unclear. One koura that consumed 13 *Aoteapsyche*, for example, may have simply stumbled upon a 'good patch' rather than methodically targeting this species.

Deleatidium, *Aoteapsyche*, and Hydrobiosidae rank among the most commonly taken prey taxa of koaro (*Galaxias brevipinnis*), rainbow trout (*Oncorhynchus*

mykiss) (Kusabs & Swales 1991) and brown trout (*Salmo trutta*) (Sagar & Glova 1995) in New Zealand streams. Chironomidae often dominant the diet of koaro, but occur less frequently in the diet of trout (Sagar & Glova 1995). Since aquatic invertebrates total only ~10% of koura diet, the consequences of koura predation are expected to be far lower than that of the native or introduced predacious fish. *Potamopyrgus* appears to be avoided as prey by many fish species in New Zealand (Kusabs & Swales 1991; Sagar & Glova 1995), and as such may be particularly susceptible to the influence of koura predation. The predilection of some crayfish species for aquatic snails is well documented (e.g. Hanson et al. 1990; Weber & Lodge 1990; Alexander & Covich 1991). Consequently, the negative relationship between koura and *Potamopyrgus* abundance in the streams of Otago (Jansma 1995) may be the result of koura predation.

P. zealandicus is capable of consuming large aquatic invertebrates (up to 65% of CL). The upper limits of the prey length, as indicated by the size of terrestrial earthworms consumed would appear to be in excess of 140% of carapace length. Invertebrates were frequently found in the gut in a whole condition, while plant material was well masticated. Shell fragments and opercula of *Potamopyrgus* were often found in the absence of snail tissue. It possible that the greater mastication of plant and hardened animal material is a result of the larger digestive effort required for these items. These observations are very similar to that recorded by Mason (1974) for *Pacifastacus leniusculus* in a woodland stream in western Oregon, USA.

Mason (1974) found that small crayfish fed extensively on small mayfly nymphs and chironomid larvae, and many of these occurred as whole animals—some were still alive at the time of dissection. These results suggests that both *P. zealandicus* and *Pacifastacus leniusculus* employ a specific feeding action for soft bodied macroinvertebrates, whereby the prey are ingested without prior mastication. However this may not be a generalised crayfish phenomenon. Kawai et al. (1995) recorded no animal remains in the diet of *Cambaroides japonicus* dwelling in a forested stream (despite the species having been observed preying on salamanders elsewhere) and attributed this to the slow moving nature of this crayfish species.

For many crayfish species, diet has been shown to be a consequence of sex, season, and biogeography (Goddard 1988). We found that small koura consumed a lower proportion of plant fragments than large koura. This ontogenetic shift in feeding habit is consistent with that found for a number of crayfish species (Mason 1974; Holdich & Reeve 1988; France 1996). Parasitism by the cosmopolitan microsporidian *Thelobania* (causative agent for the disease 'white-tail'), also has been shown to induce changes in the prey preference in crayfish (Coste et al. 1987). Although *Thelobania* is found in coastal Otago (Quilter 1976), koura used in the gut samples were not examined for infection.

Evidence of cannibalism occurred in less than 1% of the koura stomachs examined. The only definite example of cannibalism was large male that had ingested eighteen stage II koura. This percentage is very low when compared to other crayfish species (Growth & Richardson 1988). However, when this placed in the context of the stream of occurrence (Powder Creek), cannibalism

assumes a far greater magnitude. Females carrying eggs or young in Powder Creek make up less than 4% of the female population. The loss of such a large proportion of young of the year through cannibalism would be of a major consequence to the recruitment in this stream.

Crayfish in North American studies have been recognised as having a role in the comminution of leaf litter (Huryn & Wallace 1987; Griffith et al. 1994). Even if leaf processing by *P. zealandicus* is of a lower magnitude than that expected from the frequency of leaf-litter fragments in their gut, their large standing stocks in headwater areas suggests a clear role in the breakdown of leaf litter. The presence of koura in Otago streams is positively correlated with native vegetation (Jansma 1995) and therefore areas of substantial allochthonous input (Vannote et al. 1980). Given that the shredder functional feeding group is considered to be poorly represented (Winterbourn et al. 1981), the importance of koura to stream ecosystems in New Zealand may well lie in their processing of leaf litter.

The stomach contents of *Paranephrops zealandicus* appears consistent with its designation as a opportunistic omnivore. While the magnitude of koura predation in New Zealand streams is not large in comparison with predatory fish, it may be sufficient to cause localised effects on some macroinvertebrates. Because of ontogenetic shifts in diet, the size structure of the koura population may determine the direction and magnitude of these effects. Overall, it is likely that the trophic significance of *P. zealandicus*, as predators in headwater streams, will be overshadowed by their importance as detritivores.

4. Conclusions and recommendations

1. Koura are widely distributed in the lower Taieri River catchment, while they are sporadically distributed in the upper catchment. Koura are uncommon in streams on inland plains of the Taieri regardless of position within the catchment.
2. The distribution of koura within the Taieri catchment is correlated with geological discontinuities that have been caused by events in the evolution of the drainage system. The effects of land-use variables on koura distribution are obscure. The intensity of land use in the catchment shows little relationship with koura distribution.
3. A positive relationship exists between koura presence and the existence of native vegetation within the riparian zone. This may indicate a continuous history of low disturbance to streams in which koura still exist. On the other hand, streams that still have high proportions of native vegetation in their riparian zones may have morphologies that are suitable for koura while providing poor conditions for intensive grazing near the stream channel. Only large-scale experiments will be able to untangle cause-effect relationships among confounding land-use variables.

4. It is unlikely that the koura population of Powder Creek could withstand commercial harvesting. Given the strong influence of temperature on life history characteristics of koura, and the wide range of climatic conditions found across the South Island, wild populations that are capable of supporting sustainable commercial harvests will most likely occur in drainages with thermal regimes more moderate than that shown for Powder Creek.
5. Given the potential plasticity in the growth rates of koura, if commercial harvests are to occur the maximum sustainable yield would need to be set on a site by site basis.
6. While there is direct experimental evidence (and inference from overseas studies), that koura have role in structuring freshwater communities by silt removal, the relationship with koura and silt in the wild appears to run contrary to this expectation.
7. As the composition of stream communities often varies according to land use, the role of koura may also differ between streams. The methods used in this study were limited to identifying a number of the possible mechanisms by which koura may affect a single community. As such the research contained within this study is insufficient to produce a general model for the effects of the extinction of *P. zealandicus* on stream community structure.
8. Overseas literature suggests that the main influence of decapods on the stream community is often a consequence of their modification of the environment brought about by a large population biomass. Consequently, in the absence of comprehensive studies, any conservation effort directed at koura should focus on maintaining the streams characterised by large natural populations of koura within communities of high conservation status. The corollary being that harvest should be limited to areas where the freshwater community is of little conservation value, in the expectation that the removal of koura will affect the community.
9. Within the Taieri catchment koura appears to be a superb generalist, capable of surviving in a variety of natural and modified habitats, but limited in macrodistribution by historic drainage patterns. Consequently, the amalgam of these factors may prevent any reliable method of delineating 'good' from 'bad' koura habitats within this particular catchment.
10. Further studies of harvest potential of natural of koura should be directed toward:
 - Screening sites on thermal criteria as a possible indicator of koura productivity and therefore resilience
 - Long term seasonal monitoring of koura densities at harvest sites, so that the resilience of the populations can be quantified, with the aim of constructing a harvest model with an empirical rather than theoretical base.

5. Acknowledgements

This work was undertaken as part of a Department of Conservation contract (Investigation No. 1943). The authors would like to thank the many farmers who allowed them access to streams on their properties to conduct crayfish surveys. The Dunedin City Council provided access to the Silver Stream catchment. For additional information on crayfish distribution we thank Monty Wright (Fish & Game Otago), Dr Donald Scott (University of Otago), Murray Neilson (Department of Conservation), and Jody Richardson for access to the NIWA Freshwater Fish Database.

6. References

- Abrahamsson, S.A.A. 1965: A method of marking crayfish *Astacus astacus* Linne in population studies. *Oikos* 16: 228-231.
- 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.
- Anastácio, P.M.; Marques, J.C. 1995: Population biology and production of the red swamp crayfish *Procambarus clarkii* Girard in the lower Modego River valley, Portugal. *Journal of Crustacean Biology* 15(1): 156-168.
- Arbuckle, C.J.; Huryn, A.D.; Israel, S.A. 1999: Landcover classification in the Taieri River catchment: A focus on the riparian zone. *Geocarto International* 14(3): 7-13.
- Archey, G. 1915: The fresh-water crayfish of New Zealand. *Transactions and Proceedings of the New Zealand Institute* 47: 295-315.
- Begon, M.; Harper, J.L.; Townsend, C.R. 1988: Ecology: Individuals; Populations and Communities. Blackwell Scientific Press, Oxford.
- Brewis, J.M.; Bowler, K. 1983: A study of the dynamics of a natural population of the freshwater crayfish, *Austropotamobius pallipes*. *Freshwater Biology* 13: 443-452.
- Carpenter, A. 1977: Zoogeography of the New Zealand freshwater decapoda: a review; *Tuatara* 23(1): 41-48.
- Collier, K. 1992: Assessing the natural value of New Zealand rivers. In Boone, P.J. et al. (Eds) River conservation and management. John Wiley & Sons, New York.
- Collier, K. 1993: Review of the status distribution and conservation of freshwater invertebrates in New Zealand. *New Zealand Journal of Marine and Freshwater Research* 27: 339-356.
- Coste, P.; Breton, J.C.; Chaisemartin, C. 1987: Effets de la microsporidiose des acides gras alimentaires par l'ecrevisse hôte: *Austropotamobius pallipes* Lereboullet 1858. *Annales des Sciences Naturelles Zoologie et Biologie Animale* 8(1): 11-18.
- Cukerzis, J.M. 1988: *Astacus astacus* in Europe. Pp. 309-340 in Holdich, D.M.; Lowery R. S. (Eds) Freshwater crayfish: Biology management and exploitation. Croom Helm, London.
- Devcich, A.A. 1979: An ecological study of *Paranephrops planifrons* White Decapoda: Parastacidae in Lake Rotoiti, North Island. Biological Sciences, University of Waikato, Hamilton.
- Effron, B.; Tibshirani, R.J. 1993: An introduction to the bootstrap. Pp. 436 in: Monographs on statistics and applied probability 57. Chapman Hall, New York.

- Flecker, A.S. 1992: Fish trophic guilds and the structure of a tropical stream: weak direct versus strong indirect effects. *Ecology* 73(3): 927-940.
- Flint, R.W.; Goldman, C.R. 1975: The effects of a benthic grazer on the primary productivity of the littoral zone of Lake Tahoe. *Limnology and Oceanography* 20(6): 935-944.
- Fordham, R.A.; Kelton, S.D.; Leersnyder, H.; Lo, P.L. 1979: Subalpine koura, *Paranephrops planifrons* Decapoda, in Tongariro National Park: zoogeographic implications. *New Zealand Journal of Marine and Freshwater Research* 13(3): 443-446.
- France, R. 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. Pp. 145-166 in Holdich, D.M.; Lowery, R.S. (Eds) Freshwater crayfish: Biology management and exploitation. Croom Helm, London.
- Griffith, M.B.; Perry, S.A.; Perry, W.B. 1994: Secondary production of macroinvertebrate shredders in headwater streams with different baseflow alkalinity. *Journal of the North American Benthological Society* 13(3): 345-356.
- Growns, I.O.; Richardson, A.M.M. 1988: Diet and burrowing habits of the freshwater crayfish *Parastacoides tasmanicus tasmanicus* Clark Decapoda : Parastacidae. *Australian Journal of Marine and Freshwater Research* 39: 525-534.
- Hanson, J.M.; Chambers, P.A.; Prepas, E.E. 1990: Selective foraging by the crayfish *Orconectes virilis* and its impact on macroinvertebrates. *Freshwater Biology* 24: 69-80.
- Harvey, B.C.; Hill, W.R. 1991: Effects of snails and fish on benthic invertebrate assemblages in a headwater stream *Journal of the North American Benthological Society* 10(3): 263-270.
- Holdich, D.M.; Reeve I.D. 1988: Functional morphology and anatomy. Pp. 11-52 in Holdich, D.M.; Lowery, R.S. (Eds) Freshwater crayfish: Biology management and exploitation. Croom Helm, London.
- Hopkins, C.L. 1966: Growth in the freshwater crayfish *Paranephrops planifrons* White. *New Zealand Journal of Science* 9: 50-56.
- Hopkins, C.L. 1967: Breeding in the freshwater crayfish *Paranephrops planifrons* White. *New Zealand Journal of Marine and Freshwater Research* 1: 51-58.
- Hopkins, C.L. 1970: Systematics of the New Zealand freshwater crayfish *Paranephrops* Crustacea: Decapoda: Parastacidae. *New Zealand Journal of Marine and Freshwater Research* 4(3): 278-291.
- Horwitz, P. 1990: The conservation status of Australian freshwater Crustacea. Australian National Parks and Wildlife Service, Canberra.
- Hurn, A.D.; Wallace, J.B. 1987: Production and litter processing by crayfish in an Appalachian mountain stream. *Freshwater Biology* 18: 277-286.
- Jansma, F. 1995: Past and present distribution of the crayfish *Paranephrops zealandicus* in Eastern Otago New Zealand and its relationship with land use. *Wildlife Management Report number 72*. University of Otago, New Zealand.
- Jones, J.B. 1981: The growth of two species of freshwater crayfish *Paranephrops* spp. in New Zealand. *New Zealand Journal of Marine and Freshwater Research* 15(1): 15-20.
- Kawai, T.; Hamano, T.; Matsuura, S. 1995: Feeding behaviour of the Japanese crayfish *Cambaroides japonicus* Decapoda Astacoidea in a stream in Hokkaido Japan. *Fisheries Science* 61(4): 720-721.
- Kusabs, I.A.; Swales, S. 1991: Diet and food resource partitioning in koaro *Galaxius brevipinnis* Guenther and juvenile rainbow trout *Oncorhynchus mykiss* Richardson in two Taupo streams, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 15(3): 317-325.
- Kwak, T.J. 1992: Modular microcomputer software to estimate fish production parameters production rates an associated variances. *Ecology of Freshwater Fish* 1: 73-75.
- Langlois, T.H. 1935: Notes on the habit of the crayfish *Cambarus rusticus* Girard in fish ponds in Ohio. *Transactions of the American Fisheries Society* 65: 189-193.

- Lodge, D.M.; Hill, A.M. 1994: Factors governing species composition population size and productivity of cool water crayfishes. *Nordic Journal of Freshwater Research* 69: 111-136.
- Lowery, R.S. 1988: Growth, moulting and reproduction. Pp. 83-113 in Holdich, D.M.; Lowery, R.S. (Eds) *Freshwater crayfish: Biology management and exploitation*. Croom Helm, London.
- Main, M.R. 1989: Distribution and post-glacial dispersal of freshwater fishes in South Westland, New Zealand. *Journal of the Royal Society of New Zealand* 19: 161-169.
- Mason, J.C. 1974: Crayfish production in a small woodland stream. *Freshwater Crayfish* 2: 449-479.
- McDowall, R.M. 1990: *New Zealand Freshwater Fish: a Natural History Guide*. Heinemann, Auckland.
- McDowall, R.M. 1995: Understanding the absence of upland bullies from eastern Banks Peninsula. *Water & Atmosphere* 3(4): 17-19.
- McGlone, M.S. 1983: Polynesian deforestation of New Zealand: A preliminary synthesis. *Archaeology in Oceania* 18: 11-25.
- McLellan, I.D. 1979: Mountain tarn. *New Zealand's Nature Heritage* 3: 946-949.
- Merrick, J.R. 1993: *Freshwater crayfishes of New South Wales*. Linnean Society of New South Wales, Marrickville.
- Mitchell, D.J.; Smock, L.A. 1991: Distribution life history and production of crayfish in the James River Virginia. *American Midland Naturalist* 126: 353-363.
- Momot, W.T. 1967: Population dynamics and productivity of the crayfish, *Orconectes virilis* in a marl lake. *American Midland Naturalist* 78: 55-81.
- Momot, W.T. 1984: Crayfish Production: a reflection of community energetics. *Journal of Crustacean Biology* 4: 35-54.
- Momot, W.T. 1995: Redefining the role of crayfish in aquatic ecosystems. *Reviews in Fisheries Science* 3(1): 33-63.
- Momot, W. 1988: *Orconectes* in North America and elsewhere. Pp. 262-282 in Holdich, D.M.; Lowery, R.S. (Eds) *Freshwater crayfish: Biology management and exploitation*. Croom Helm, London.
- Musgrove, R.J. 1988: The diet energetics and distribution of the freshwater crayfish *Paraneoprops zealandicus* White in Lake Georgina South Island New Zealand. Department of Zoology, University of Canterbury, Christchurch.
- Nilsen, H.C.; Larimore, R.W. 1973: Establishment of invertebrate communities on log substrates in the Kaskaskia River Illinois. *Ecology* 54: 366-374.
- Otago Catchment Board 1983: *The Taieri River: A Water Resource Inventory*. Otago Catchment Board and Regional Water Board, Dunedin.
- Peckarsky, B.L.; Penton, M.A. 1990: Effects of enclosures on stream microhabitat and invertebrate community structure. *Journal of the North American Benthological Society* 9(3): 249-261.
- Power, M.E. 1990: Effects of fish in river food webs. *Science* 250: 811-814.
- Pratten, D.J. 1980: Growth in the crayfish *Austropotamobius pallipes* Crustacea: Astacidae. *Freshwater Biology* 10: 401-412.
- Pringle, C.M.; Blake, G.A. 1994: Quantitative effects of Atyid shrimp Decapoda: Atyidae on the depositional environment in a tropical stream: use of electricity for experimental exclusion. *Canadian Journal of Fisheries and Aquatic Science* 51: 1443-1450.
- Pringle, C.M.; Blake, G.A.; Covich, A.P.; Buzby, K.M; Finley, A. 1993: Effects of omnivorous shrimp in a montane tropical stream: sediment removal disturbance of sessile invertebrates and enhancement of understory algal biomass. *Oecologia* 93: 1-11.
- Quilter, C.G. 1976: Microsporidian parasite *Thebonia contejeani* Henneguy from New Zealand freshwater crayfish. *New Zealand Journal of Marine and Freshwater Research* 10(1): 225-231.

- Quilter, C.G.; Williams, B.G. 1977: Circadian activity rhythms in the crayfish *Paranebrops zealandicus* Crustacea. *Journal of Zoology* 182: 559-571.
- Quinn, J.M.; Davies-Colley, R.J.; Hickey, C.W.; Vickers, M.L.; Ryan, P.A. 1992: Effects of clay discharge on streams. *Hydrobiologica* 248: 235-247.
- Reed, J.; Creed, R. 1996: The effect of the crayfish *Cambarus bartoni* on a headwater stream community. *Bulletin of the North American Benthological Society* 13(1): 222-223.
- Roell, M.J.; Orth, D.J. 1992: Production of three crayfish populations in the New River of West Virginia USA. *Hydrobiologia* 228: 185-194.
- Ryder, G.I. 1989: Experimental studies on the effects of fine sediments on lotic invertebrates. Department of Zoology, University of Otago, Dunedin. 216 p.
- Sagar, P.M.; Glova, G.J. 1995: Prey availability and diet of juvenile brown trout *Salmo trutta* in relation to riparian willows *Salix* spp. in three New Zealand streams. *New Zealand Journal of Marine and Freshwater Research* 29(4): 527-537.
- Shave, C.R.; Townsend, C.R.; Crowl, T.A. 1994: Anti-predator behaviours of a freshwater crayfish *Paranebrops zealandicus* to a native and introduced predator *New Zealand Journal of Ecology* 18(1): 1-10.
- Sokal, R.R.; Rohlf, F.J. 1981: Biometry: the principles and practice of statistics in biological research. W. H. Freeman and Company, New York.
- Thompson, G.M. 1922: The naturalisation of animals and plants in New Zealand. Cambridge University Press, London.
- Vannote, R.L.; Minshall, G.W.; Cummins, K.W.; Sedell, J.R.; Cushing, C.E. 1980: The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37: 130-137.
- Velleman, P.F. 1992: DataDesk4: Statistics guide. Data Description Inc., Ithaca, N.Y.
- Waters, T.F. 1969: Sub-sampler for dividing large samples of stream invertebrate drift. *Limnology and Oceanography* 14: 813-815.
- Weber, L.M.; Lodge, D.M. 1990: Periphytic food and predatory crayfish: relative roles in determining snail distribution. *Oecologia* 82: 33-39.
- Wells, S.M.; Pyle, R.M.; Collins, N.M. 1983: The IUCN invertebrate red data book. IUCN, Gland, Switzerland.
- Winterbourn, M.J. 1973: A guide to the freshwater Mollusca of New Zealand. *Tuatara* 20(3): 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.
- Winterbourn, M.J.; Rounick, J.S.; Cowie, B. 1981: Are New Zealand stream ecosystems really different? *New Zealand Journal of Marine and Freshwater Research* 15: 321-328.