

Land use, associated eel production, and abundance of fish and crayfish in streams in Waikato, New Zealand

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Abstract The density and biomass of fish and crayfish, and the production of eels, was compared among streams in native forest, exotic forest, and pasture. Populations were estimated by multiple-pass electroshocking at 11 sites in hill-country streams in the Waikato region, North Island. Three sites were in native forest, four in exotic forest, and four in pasture. Length of stream sampled at each site was 46–94 m (41–246 m² in area), and catchment areas up stream of the sites ranged from 0.44 to 2.01 km².

A total of 487 fish were caught. The species were longfinned and shortfinned eels, banded kokopu, Cran's and redfinned bullies, and common smelt. Eels were the most abundant fish in all three land-use types, and shortfinned eels were more abundant at pastoral sites (mean density 1.11 fish m⁻²) than longfinned eels (mean density 0.129 fish m⁻²). Banded kokopu were present only at forested sites. Mean fish densities were greater at pastoral sites (1.55 fish m⁻²) than under either native forest (0.130 fish m⁻²) or exotic forest (0.229 fish m⁻²). Mean fish biomass was also greater at pastoral sites (89.7 g m⁻²) than under native forest (12.8 g m⁻²) or exotic forest (19.3 g m⁻²). Longfinned eels made a greater contribution to the fish biomass at all sites than did shortfinned eels. Densities of crayfish were high (0.46–5.40 crayfish m⁻²), but were not significantly different between land-use types.

Crayfish biomass ranged from 1.79 to 11.2 g m⁻². Total eel production was greater at pastoral sites (mean 17.9 g m⁻² year⁻¹) than at forest sites (mean 2.39 g m⁻² year⁻¹).

Keywords eels; bullies; common smelt; density; biomass; land use; native forest; exotic forest; pasture; streams; production

INTRODUCTION

Catchment vegetation, especially streamside or riparian vegetation, has been implicated as a major factor controlling fish populations in streams through its influence on light availability, water temperature, and channel stability (Hicks et al. 1991). In the ecology of New Zealand's freshwaters, a long-held belief has been that widespread habitat modification caused by a land-use change from forest to pasture has been detrimental to fish communities. Land-use change has been held at least partly responsible for reduced viability and species diversity of indigenous freshwater fish populations, especially in the instances of the extinction of the southern grayling (*Prototroctes oxyrhynchus*) and the apparent decline in galaxiid whitebait abundance (McDowall 1990).

Density, biomass, size of animals, growth rates, and annual production are important variables with which to compare the effects of land uses. Though estimates of these variables have been made previously in New Zealand streams (e.g., Allen 1951; Burnet 1952; Hopkins 1971; Chisnall & Hicks 1993), rarely have all five variables been related to land use at one suite of study sites.

Land use has implications for the estimation of production rates and fishery management, especially for eels, the most commercially important of New Zealand's freshwater fish. As sustainability of eel fishing is a current issue, evaluation of the impact of land-use changes on eel productivity in streams is particularly important. The predominant land use in the Waikato region is pastoral farming,

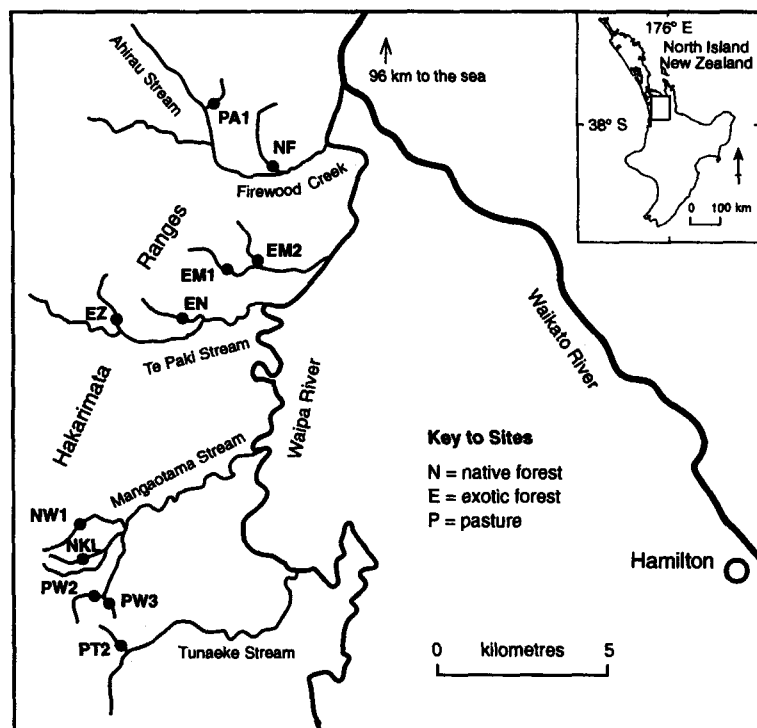


Fig. 1 Location of the study sites in the Hakarimata Ranges, Waikato region, North Island, New Zealand.

though some areas of hill country have exotic or native forests. Growth and production estimates have often been obtained from seasonal sampling (e.g., Hopkins 1971), usually involving repeated electroshocking. Instead of repeated sampling, this study used a single intensive sampling at each study site to determine fish density, biomass, and growth rates. The aim of this project was to investigate the influence of native forest, exotic forest, and pastoral land uses on fish and crayfish populations in streams as part of the wider study of land use by the National Institute of Water and Atmospheric Research (NIWA).

STUDY SITES

Eleven study sites were chosen on streams draining the Hakarimata Ranges that reflected the three land uses in the Waikato region ($37^{\circ}39' - 37^{\circ}50'S$, $175^{\circ}02' - 175^{\circ}08'E$; Fig. 1). Three sites were in native forest, four in exotic forest, and four in pasture. The land-use type is designated in Table 1 by the beginning letter of each site name: N for

native forest, E for exotic forest, or P for pasture. The forested sites had a dense riparian vegetation of trees and shrubs, whereas the riparian zones of the pastoral sites were dominated by pasture grasses, with very few trees or shrubs (Quinn et al. 1997). Catchment areas ranged from 0.44 to 2.01 km², and channel gradients ranged from 0.008 to 0.057 m m⁻¹ (Table 1). Mean depth ranged from 0.073 to 0.125 m, and mean water surface width ranged from 0.64 to 2.62 m. Discharge ranged from 7.0 to 31.6 litres s⁻¹ in November, when stream widths were measured (Table 1). Substrates were predominantly gravels and cobbles, though silt and clay were also common at exotic forest and pasture sites.

Most sites were up stream of cascades and small waterfalls ranging from 1 to 3 m in height (sites NW1, PA1, PW2, and PW3). There was a 4-m waterfall just down stream of the study reach at site NF, and a 10-m waterfall c. 200 m down stream of site NKL. Because of the small size of streams at the study sites, and their limited accessibility, the eel populations were unexploited.

Table 1 Physical characteristics of study sites in native forest, exotic forest, and pasture streams in the Waikato region, North Island, New Zealand, including dates of fish sampling, and map references from sheet S14, NZMS 260 (Department of Lands and Survey 1979).

Site	Catchment area (km ²)	Length fished (m)	Elevation (m)	Mean depth (m)	Mean water width (m)	Surface area (m ²)	Channel gradient (m m ⁻¹)	Discharge (litres s ⁻¹)	Map reference	Date sampled
Native forest										
NF	2.01	94	36	0.125	2.62	246	0.008	31.6	26974 63888	11 Jan 1993
NKL	0.53	85	112	0.073	1.54	130	0.039	10.0	26919 63775	28 Jan 1993
NW1	0.98	67	97	0.108	1.74	116	0.019	11.0	26917 63785	4 Feb 1993
Exotic forest										
EM1	0.88	72	50	0.081	1.35	97	0.012	11.0	26961 63859	29 Jan 1993
EM2	1.31	84	37	0.129	1.21	101	0.018	17.0	26967 63861	18 Jan 1993
EN	0.69	73	54	0.074	1.47	107	0.021	8.0	26946 63845	3 Feb 1993
EZ	0.96	58	95	0.112	1.48	85	0.020	12.0	26928 63845	13 Jan 1994
Pasture										
PA1	0.44	64	55	0.095	0.64	41	0.057	11.0	26954 63906	13 Jan 1993
PT2	0.76	46	62	0.094	1.31	60	0.021	8.0	26928 63747	25 Jan 1993
PW2	0.95	75	97	0.104	1.11	83	0.032	16.0	26923 63764	22 Jan 1993
PW3	0.49	71	98	0.088	0.82	58	0.035	7.0	26924 63763	20 Jan 1993
Kruskal-Wallis P	0.227	0.273	0.310	0.931	0.016	0.012	0.107	0.569		

METHODS

Fish and crayfish populations

Fish and crayfish populations were estimated at each site by multiple-pass electroshocking in January and February 1993, except for EZ, which was sampled in January 1994 (Table 1). Reaches fished ranged from 46 to 94 m in length (41–246 m² in area). Each reach was blocked with a 5-mm mesh net at its up-stream and down-stream ends, and then fished using the removal method (White et al. 1982) in an up-stream direction, using a 90 W backpack electroshocker powered by 12 V battery. Fish from each pass were identified to species, counted, weighed, and their total lengths were measured.

Number of fish and crayfish at each site, the variance of each estimate, and the capture probability (\hat{p}) was calculated from two-pass removal estimates (White et al. 1982; Armour et al. 1983). Generally, \hat{p} estimated from two passes was ≥ 0.6 , but site PT2 was fished 3 times because the \hat{p} for smelt and bullies was $<< 0.6$. For the three-pass estimates, number of fish and crayfish and variance estimates were calculated using the methods of Zippin (1958; in Armour et al. 1983). Where the population estimate failed because no reduction in numbers occurred between successive passes, the sum of the fish or crayfish caught was used as the estimate. This occurred in only 4 out of 51 estimates. Biomass was calculated from the density multiplied by the arithmetic mean of the untransformed weights for each species at each site.

Total length of fish was measured to the nearest millimetre. For crayfish, the width of the first tail segment behind the cephalothorax was measured with Vernier-scale callipers. Fish and crayfish were wet-weighted on electronic balances that were accurate to 0.01 g for animals < 250 g, and to 0.1 g for animals ≥ 250 g. Crayfish that had shed chelipeds or legs as a result of capture or during handling were omitted from the regression calculations.

Eel growth and production

To calculate growth rates of eels, otoliths embedded in epoxy resin were first sectioned vertically through the nucleus along the longest axis with a double-bladed saw, then mounted on glass slides, and ground to thin sections. These sections were examined for seasonal annuli

along the longest axis from the nucleus (McCaughan 1995).

In back-calculating length at age, the relationship between length and otolith radius was first established (McCaughan 1995). Curvilinear relationships between total fish length, L , the longest radius on the otolith, R , of the form:

$$R = u L^v \quad (1)$$

were calculated for each eel species. For longfinned eels:

$$R = 0.0104 L^{0.789}$$

($r^2 = 0.934$, $P < 0.001$, N otoliths = 87, N eels = 79), and for shortfinned eels:

$$R = 0.00541 L^{0.908}$$

($r^2 = 0.957$, $P < 0.001$, N otoliths = 47, N eels = 38). Curvilinear relationships fitted the data better than linear relationships, and overcame the problem of positive otolith radius at fish length 0 mm that resulted from linear relationships.

Body length at previous ages was back-calculated using the equation:

$$L_i = L_c (S_i / S_c)^v \quad (2)$$

where L_i = total length of the eel in mm at the i th annulus, L_c = total length of the eel in mm at capture, S_i = length of the longest radius in mm from the otolith nucleus to the i th annulus, S_c = length of the longest radius in mm from the nucleus at the time of capture, and v = the exponent for each species from Equation 1 above (Francis 1990).

For eels, average growth in weight was estimated from the annual growth in length in each land-use type. As growth in weight depended on the initial size, production depended on the size-frequency distribution of eels at each site, and therefore instantaneous weight gains were calculated for each eel caught by electroshocking. Assuming a weight-length relationship of the form

$$W = e^a L^b \quad (3)$$

where W is weight in g and L is total length in mm:

$$\frac{dW}{dL} = b e^a L^{b-1} \text{ g mm}^{-1} \quad (4)$$

Rearranging Equation 3:

$$L = (W e^{-a})^{\frac{1}{b}} \quad (5)$$

Substituting Equation 5 into Equation 4:

$$\frac{dW}{dL} = b e^a (W e^{-a})^{\frac{b-1}{b}} \text{ g mm}^{-1} \quad (6)$$

To estimate the weight gain for individual eels, Equation 6 was parameterised with the constants a

and b for each species (Table 4), dW/dL was determined for each eel by inserting its weight in Equation 6, and dW/dL was then multiplied by the average length increase in mm year⁻¹ for each land-use type and eel species, to give average biomass increase in g year⁻¹. Thus, using Equation 6, $dW/dL \text{ g mm}^{-1} \times$ annual length increment in mm year⁻¹ yielded production in g year⁻¹.

To estimate production, annual weight gains of individual eels were summed for each site, and these biomass increases were then scaled. The scaling factor was total estimated biomass (mean weight times density) divided by the sum of the weight of the eels actually caught at each site. Scaled biomass increases were then divided by the site area to give production in g m⁻² year⁻¹.

Physical site attributes, fish and crayfish densities, biomasses, and eel production estimates were compared among land-use types using Kruskal-Wallis nonparametric one-way analysis of variance (ANOVA) and Tukey's multiple comparison test (Zar 1984; Wilkinson et al. 1994). Parallelism of slopes of weight-length regressions was tested using ANCOVA (Wilkinson 1994).

RESULTS

Catchment variables and stream channel morphology

Catchment areas were not different among the land-use types ($P = 0.227$; Table 1). Similarly, there was no difference in length fished at each site ($P = 0.273$), elevation ($P = 0.310$), mean water depth ($P = 0.931$), channel gradient ($P = 0.107$), or discharge ($P = 0.569$). However, mean water surface width differed among land-use types ($P = 0.016$). Pastoral streams were narrower than streams in native forest ($P = 0.015$; Tukey's multiple comparison test). Area fished also differed among land-use types ($P = 0.012$), largely as a consequence of the wider streams in forest.

Efficiency and effort of electroshocking

Efficiency of fish capture, as estimated by capture probability (\hat{p}) between passes in multiple-pass electroshocking, was ≥ 0.6 at 10 out of 11 sites and homogeneous among land-use types ($P = 0.931$; Table 2). The time taken to fish each site ranged from 144 to 246 min for all passes combined, and depended on the area and habitat complexity. The fishing effort was $2.38 \pm 0.69 \text{ min m}^{-2}$ (mean \pm 95% confidence interval; $N = 11$). On average, each

second pass took $69 \pm 2\%$ ($N = 11$) of the time required for the first pass.

Density

A total of 487 fish were caught in the 1125 m² fished (mean density 0.433 fish m⁻²). The fish species caught were longfinned eel (*Anguilla dieffenbachii*, $N = 114$); shortfinned eel (*A. australis*, $N = 263$); banded kokopu (*Galaxias fasciatus*, $N = 8$); Cran's bully (*Gobiomorphus basalis*, $N = 38$); common smelt (*Retropinna retropinna*, $N = 63$); and redfinned bully (*G. huttoni*, $N = 1$). In addition, 766 crayfish (*Paranephrops planifrons*) were caught by electroshocking. From these catches, the total population estimates were made for each site. The number of species found at any one site ranged between 1 and 4, and was homogeneous across land-use types ($P = 0.610$; Table 2). Longfinned and shortfinned eels were found in all streams except NKL, where longfinned eels were the only fish species. Sites NF, NW1, and EM2 had banded kokopu in addition to the two eel species, and both EM1 and EM2 had Cran's bully. One redfinned bully was found at site EN, and site PT2 had both eel species, Cran's bully, and common smelt. Crayfish were found at all sites.

Fish abundance varied with land use. Density of all fish species combined was the same under both forest types, but was higher at pastoral sites

($P = 0.020$; Table 2; $P \leq 0.008$: Tukey multiple comparisons test). Total fish density on an areal basis was correlated with site area (Spearman correlation with density in fish m⁻²: $r_s = -0.891$, $P < 0.001$), but so was fish density in a lineal basis (fish lineal m⁻¹, $r_s = -0.718$, $P < 0.01$). Thus comparisons of density in fish m⁻² were justified.

Mean density was 0.130 fish m⁻² in native forest, 0.229 fish m⁻² in exotic forest, and 1.55 fish m⁻² at pastoral sites (Fig. 2). Densities of longfinned eels were similar in all land-use types (mean densities 0.092–0.129 fish m⁻²; $P = 0.401$; Kruskal-Wallis ANOVA), but densities of shortfinned eels were much greater at pastoral sites than at forest sites ($P = 0.032$; Table 2). Mean density of shortfinned eels was 0.022 fish m⁻² in native forest, 0.056 fish m⁻² in exotic forest, and 1.11 fish m⁻² in pastoral streams (Fig. 2).

Banded kokopu densities were 0.012 fish m⁻² (0.032 fish m⁻¹) at NF, 0.039 fish m⁻² (0.068 fish m⁻¹) at NW1, and 0.010 fish m⁻² (0.012 fish m⁻¹) at EM2. A high density of common smelt occurred at PT2 (1.063 fish m⁻²). Densities of Cran's bullies were 0.010 fish m⁻² at EM1, 0.158 fish m⁻² at EM2, and 0.473 fish m⁻² at PT2. At site EN, redfinned bully density was 0.009 fish m⁻².

The greatest range of crayfish densities occurred at native forest sites (Fig. 2; Table 2). The confidence intervals around the density estimates

Table 2 Density of fish and crayfish in streams native forest, exotic forest, and pasture in the Waikato region, New Zealand. Probability (P) for Kruskal-Wallis ANOVA is shown for the comparison of variables by land-use type.

Site	Capture probability (\hat{p})	No. of fish species	Density (number m ⁻²)			
			All fish species combined	Longfinned eels	Shortfinned eels	Crayfish
Native forest						
NF	0.8	3	0.123	0.055	0.058	0.69
NKL	0.6	1	0.125	0.125	0.000	1.67
NW1	0.9	3	0.141	0.096	0.009	5.40
Exotic forest						
EM1	0.7	3	0.249	0.165	0.083	2.80
EM2	0.8	4	0.337	0.152	0.020	0.66
EN	0.5	3	0.188	0.119	0.037	1.65
EZ	0.9	2	0.142	0.059	0.085	0.71
Pasture						
PA1	0.6	2	1.405	0.194	1.369	1.37
PT2	0.7	4	2.614	0.073	1.089	0.46
PW2	0.7	2	1.123	0.181	0.986	1.63
PW3	0.8	2	1.076	0.069	0.996	1.40
Kruskal-Wallis P	0.931	0.610	0.020	0.401	0.032	0.782

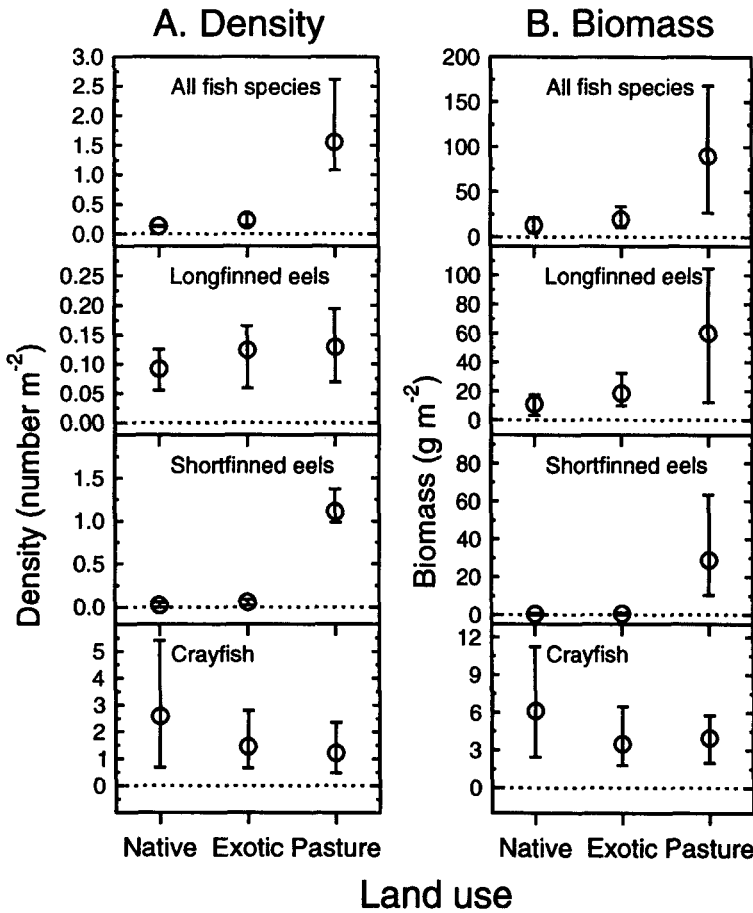


Fig. 2 Density and biomass of fish and crayfish in streams in native forest, exotic forest, and pasture, in the Waikato region. Means and ranges of estimates from removal electroshocking are shown.

were usually large, showing that the population estimates were not particularly reliable. In one instance (EZ), the number caught in the second pass exceeded that caught in the first, and thus the sum of the two passes was used to calculate density. Densities ranged from 0.46 to 5.40 crayfish m⁻², and were not different among land-use types ($P = 0.782$: Table 2).

Weight and length

Mean weight of all fish in this study was 63.0 g ($N = 487$). Mean weights of longfinned eels in each stream ranged from 56.6 to 1012 g, whereas mean weights of shortfinned eels were less at every site, ranging from 1.4 to 46.2 g (Table 3). Mean weights for both species were homogeneous among land-use types ($P = 0.101$). Crayfish ranged in mean weight from 1.96 to 4.27 g, and were similarly homogeneous across land-use types ($P = 0.556$). Mean weight of banded kokopu was 67.5 g ($N = 3$)

in NF, and 80.4 g ($N = 4$) in NW1. The single banded kokopu at EM2 weighed 26 g. The mean weight of Cran's bullies was 5.2 g ($N = 15$) at EM2, and 2.5 g ($N = 22$) at PT2, and the single Cran's bully at EM1 weighed 9.6 g. Mean weight of common smelt at PT2 was 2.6 g ($N = 63$), and the single redfinned bully at EN weighed 7.9 g.

Two size modes were apparent for longfinned eels (Fig. 3A). There was limited overlap of ages between the modes, but eels in the longer length modes were older than the shorter modes (for native forest: $P = 0.021$, $N = 11$; for exotic forest: $P = 0.001$, $N = 24$; for pasture: $P = 0.014$, $N = 12$; Kruskal-Wallis ANOVA). Size modes were not apparent for shortfinned eels (Fig. 3B). Two size modes were also apparent for crayfish, which were probably related to age classes (Fig. 3C). Cran's bullies were larger under exotic forest than at pastoral sites (Fig. 3D). Slopes of the weight-length relationships for longfinned eels were homogeneous

across land-use types ($P = 0.224$; ANCOVA), so weight-length regressions were calculated from data pooled across all sites (Table 4). However, there were too few shortfinned eels at forest sites to make valid weight comparisons with pasture sites. Weight-length regressions were also calculated for Cran's bullies and banded kokopu. For crayfish, the regression between weight and tail width was calculated, and the weight-OCL relationship was calculated from tail width using the equation $OCL = 0.5592 + 1.5534 TW$, where TW = tail width in mm, and OCL = orbit-carapace length in mm ($r^2 = 0.981$, $N = 81$; Table 4; S. Parkyn, NIWA, Hamilton unpubl. data).

Biomass

The mean weights of fish and crayfish for each site were multiplied by density to calculate biomass. Fish biomass was homogeneous across land-use types ($P = 0.051$; Table 5), despite the considerably greater mean and range at pastoral sites than forest sites (Fig. 2). At all sites, biomass was dominated by eels, which on average comprised 95% of the total fish biomass. At forest sites, longfinned eels were by far the greatest proportion of the fish biomass, but at pastoral sites shortfinned eel biomass was of the same order of magnitude as longfinned eels (Table 5). Longfinned eel biomass

was not different among land-use types ($P = 0.135$), but shortfinned eel biomass was much greater at pastoral sites (mean 28.8 g m^{-2}) than at forested sites (mean $0.403\text{--}0.502 \text{ g m}^{-2}$; $P = 0.038$; Kruskal-Wallis ANOVA).

The biomass of banded kokopu at the native forest site NW1 was 3.12 g m^{-2} , but was lower at a NF (0.82 g m^{-2}). At EM2, banded kokopu biomass was 0.26 g m^{-2} . Common smelt biomass at PT2 was 2.81 g m^{-2} . Biomass of Cran's bullies was 0.10 g m^{-2} at the exotic forest site EM1, 0.82 g m^{-2} at EM2, and 1.18 g m^{-2} at the pastoral site PT2. Redfinned bully biomass at EN was 0.07 g m^{-2} . Crayfish biomass was similar in all land-use types ($1.79\text{--}11.22 \text{ g m}^{-2}$; $P = 0.620$; Table 5).

Eel growth and production

For each land-use type, lengths at previous ages for the two eel species were back-calculated from the width of annual check rings on the otoliths, by substituting values of v determined from Equation 1 into Equation 2. Growth in length generally was close to linear up to 27 years for longfinned eels, and 14 years for shortfinned eels (Fig. 4), so a linear growth model was assumed. The small amount of data did not justify the use of a curvilinear growth model. A linear regression between back-calculated length in mm and age in years was calculated for

Table 3 Mean weights of longfinned eels, shortfinned eels, and crayfish in 11 streams in native forest, exotic forest, and pasture in the Waikato region, New Zealand. Probability (P) for Kruskal-Wallis ANOVA is shown for the comparison of variables by land-use type.

Stream	Number and mean weight					
	Longfinned eels		Shortfinned eels		Crayfish	
	<i>N</i>	Weight (g)	<i>N</i>	Weight (g)	<i>N</i>	Weight (g)
Native forest						
NF	13	56.6	13	14.8	48	3.55
NKL	13	102.7	0	—	71	2.83
NW1	11	181.2	1	40.7	96	2.08
Exotic forest						
EM1	15	195.6	6	11.3	179	2.32
EM2	15	135.5	2	1.4	38	3.66
EN	11	93.2	4	2.3	83	1.96
EZ	5	166.6	7	11.4	60	2.54
Pasture						
PA1	8	537.8	40	46.2	24	4.23
PT2	4	167.4	65	9.5	26	4.27
PW2	15	295.6	68	21.2	106	2.08
PW3	4	1012.3	57	20.6	32	3.35
Kruskal-Wallis P		0.101		0.101		0.556

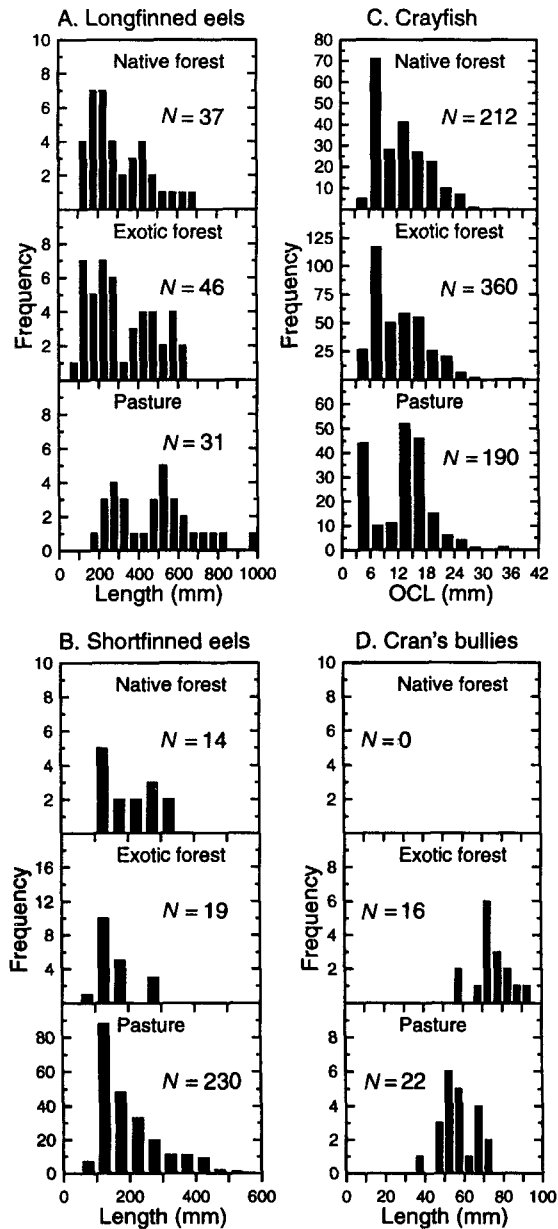


Fig. 3 Frequency distributions of: **A**, total length of longfinned eels and **B**, shortfinned eels; **C**, orbit-carapace length (OCL) of crayfish; and **D**, total length of Cran's bullies in streams in three land-use types in the Waikato region of New Zealand.

each otolith, and the means of all regression slopes in mm year^{-1} was compared among land-use types. For longfinned eels, mean annual growth in length was higher at pastoral sites than in either forest type

($P = 0.049$; Kruskal-Wallis ANOVA: Table 6). For shortfinned eels, mean annual growth in length was greater in pasture than in exotic forest ($P = 0.003$; Mann-Whitney U test). There was no difference between the growth rates of longfinned eels and shortfinned eels in either exotic forest ($P = 0.507$; Mann-Whitney U test) or in pastoral streams ($P = 0.073$; Mann-Whitney U test).

Production of eels in each land-use type was calculated using mean annual length increase from Table 6 multiplied by the instantaneous weight increase (Equation 6) for each eel at each site. The annual growth in weight for eels at a site was then summed, scaled by the site and species-specific factor, and finally divided by site area (Table 1) to estimate production in $\text{g m}^{-2} \text{ year}^{-1}$. The mean of 21 scaling factors was 1.07, and all except one were ≤ 1.23 .

Total eel production was greater at pastoral sites (mean $17.9 \text{ g m}^{-2} \text{ year}^{-1}$) than at forest sites (mean $2.39 \text{ g m}^{-2} \text{ year}^{-1}$, $P = 0.032$; Table 7). Production of longfinned eels was similar in all land-use types ($P = 0.135$; Table 7), but the greatest range was at pastoral sites. For shortfinned eels, production was similar in both forest types but was much greater at pastoral sites than at forest sites ($P = 0.038$). At pastoral sites the production by both species was about equal, but in both forest types, most of the production was contributed by longfinned eels because their biomass was greater than shortfinned eels (Table 5).

Production (P) to biomass (B) ratios for eels ranged from 0.142 to 0.322, and were greater at pastoral sites than at forest sites ($P = 0.038$; Table 7). Considering that eels formed on average 95% of the fish biomass at each site, these estimates of production and $P:B$ ratio should be close to total production.

DISCUSSION

Fish densities and land use

Pastoral streams in our study had greater total fish abundance than did streams in either forest type, caused mainly by the greater abundance of shortfinned eels at pastoral sites. Fish densities at pastoral sites were c. 5 times greater than those in exotic forest, and c. 10 times greater than those in native forest. Similar results were found in the Grey River system on the West Coast of the South Island, where the only stream to contain shortfinned eels was also the only purely pastoral stream in the study

Table 4 Relationship of weight to length for fish, and weight to orbit-carapace length (OCL) for crayfish, in 11 streams in the Waikato region, New Zealand. Model for regression: $\ln(Y)=a+b\ln(X)$; Y = wet weight in g; X = length in mm for fish, or OCL in mm for crayfish. Model P for all regressions was <0.001 .

Species	N	Constant (a)	Slope (b)	r^2	Length or OCL (mm)	
					Min.	Max.
Fish						
Shortfinned eels	261	-13.95	3.102	0.993	93	498
Longfinned eels	113	-15.12	3.353	0.996	94	987
Cran's bullies	38	-11.81	3.123	0.974	39	95
Banded kokopu	8	-12.00	3.135	0.990	95	242
Common smelt	62	-14.91	3.750	0.943	56	85
Crayfish						
Tail width	346	-5.40	2.888	0.994	1.70	23.0
OCL	346	-7.30	3.076	0.994	3.2	36.3

Table 5 Biomass of fish and crayfish in streams native forest, exotic forest, and pasture in the Waikato region, New Zealand. Probability (P) for Kruskal-Wallis ANOVA is shown for the comparison of variables by land-use type.

Site	Biomass (g m^{-2})			
	All fish species combined	Longfinned eels	Shortfinned eels	Crayfish
Native forest				
NF	4.77	3.09	0.86	2.44
NKL	12.79	12.79	0.00	4.73
NW1	20.86	17.38	0.35	11.22
Exotic forest				
EM1	33.36	32.33	0.93	6.49
EM2	21.71	20.60	0.03	2.40
EN	11.30	11.14	0.08	3.24
EZ	10.75	9.79	0.97	1.79
Pasture				
PA1	167.82	104.55	63.27	5.78
PT2	26.47	12.15	10.34	1.97
PW2	73.64	53.38	20.26	3.39
PW3	90.93	69.79	21.14	4.68
Kruskal-Wallis P	0.051	0.135	0.038	0.620

Table 6 Mean annual growth in length of eels in native forest, exotic forest, and pasture determined from slopes of back-calculated length-age regressions of individual otoliths. (CI = confidence interval.)

Species	Land-use type	N otoliths	Mean annual growth (mm year^{-1})	
			Length increase	95% CI
Longfinned eels	Native forest	11	21.1	3.7
	Exotic forest	24	20.4	2.6
	Pasture	12	25.9	5.0
Shortfinned eels	Native forest	1	19.8	—
	Exotic forest	15	20.4	3.9
	Pasture	13	29.7	2.6

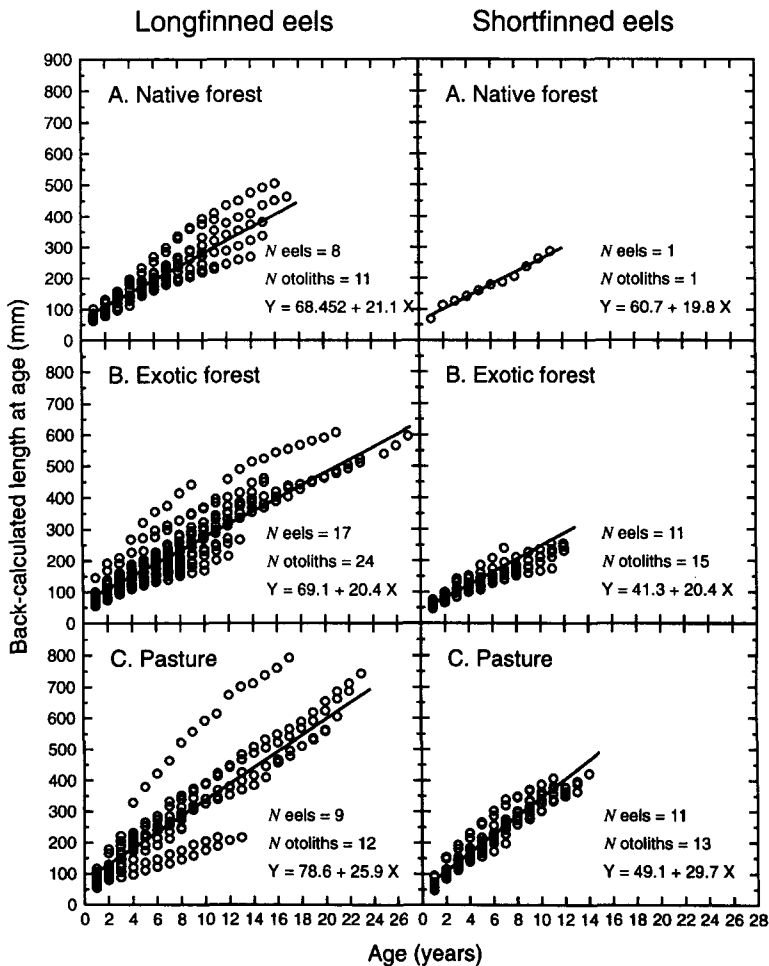


Fig. 4 Back-calculated length at age for longfinned and shortfinned eels in streams in three land-use types in the Waikato region, New Zealand. Coefficients for the linear equations are the means of the constants and slopes from regressions of length on age for each otolith.

(Jowett et al. 1996). Other differences of fish abundance caused by land use in the study of Jowett et al. could not be distinguished from the effects of significantly different stream sizes.

Fish density in a wide range of New Zealand rivers was estimated as 0.005–2.0 fish m^{-2} (Jowett & Richardson 1996). Densities in our study fell within this range, with the exception of the pasture site PT2, which had 2.61 fish m^{-2} . High densities have usually been associated with large numbers of small fish (e.g., up to 266 fish m^{-2} for the bully *Gobiomorphus breviceps* in December just after spawning in the Hinaki Stream, Wairarapa; Hopkins 1971). Globally, fish densities have been found to be inversely correlated with mean fish weight (Randall et al. 1995). Consistent with this, PT2 had the lowest mean weight of eels of both species

among pasture sites, and also had smelt and Cran's bullies, which are small fish.

Catchment sizes were much smaller in our study (0.44–2.01 km^2) than in the study of Jowett & Richardson (38–1760 km^2), but all reaches except PA1 (41 m^2) exceeded the minimum 50 m^2 they recommended for making representative density estimates. Reach areas sampled in native forest streams were larger than for pastoral streams (Table 1), largely because forest streams were wider than pastoral streams.

One obvious criticism of our study from the viewpoint of diadromous fish, which must migrate from the sea into fresh water, is the influence of distance inland and barriers to migration on structuring stream fish communities (Jowett & Richardson 1995; McDowall 1993, 1995). All fish

species found in this study except Cran's bully are diadromous (McDowall 1990). It could be argued that access from down stream controlled fish abundance more than land use, because the native forest sites NF and NKL had substantial waterfalls down stream, and NW1 had a series of 1–3 m cascades down stream. Common smelt, a diadromous fish with no climbing ability, were restricted to one site (PT2), probably by barriers to migration at all other sites. On the other hand, the remaining pastoral sites had only the two eel species. Also, total fish biomass was not different among land-use types (Table 5), and thus it seems fair to conclude that land use had more influence on overall fish density and abundance of shortfinned eels than did diadromy.

Climbing ability is an important factor controlling fish access. From the sites at which they were found in our study, banded kokopu appear to climb as well as eels. However, banded kokopu were found only at forest sites. Assuming that waterfalls and cascades alone did not limit the abundance of banded kokopu, we must look for other explanations. Banded kokopu seem to inhabit only small streams; in Westland, banded kokopu were found in four of the five streams fished with flows <20 litres s⁻¹ (Jowett et al. 1996), but not in larger streams. From the size of our pastoral streams (discharge 7–32 litres s⁻¹: Table 1), banded kokopu

should have been present, so we assume that habitat conditions in these pastoral streams were not suitable. Banded kokopu also preferred forest sites in a study of 55 stream sites ≤3 m wide in the Waikato region (Hanchet 1990). Of these sites, 26 were in native forest, 10 were in exotic forest, and 19 were in pasture. Banded kokopu occurred at 73% of the native forest sites, 30% of the exotic forest sites, but only 21% of the pasture sites. Two of Hanchet's four pasture sites with banded kokopu were down stream of native forest; such sites had lower temperatures and coarser substrates than pastoral sites well away from native forest. Our pasture sites were not down stream from native forest, but the absence of banded kokopu might have been partly attributable to the small number of sites we sampled, which was only one-fifth the number of sites in Hanchet's study.

Banded kokopu densities in our study were low (0.010–0.039 fish m⁻²; 0.012–0.068 fish m⁻¹) compared to other studies. In Ship Creek, South Westland, a density of 0.9 fish m⁻² was recorded (Taylor & Main 1987), and in tributaries of the Whanganui Inlet, northwest Nelson, a mean density of 0.61 fish m⁻² was estimated at eight sites, with a maximum density of 1.96 fish m⁻² (Eldon & Ward 1991). In the Waikato, Hanchet (1990) also found low densities of banded kokopu (generally <0.039 fish m⁻¹). At only one site did Hanchet find a higher

Table 7 Production of longfinned and shortfinned eels, and production (P) to biomass (B) ratios of both eel species together, in 11 streams in native forest, exotic forest, and pasture in the Waikato region, New Zealand. Probability (*P*) for Kruskal-Wallis ANOVA is shown for the comparison of variables by land-use type.

Stream	Production (g m ⁻² year ⁻¹)			P/B ratio
	Total	Longfinned eels	Shortfinned eels	
Native forest				
NF	0.792	0.54	0.250	0.201
NKL	2.06	2.06	0.000	0.161
NW1	2.70	2.61	0.085	0.152
Exotic forest				
EM1	4.71	4.41	0.298	0.142
EM2	2.99	2.97	0.019	0.145
EN	1.69	1.64	0.050	0.151
EZ	1.76	1.43	0.332	0.164
Pasture				
PA1	32.92	13.78	19.14	0.196
PT2	7.25	2.36	4.90	0.322
PW2	16.04	8.49	7.55	0.218
PW3	15.21	7.16	8.05	0.167
Kruskal-Wallis <i>P</i>	0.032	0.135	0.038	0.038

density (Waioteatua Stream; $0.102 \text{ fish m}^{-1}$), though this is still low by national standards.

Fish biomass

Eel biomass similar to ours ($4.8\text{--}33.4 \text{ g m}^{-2}$ in forest streams; $26.5\text{--}168 \text{ g m}^{-2}$ in pastoral streams: Table 5) have been measured previously in New Zealand. Eel biomass in other Waikato studies was $5.4\text{--}10.7 \text{ g m}^{-2}$ in native forest streams, and $12.9\text{--}51.9 \text{ g m}^{-2}$ in pastoral streams (Chisnall & Hicks 1993). In the forested Ngakoahia River, eel biomass was 6.2 g m^{-2} , and was 58 g m^{-2} in the pastoral Kaniwhaniwha Stream (Burnet 1952). However, Burnet had doubts about the proportion of the eel population that was susceptible to traps in the Ngakoahia River, so he may have underestimated eel biomass. In Canterbury streams, eel densities ranged from 13.0 to 25.4 g m^{-2} (Burnet 1969). In the Wairarapa, total fish biomass in the pastoral Hinau and Hinaki Streams were $13.5\text{--}140 \text{ g m}^{-2}$ (Hopkins 1971). In Hopkins' estimate, eels comprised $63\text{--}93\%$ of the fish biomass, compared to our average of 95% .

Total fish biomass in our streams (mean 43.1 g m^{-2} , $N=11$) was higher than estimates from streams and rivers in other countries (mean 14.6 g m^{-2} , $N=58$; Randall et al. 1995: $P=0.005$; Kruskal-Wallis ANOVA). Our pastoral stream biomasses exceeded all the estimates reported by Randall et al. except for the Amazon River, Venezuela (160 g m^{-2}). Fish biomass in our pasture site PA1 (168 g m^{-2}) exceeded the Amazon River estimate. Thus small streams in New Zealand with eels can have very high fish biomass by global standards.

The validity of using the means of untransformed weights to calculate biomass was investigated. Biomass cannot be less than the sum of the weights of fish actually caught at a site, so

this is a useful value with which to compare the validity of other biomass estimates. The sum of fish weight caught in all electroshocking passes at each site was divided by the site area. This minimum possible biomass was used as the independent variable, which was regressed on other biomass estimates. These estimates were calculated by multiplying fish density by the means of: (1) untransformed weights; (2) natural-log transformed weights; and (3) square-root transformed weights. Lastly, biomass was estimated by: (4) substituting total fish weight from each electroshocking pass into the equations for calculating removal population estimates (Armour et al. 1983).

It is clear that both natural-log and square-root transformations give invalid biomass estimates, because they seriously underestimated the minimum biomass (Table 8). The slopes of the regressions were 0.486 for the log-transformed weights, and 0.748 for the square-root transformed weights, indicating that biomass estimates were c. 50 and 25% less respectively than the biomass caught. For biomass calculated from untransformed data, the slope was 1.033 , i.e., estimated biomass was c. 3% greater than the biomass caught. An alternative method of calculating biomass, which appears to give equally reliable results, is to use the weight of fish caught in each electroshocking pass to estimate biomass by the removal method. The slope of this regression was 1.024 , which means the estimated biomass was c. 2% greater than the sum of the biomass caught. The regression constants in every instance were effectively zero.

Crayfish

Previous estimates of crayfish densities in New Zealand have ranged in February from 2.8 to $27.5 \text{ crayfish m}^{-2}$ in the Wairarapa, and 0.8 to 1.1

Table 8 Coefficients for the regressions of fish biomass calculated by four different methods. Regression equation is $Y = a + bX$, where X = sum of the biomass of fish caught in all electroshocking passes at each site, divided by the site area. Y = biomass estimated by multiplying fish density by the mean weight, except for the Removal method, in which biomass was estimated by substituting total fish weight for number of fish into equations for calculating removal population estimates. ($N=29$, and $P<0.001$ in all instances; standard errors of the coefficients are in parentheses.)

Biomass calculation method	Constant (<i>a</i>)	Slope (<i>b</i>)	r^2_{adj}
Untransformed data	0.579 (0.743)	1.033 (0.026)	0.983
Log-transformed data	0.519 (1.787)	0.486 (0.063)	0.690
Square-root transformed data	0.164 (0.571)	0.748 (0.020)	0.981
Removal method	0.523 (0.470)	1.024 (0.017)	0.993

crayfish m^{-2} on the west coast north of Wellington (Hopkins 1966). Our densities in the same season (0.66–5.40 crayfish m^{-2}) were closer to north Wellington estimates than to densities in the Wairarapa streams.

Our crayfish density estimates should be treated with caution, as site lengths were chosen to optimise fish capture rather than crayfish capture. In a comparison of sampling methods (Rabeni et al. 1997), two-pass removal-method electroshocking produced density estimates (3.86 crayfish m^{-2}) that were only 76% of density estimated in a 14-m-long reach by a combination of 5-pass removal electroshocking and mark-recapture (5.10 crayfish m^{-2}). Thus our density estimates may be c. 24% lower than actual densities. Greater effort than our mean of 2.4 min m^{-2} is required if electroshocking is to be used as the sole method for estimating crayfish abundance.

Few crayfish in our study appeared to survive past age 1, as there were only two size modes (Fig. 3C), in contrast to Hopkins' (1966) study where three size modes were apparent in February. In Wairarapa streams, mean OCL of crayfish (*Paranephrops planifrons*) was 3.5 mm on leaving the parent, 11.4–11.8 mm after 1 year, 18.2–19.3 mm after 2 years, 22.1–23.8 mm after 3 years, and 26.7–29.6 mm after 4 years (Hopkins 1967). This suggests that the two modes of OCL that we found correspond to age 0 and age 1 animals. The presumed age of our size modes should be treated with caution, as genetic differences in growth rates have been shown (Jones 1981). Also, crayfish growth is density-dependent; the densest population in Hopkins' (1966) study had the slowest growth.

Eel growth

For eels in New Zealand, the opaque annuli seen in sectioned otoliths correspond to annual checks in growth (Chisnall & Kalish 1993), and growth in length was linear for eels up to 29 years of age (Cairns 1941; Chisnall & Hayes 1991; Chisnall & Hicks 1993), so these assumptions in our study were valid. However, our length increments (20–30 mm $year^{-1}$) were much less than those estimated by Cairns, whose estimates ranged from c. 55 to 94 mm $year^{-1}$ between ages 3 and 15 years, depending on species. When eels are older than those in our study, growth in length has been shown to become curvilinear, and to reduce with age and size (Burnet 1969). Growth in Canterbury streams was very habitat-specific; in Doyleston Drain, most annual length increments ranged from c. 10 to 80 mm

$year^{-1}$, whereas in the Main Drain they were more consistently between c. 10 and 40 mm $year^{-1}$. Our mean length increment (26 mm $year^{-1}$) for longfinned eels in pastoral streams were similar to estimates given by Chisnall & Hicks (1993) for pastoral streams in the Waikato (24–36 mm $year^{-1}$). However, our estimates for longfinned eels in native and exotic forest (21 and 20 mm $year^{-1}$ respectively) are higher than Chisnall & Hicks estimated in forested streams (12–15 mm $year^{-1}$). Similarly for shortfinned eels, our estimated growth in pastoral streams (30 mm $year^{-1}$) was greater than a previous estimate of growth in pastoral Waikato streams (16 mm $year^{-1}$; Chisnall & Hayes 1991), indicating site-to-site differences within one land-use type.

Longfinned and shortfinned eels in our study had similar growth rates in the forested streams, but shortfinned eels grew faster, and reached lower ages than longfinned eels, probably reflecting the earlier age at maturity of shortfinned eels (Todd 1980). Shortfinned eels were also considerably lighter than longfinned eels for equivalent lengths, which combined with their earlier age at maturity, suggests that shortfinned eels require less somatic growth to achieve maturity than longfinned eels.

The faster eel growth seen in our pastoral streams probably resulted from the greater primary productivity in pastoral streams than in forest streams. Quinn et al. (1997) showed that gross photosynthesis, chlorophyll *a*, and epilithon biomass were greater in our pastoral streams than in our forested streams. Greater primary productivity appears to have been a response to the increased light and dissolved inorganic nitrogen that were available at the pastoral sites, and to their higher water temperatures, compared to the forested sites. Mean density and biomass of invertebrates other than crayfish had greater ranges and maxima at pastoral sites than at forested sites, but were not different between land-use types because of site-to-site variability.

Eel production

We estimated eel production from a single sample by applying growth rates for each species and land-use type to the species-specific weight-length relationships. We calculated annual weight increment for individual eels caught at each site, thus taking into account the size distribution of the population. Our eel production estimates (0.792–32.9 g $m^{-2} year^{-1}$) were lower than previous New Zealand estimates; in the Hinau and Hinaki Streams,

eel production was estimated at 10 and 59 g m⁻² year⁻¹ (Hopkins 1971). Mean eel production in our study (8.0 g m⁻² year⁻¹; $N = 11$) was also lower than global stream fish production estimates (mean 27.4 g m⁻²; $N = 55$; Randall et al. 1995: $P = 0.003$; Kruskal-Wallis ANOVA).

Our methods of calculating growth and production were quite different from Hopkins, who used repeated electroshocking to estimate changes in biomass. Because of the assumptions underlying back-calculation of length at age (e.g., Francis 1990), our methods are open to criticism. However, studies that use repeated electroshocking are equally problematic, because electroshocking can affect fish growth rates (e.g., Mesa & Schreck 1989), and probably disturbs fish communities profoundly.

Production in our study was positively related to biomass. The regression equation for our values for total P and B for eels in all land-use types was:

$$\log_{10}P \text{ (kg ha}^{-1} \text{ year}^{-1}\text{)} = -0.82 + 1.03 \log_{10}B \text{ (kg ha}^{-1}\text{)}$$

($r^2 = 0.96$, $P < 0.001$, $N = 11$). Randall et al. (1995) also found that P and B in rivers were positively related, according to the regression equation:

$$\log_{10}P \text{ (kg ha}^{-1} \text{ year}^{-1}\text{)} = 0.38 + 0.89 \log_{10}B \text{ (kg ha}^{-1}\text{)}$$

($r^2 = 0.80$, $P < 0.001$, $N = 40$). Considering our small sample size, these regression equations are similar, and we conclude that production in our streams was strongly dependent on biomass.

Production (P) to biomass (B) ratios have been used to characterise ecosystem maturity (Johnson 1994), with low P/B ratios indicative of mature ecosystems. Also, P/B ratios have been used to estimate production from biomass when growth and mortality are unknown (Randall et al. 1995). Our results support the conclusions of Randall et al. (1995) that P/B ratios are negatively related to mean fish weight, and that comparisons of P/B ratios that do not consider biomass are invalid. However, our data did not fit the regression line of Randall et al. particularly well, suggesting instead that the slope that Randall et al. calculated would have been more steeply negative had they included P/B ratios associated with higher biomasses. Our P/B ratios (mean 0.183, $N = 11$) were lower than those quoted by Randall et al. for rivers (mean 1.64, $N = 51$: $P < 0.001$, Kruskal-Wallis ANOVA), probably because of greater mean fish weights in our study. Low P/B ratios have also been associated with long mean life-span, and eels in our study were long-lived (up to 27 years). In slow-growth environments, such

as forested streams, longfinned eels can live for 60 years (Chisnall & Hicks 1993). Hopkins' (1971) P/B ratios (0.25–2.12) were generally greater than ours, probably also because his mean fish weight was less than ours, as his P and B estimates included small fish such as bullies and juvenile trout. Thus P/B ratios seem principally to reflect fish size and longevity, and low values indicate unexploited populations of long-lived species.

Longfinned eels were the only fish common enough in all streams to compare length frequencies across land-use types, and were the dominant organism in these small Waikato streams, with by far the greatest biomass of any single fish species. The dominant species in an aquatic ecosystem can be expected to exert a "top-down" influence on smaller fish and invertebrates, while at the same time stimulating their turnover rate (Northcote 1988; Johnson 1994). The length-frequency distribution of longfinned eels in all land-use types appeared bimodal, with modes c. 200 mm apart (Fig. 3).

Size modes that are unrelated to age classes may reflect a stable size structure of the dominant organism, which is a feature of unexploited populations. Johnson (1994) has suggested that underlying ecosystem bioenergetics are responsible for stable size modes, which minimise energy loss in unexploited populations. Such size modes often contain a mix of ages. Whether the size modes we observed correspond to energetically stable sizes of longfinned eels for these environments, or instead reflect variation in recruitment, cannot be answered from our limited data. We suggest that variable recruitment is a more plausible explanation because, despite some overlap, the mean ages of eels in the length modes were different.

Our findings have implications for the effects of land-use practices on fish in Waikato streams. Widespread conversion of land use from forest to pasture has increased the abundance of shortfinned eels, while reducing the abundance of banded kokopu. Removal of forest cover has also increased growth rates of both eel species. The combination of increased growth rates and higher shortfinned eel biomass has resulted in a c. 7-fold increase in eel production in pastoral streams compared to forested streams. These changes in the fish community seem certain to have been caused by the increased light, inorganic nitrogen, water temperatures, and in-stream primary production associated with removal of forest cover.

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