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Age and growth of longfinned eels (*Anguilla dieffenbachii*) in pastoral and forested streams in the Waikato River basin, and in two hydro-electric lakes in the North Island, New Zealand

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Abstract Growth rates of New Zealand endemic longfinned eels (*Anguilla dieffenbachii*) from streams in pasture and indigenous forest, and from two hydro-electric lakes (Lakes Karapiro and Matahina), were estimated by otolith examination. Habitat-specific growth was further investigated with measurement of widths of annual bands in otoliths. Longfinned eels 170–1095 mm in length ranged between 4 and 60 years old ($N = 252$). Eels in pastoral streams grew faster (mean annual length increment ± 95% CL = 24 ± 3 mm to 36 ± 7 mm) than eels in streams in indigenous forest (annual length increment 12 ± 2 mm to 15 ± 3 mm). Eels from the hydro-electric lakes had growth rates (annual length increments 19 ± 4 and 19 ± 7 mm) similar to eels from pastoral streams. Otoliths of most eels showed annual band widths that indicated growth in several different habitats, corresponding to growth during upstream migration, and limited movement among adult habitats. Estimated age at marketable size (220 g) ranged between 7 and 26 years. The particularly slow growth of longfinned eels in streams in indigenous forest has considerable implications for management. The fast growth rates of eels in hydro-electric lakes provides evidence for the potential of increased eel production by stocking. The probable selective production of female eels in these lakes may be nationally important to allow enhancement of breeding stocks.

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INTRODUCTION

The New Zealand commercial eel fishery exploits wild longfinned (*Anguilla dieffenbachi* Gray, 1842) and shortfinned eels (*Anguilla australis* Richardson, 1848). Longfinned eels are endemic to New Zealand, and constitute 42% of the average annual national catch, which fluctuates around 1200 t (Ministry of Agriculture and Fisheries statistics). One of the most productive eel fisheries in New Zealand is in the Waikato River basin, where longfinned eels comprise up to 30% of the 150–200 t annual catch. Longfinned eels are found throughout the Waikato River catchment but are more abundant in the upper reaches of streams and rivers, and mainstem hydro-electric impoundments, than in lowland rivers, lakes, or wetlands (e.g., Chisnall 1989; Chisnall & Hayes 1991; Swales & West 1991).

Methods for studying growth rates of New Zealand eels have been established (Jellyman 1977, 1979; Todd 1980; Hu & Todd 1981; Chisnall 1989; Chisnall & Hayes 1991). Otoliths of both shortfinned and longfinned eels show alternating concentric transparent and opaque bands; each transparent zone delimits 1 year's growth. The width of opaque bands (growth bands), appears to be correlated with habitat type, as do growth rates (e.g., Chisnall 1989; Chisnall & Hayes 1991). The main aims of the present paper were to determine to what extent growth rates of longfinned eels vary among habitat types, and to test objectively whether growth bands in the otoliths of longfinned eels have characteristic widths in different habitats.

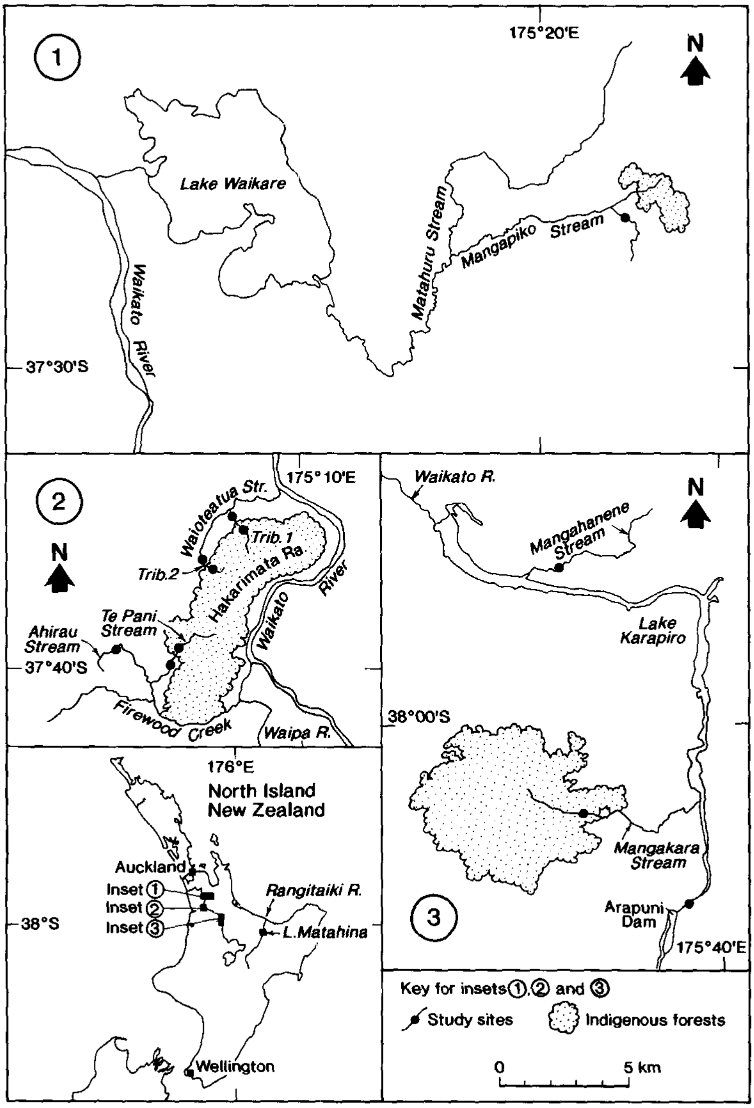

Fig. 1 Location of study sites in the Waikato River basin, and Rangitaiki River, North Island, New Zealand.

STUDY SITES

Stream study sites were located in tributaries of the lower Waikato River in the North Island, south of Auckland (Fig. 1), between 86 km and 175 km upstream from the sea (Table 1). Channel morphology and water temperature were measured for each stream site, and gradients were estimated from topographical maps (Table 1). Four study sites were in indigenous forest, and seven in pasture. Stream sites that had not been previously commercially fished (local knowledge) were chosen to ensure that eels sampled came from unexploited stocks. Commercial harvest has been shown to rapidly reduce the number of large eels in the population (e.g., Jellyman 1992).

In addition to the stream sites, eels were also collected from two hydro-electric impoundments: Lake Karapiro on the Waikato River, and Lake Matahina on the Rangitaiki River (Fig. 1). Lake Karapiro is an impoundment formed in 1947 above Karapiro dam, the lowest of nine dams on the Waikato River. The lake is 150 km upstream from the sea and has an area of 5.4 km^2 (Strachan 1979; Livingston et al. 1986). During October and November 1989 the tailrace of Arapuni hydro-dam (immediately upstream of Lake Karapiro) was drained. An earth coffer-dam was constructed 1.5 km below the Arapuni dam, and the water was pumped out. Eels were collected for the present study from residual pools in this upstream end of Lake Karapiro (Boubée et al. 1989).

Lake Matahina is a hydro-electric impoundment on the Rangitaiki River that was formed in 1967 behind a 60-m earth-core dam. The lake has an area of 2.5 km^2 (Phillips & Nelson 1981), and is 30 km upstream from the east coast of the North Island. Eels were collected for this study from Lake Matahina in April 1988 when the lake level was lowered to facilitate repairs to the dam.

METHODS

Eel capture

Eels were collected from stream sites using a combination of electric fishing to depletion (using a 90 *W*, 12 *V* back-pack machine, delivering pulsed DC current), and unbaited fyke nets set overnight (12 mm and 6 mm stretched mesh). Eels were removed from the drained section of Lake Karapiro with baited fyke nets set along the shorelines of residual pools that were 1–2 m deep (Boubée et al. 1989). Lake Matahina was fished in a similar fashion in April 1988.

Tributary streams of the Waikato River were fished during March and April 1987, July and August 1988, and August 1989. Lake Karapiro was fished in November 1989, and its tributary streams in December 1989 and March 1990. Captured eels were measured in length and weighed whole to the nearest mm and g, respectively, while fresh. Eels < 200 mm total length (TL) were inadequately sampled because of the mesh size of nets used, and the evasive behaviour of small eels when electro-shocking. Thus, few small eels were included in subsequent analysis.

Growth determination and analysis

The sagittal otoliths were extracted and prepared using the crack-and-burn method (Jellyman 1979). Otolith halves were mounted on microscope slides in silicone rubber sealant (Hu & Todd 1981). Transparent zones (dark when burnt), were counted to determine age. Age was expressed as years spent in freshwater, ignoring the central zone of larval growth (Jellyman 1979).

To investigate the relationship between otolith growth-band width and habitat type, mounted otolith halves were selected for growth-band width measurement from several locations, representative of three main habitat types (pastoral and forested sections in the three Hakarimata Range streams, Mangakara and Mangahanene streams, and Lake Karapiro, N = 153). Only otoliths that could be easily read and which had been cleanly axially fractured

Table 1 Environmental variables recorded from streams in the Waikato River basin. Gradients, distance from sea, and catchment areas measured from 1:50 000 topographical maps (NZMS 260); water temperatures measured in March 1990.

Location	Distance fished (m)	Gradient (m km^{-1})	Proportions of channel types (%) Run	Riffle	Pool	Pool dimensions Width (m)	Depth (m)	Water temperature (°C)	Distance upstream (km)	Catchment area (km^2)
Lowland pasture										
Mangahanene	400	10	57	20	23	2.5	0.68	14.5	154	11.39
Ahirau	400	25	66	15	21	1.4	0.45	14.5	100	1.44
Pasture below forest										
Hakarimata Ranges										
Te Pani	130	31	56	24	20	1.9	0.54	14.0	101	4.80
Waioteatua trib. 1	220	40	55	24	21	1.2	0.28	13.5	86	1.56
Waioteatua trib. 2	400	49	63	27	10	1.0	0.18	14.5	86	0.64
Mangapiko	700	57	58	27	15	2.1	0.45	14.0	86	2.93
Mangakara	200	60	59	27	14	2.0	0.35	13.0	175	4.84
Indigenous forest										
Hakarimata Ranges										
Te Pani	387	42	58	25	17	2.4	0.42	12.0	101	2.40
Waioteatua trib. 1	205	89	71	18	11	1.3	0.18	11.5	86	0.86
Waioteatua trib. 2	218	67	41	41	18	1.4	0.25	12.5	86	0.36
Mangakara	1000	80	60	32	8	2.0	0.30	11.5	175	3.90

across the central larval zone were used (N = 74).

Widths of growth-bands were measured with a calibrated eyepiece graticule (100 μm = 63.8 graticule units, SD = 1.4) under 80× magnification. Growth bands, determined as the distance between successive transparent zones, were individually measured beginning at the outer perimeter of each otolith fragment and following along the longitudinal axis to the centre (Jearld 1983: fig. 16.11C). The width of each growth band was visually classified as wide, intermediate, or narrow before measurement to test the assumption that band frequency is characteristic of habitat type.

Growth was described by Model I least-squares linear regression of length-at-age and weight-at-age, calculated using the MGLH package of SYSTAT (Wilkinson 1990). Linear equations were only presented and fitted to data sets with sufficient correlated data. The ages at which longfinned eels reached threshold commercial weights in each location were estimated from weight-age regressions. The 95% confidence limits of these estimates were calculated following Sokal & Rohlf (1981: 498), using age-weight regressions.

Length-weight relationships were determined for longfinned eels from each location. Comparisons of condition between locations were made by using condition factors calculated for isometric growth ($K = 10^6\ W/L^3$; where W = weight in g, and L = length in mm, Bagenal 1978), to facilitate comparison between habitats.

Eel density and biomass in streams were estimated by relating the number and total weight of eels removed from the section fished to distance and area fished.

RESULTS

Classification of growth bands

Growth bands visually classified as wide, intermediate, or narrow formed clearly distinct groups of widths when measured (N = 74, Table 2). Growth-band widths in otoliths from individual eels, visually classified as wide, intermediate, or narrow were normally distributed (Kolmogorov-Smirnov test, standardised by Lilliefors test; $P > 0.3$), and analysis of variance showed that each group was significantly different (Tukey HSD, with Tukey-Kramer adjustment for unequal N; $P < 0.001$). Otolith pairs with > 80% of their growth bands visually categorised as the same width (N = 30) were used to derive mean band widths characteristic of growth in each of the three habitat types (e.g., Fig. 2A, B, C and F). The mean width of narrow growth bands in this group was half that of intermediate bands, and intermediate bands were half the width of wide bands (Table 3).

Age and growth in different habitats

Relationship of length and weight to age

Ages were determined from otoliths of 252 eels. Otoliths from a further 10 eels (4% of total) were unreadable. Interpretation of otoliths from large longfinned eels was sometimes difficult, because growth-bands were numerous and closely spaced (e.g., Fig. 2F).

Length-age relationships of eels in different habitats showed that consistent differences in growth occurred. Longfinned eels 170–1095 mm TL ranged in age between 4 and 60 yrs. Average annual length increments, calculated from length-age relationships, ranged between 24 and 36 mm in pastoral streams with N > 10, between 12 and 15 mm in forested

Table 2 Mean widths of growth bands visually identified as wide, intermediate, and narrow, averaged for 74 individual eels (N_1) from habitats in the Waikato River basin. N_2, number of bands examined; CL, 95% confidence limits; –, no data.

	Wide			Intermediate			Narrow		
Habitat	N_1	N_2	Mean ± CL (μm)	N_1	N_2	Mean ± CL (μm)	N_1	N_2	Mean ± CL (μm)
Lake Karapiro	22	387	110 ± 6	15	140	60 ± 2	9	123	23 ± 5
Pastoral streams									
Mangahanene	2	15	87 ± 0	5	105	56 ± 5	0	0	
Mangakara	1	4	86 ± 0	2	29	54 ± 9	2	11	18 ± 0
Hakarimata (3 streams)	12	59	88 ± 2	24	261	57 ± 2	18	68	31 ± 0
Forested streams									
Mangakara	6	34	77 ± 5	5	51	48 ± 5	7	268	23 ± 2
Hakarimata (3 streams)	0	0	–	13	101	45 ± 2	14	388	25 ± 2

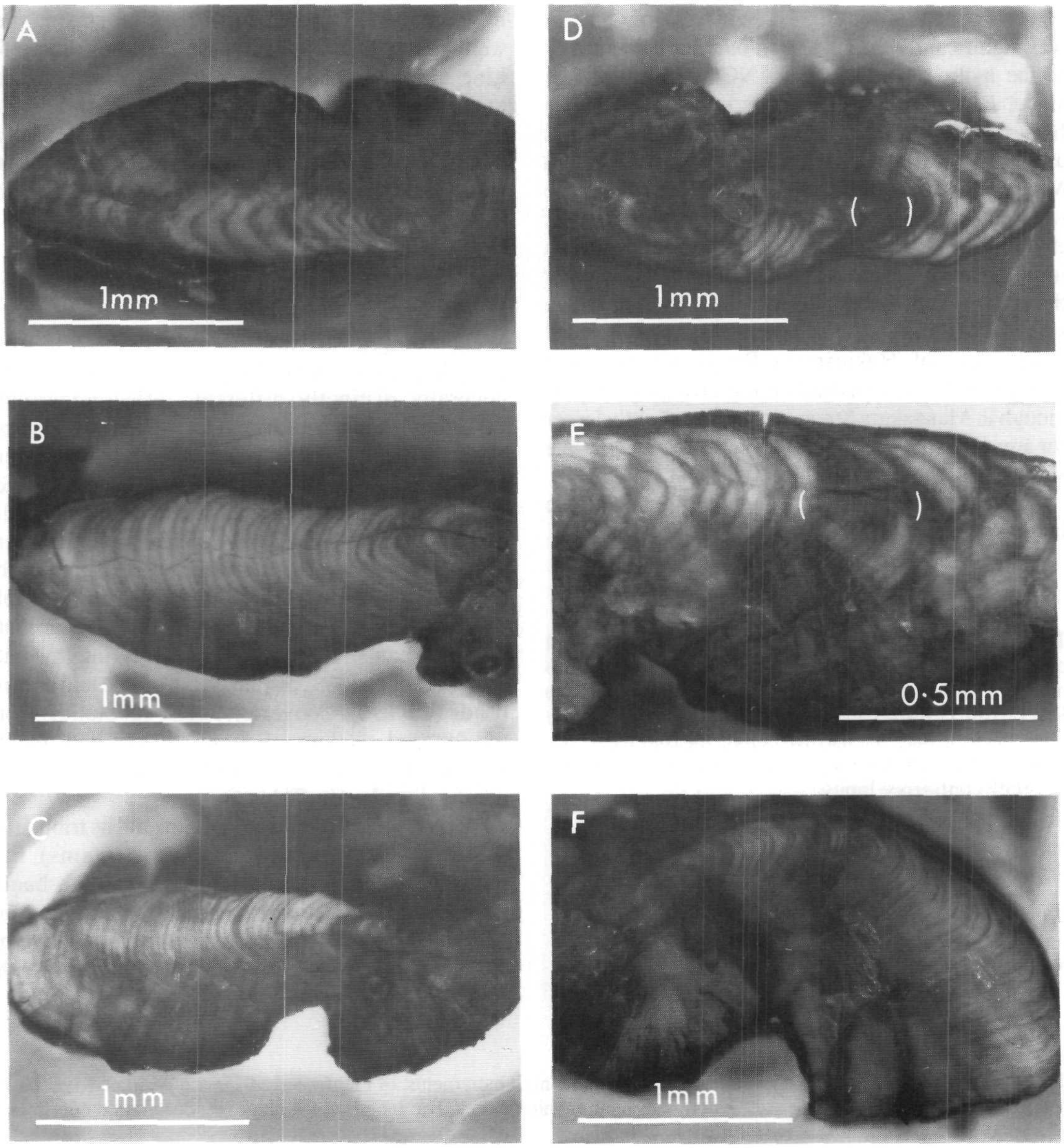

Fig. 2 Otoliths from longfinned eels (*Anguilla dieffenbachii*) from the Waikato River basin, North Island. Axial fracture plane shown; otoliths A–C and F have 80% of their bands of consistent width, characteristic of growth in three different habitat types: (A) Lake Karapiro eel, length 760 mm, age 25 years; (B) Mangahanene Stream (pastoral) eel, length 662 mm, age 43 years; (C) and (F) Mangakara Stream (forest), length 705, age 37 years, and length 915 mm, age 53 years; (D) and (E) Lake Karapiro eel, length 830 mm, age 30 years, with mixed band widths (bracketed section thought to be stream growth).

streams, and was 19 mm in both hydro-electric lakes (Table 4). The fit of data to Model I regression lines is shown in Fig. 3. Fastest growth occurred in the lowland pastoral Ahirau Stream, followed by growth in other pastoral streams. Growth of longfinned eels in forested streams was considerably slower, and growth in the hydro-electric lakes was similar to pastoral streams.

The growth of longfinned eels in Ahirau Stream was significantly faster than in other stream sites or in the hydro-electric lakes (ANCOVA: length-age slope, $P < 0.001$). Growth rates of longfinned eels from pastoral stream sites in the Hakarimata Ranges and in Mangapiko Stream were similar, though Mangapiko Stream eels were larger for any given age (ANCOVA: length and weight-age slope, $P > 0.05$; elevation, $P < 0.001$) (Fig. 3). Longfinned eel growth in all pastoral stream sites was considerably faster than in forested stream sites (ANCOVA: length-age slope, $P < 0.001$). Longfinned eels from forested headwaters of Hakarimata Range streams and Mangakara Stream eels had similar slow growth rates, though in Mangakara Stream, eels were slightly larger for any given age (ANCOVA: length and weight-age slope, $P > 0.05$; elevation, $P = 0.003$).

Increase in weight with age largely reflected the increase in length with age for the same sites.

Table 3 Mean widths of annual growth bands of sagittal otoliths from 30 longfinned eels, that had more than 80% of their bands that were of similar width, in the Waikato River basin. Growth-bands were visually determined to be wide, intermediate, or narrow before measurement. N_1, number of individuals; N_2, number of bands examined; CL, 95% confidence limits.

Growth band type	N_1	N_2	Growth-band width, mean ± CL (μm)
Wide	9	171	106 ± 9
Intermediate	10	193	55 ± 4
Narrow	11	382	26 ± 2

Regression line slopes (b) of pastoral stream sites were greater than for forested stream sites (Table 5). Line slopes for the hydro-electric lakes were similar to pastoral stream sites. Length-age and weight-age regressions of eels from the lakes had smaller r^2 values than pastoral streams, showing that growth was more variable in hydro-lakes than in streams (Table 4 and 5).

Relation of growth-band widths to habitat-specific growth

Widths of growth bands in otoliths of eels from pastoral streams, forested streams, and the lakes were generally distinctly different, reflecting growth variations established by length-at-age relationships. Most eel otoliths examined had a mixture of different growth-band widths, numerically dominated by band-widths that were common amongst eels from the same location (e.g., Fig. 4). Eels from different locations, but similar habitat types, had otoliths dominated by growth-bands of similar width (Table 2). Some otoliths of eels from pastoral Hakarimata Range streams, though dominated by intermediate growth-band widths, displayed both wide and narrow bands (Table 6). Conversely, most eel otoliths from the forested sections of these streams had mainly narrow bands but also had small numbers of intermediate bands (Table 6).

Several eels from Lake Karapiro and its tributaries (Mangahanene and Mangakara Streams) had particularly high percentages of growth-bands uncharacteristic of the habitat, suggesting that long periods of growth had occurred in other habitats (e.g., Table 6). Eels from Lake Karapiro that had otoliths

Table 4 Length-age relationships, and relative annual length increments, of longfinned eels in the Waikato River basin, and Lake Matahina. N, sample size; length-age relationship of the form: length = $a + b$ age; r^2, correlation coefficient; CL, 95% confidence limits; P for all models < 0.001.

Habitat	N	Length range (mm)	Age range (yr)	a	$b \pm$ SE	r^2	Annual length increment ± CL (mm)
Pastoral streams							
Ahirau	29	231–1095	4–25	58.7	35.8 ± 3.5	0.80	36 ± 7.2
Hakarimata (3 streams)	53	200–1055	7–39	27.7	24.1 ± 1.3	0.88	24 ± 2.6
Mangapiko	30	521–1086	14–33	150.6	25.1 ± 0.9	0.87	25 ± 1.8
Forested streams							
Hakarimata (3 streams)	22	320–1080	18–60	68.2	14.7 ± 1.3	0.86	15 ± 2.7
Mangakara	11	568–915	27–53	249.9	11.9 ± 1.1	0.93	12 ± 2.5
Hydro-electric lakes							
Lake Karapiro	62	345–980	6–30	318.7	19.4 ± 2.2	0.57	19 ± 4.4
Lake Matahina	22	398–960	15–40	190.7	18.8 ± 3.4	0.62	19 ± 7.1

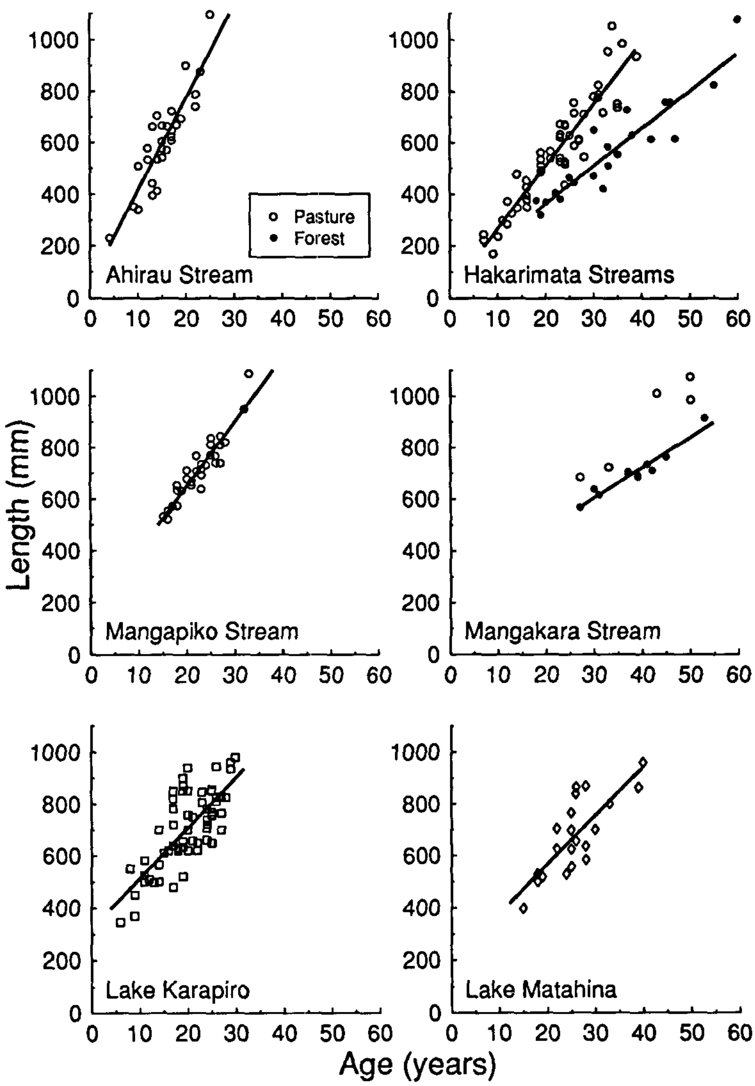

Fig. 3 Length-age relationships of longfinned eels in pastoral and forested streams, and Lake Karaprio, in the Waikato River basin, and in Lake Matahina, Rangitaiki River, North Island.

with more than 55% of their growth-bands uncharacteristic of lake growth ($N = 8$, e.g., Fig. 2D and E), were excluded from regression calculations (Tables 4 and 5), and from the plots of length-at-age (Fig. 3).

Length-weight relationships and condition

Length-weight relationships (Table 7) were compared between locations using condition factors (CF). Condition was not correlated with length, and so comparison was made across all available data. Condition factors from each location were normally distributed and mean CF did not vary significantly between locations (Tukey HSD tests, $P > 0.05$, Table 7). The mean CF (± 95% CL) for all longfinned eels sampled was 2.63 ± 0.09.

Eel density and biomass in Waikato River tributaries

Total eel biomass was greater at pastoral sites than at forested sites, generally reflecting densities (Table 8). Biomass was also related to channel gradient and proportion of pool habitat (Fig. 5A and B). The inverse relation of proportion of pool habitat to gradient appears to be the factor controlling eel biomass (Fig. 5C), and pastoral sites had lower

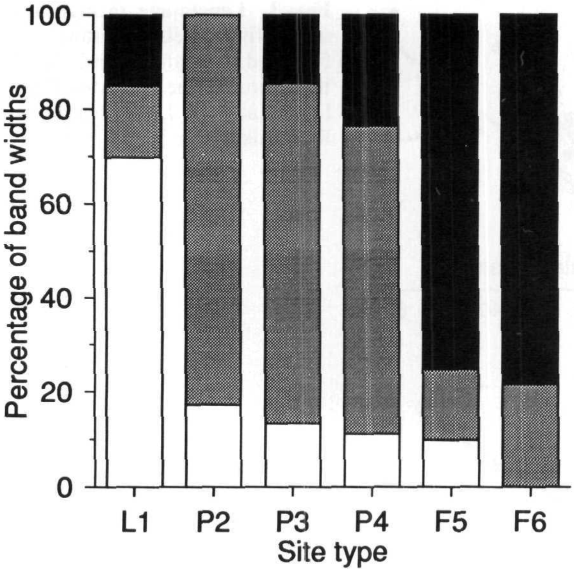

Fig. 4 Proportions of wide (white), intermediate (grey), and narrow (black) growth bands in otoliths of longfinned eels in Waikato streams, and Lake Karapiro. L1, Lake Karapiro (N = 22); P2, Mangahanene (pasture, N = 5); P3, Hakarimata Range streams (pasture, N = 24); P4, Mangakara (pasture, N = 2); F5, Mangakara (forest, N = 7); F6, Hakarimata Range streams (forest, N = 14).

gradient than forested sites. Shortfinned eel biomass was also greatest in lowland sites (Table 8).

Forested sites had low eel biomass, but Hakarimata Range streams had double the biomass of Mangakara Stream (Table 8) despite eels from these streams having similar growth rates (Table 4). The Mangakara Stream site had a higher gradient and much lower percentage of pool habitat available (Table 1).

Eel fishery management

Age at maturity

Reproductive maturity in *Anguilla* species is considered to be related to length (Tesch 1977). Longfinned males migrate to sea at 50–70 cm, and females at > 80 cm (Todd 1980; Jellyman & Todd 1982). Age at maturity was estimated for longfinned eels in the present study from length-age regressions, ignoring possible differences in growth rates between sexes (Table 4). Estimates varied with growth rates from each location, and ranged between 12 and 45 years for males and from ≥ 22 to ≥ 48 years for females (Table 9).

Commercial threshold

Habitat-specific differences in growth have implications for management of the Waikato eel fishery. Entry of eels into the commercial fishery is governed by weight, which is nationally set at a lower limit of 150 g, with the single exception of Lake Ellesmere. However, variation in growth means that eels of a given size from different habitats will have different ages. Weight-age relationships (Table 5) were used to estimate age at marketable size, and at a possible new weight restriction (220 and 250 g respectively, Table 9). Age at which longfinned eels were estimated to reach 220 g ranged from 7 to 19 years in hydro-electric lakes and pastoral streams, to 26 years in forested Hakarimata Range streams (Table 9). The low age estimate of 7 years for 220 g longfinned eels from the forested section of Mangakara Stream is probably the result of fast growth in Lake Karapiro before movement into the stream. Longfinned eels from forested sites attained a weight of 1500 g at the age of 48 years (Table 9), but attained this size at 26–31 years in hydro-electric lakes.

Table 5 Weight-age relationships of longfinned eels in the Waikato River basin, and Lake Matahina. N, sample size; weight-age relationship form of $\ln W = a + b$ age; W, weight in g; r^2, correlation coefficient; P for all models < 0.001. Age range as for Table 3.

Habitat	N	Weight range (g)	a	$b \pm SE$	r^2
Pastoral streams					
Ahirau	29	25–4191	3.05	0.21 ± 0.02	0.81
Hakarimata (3 streams)	53	7–3650	2.39	0.16 ± 0.01	0.86
Mangapiko	30	366–3581	4.52	0.10 ± 0.01	0.78
Forested streams					
Hakarimata (3 streams)	22	80–3765	3.30	0.08 ± 0.01	0.87
Mangakara	11	895–2391	5.07	0.05 ± 0.01	0.83
Hydro-electric lakes					
Lake Karapiro	62	80–2910	4.63	0.10 ± 0.01	0.59
Lake Matahina	22	120–2400	4.18	0.10 ± 0.02	0.66

DISCUSSION

Age validation

Conclusive evidence that transparent zones in otoliths do represent annual growth checks has been provided for several anguillid species, e.g., *A. australis* (Jellyman 1979), *A. rostrata* (Helfman et al. 1984a, 1984b), *A. mossambica* (McEwan & Hecht 1984), and *A. anguilla* (Berg 1985; Dekker 1986; Aprahamian 1987; Vollestad & Naesje 1988). Evidence that transparent zones are formed annually in otoliths of longfinned eels (*A. dieffenbachii*) has been provided by three studies. In a mark/recapture study of New Zealand eels in three Canterbury streams, annual length increments in recaptured, marked longfinned eels concurred with growth estimated from otolith-determined ages and length (Burnet 1969). In Lake Pounui (lower North Island), annual length increments from a large number of tagged longfinned eels were in overall agreement with growth estimated from otolith-determined ages (D. Jellyman unpubl. data). In a mark-recapture study in the pastoral Ahirau Stream (present study), the number of transparent zones following fluorescent labels (tetracycline) on the otoliths of tagged recaptured longfinned and shortfinned eels corresponded to the number of years these eels were at liberty (Chisnall & Kalish 1993).

Growth in different habitats

Causes of variable growth rates

New Zealand eels move upstream for several years as elvers and juveniles, documented as successive summer migrations (Jellyman 1977). Afterwards, eels are likely to live in specific areas, usually with limited home ranges (Burnet 1969; Jellyman & Todd 1982; Chisnall 1987; Chisnall & Kalish 1993). Growth

Table 6 Numbers of individual longfinned eels and proportions of wide, intermediate (int.), or narrow growth-band widths, in habitats of the Waikato River basin. *N*, total number of eels examined.

		Proportions of growth bands								
		> 60%			30–60%			< 30%		
Habitat	*N*	Wide	Int.	Narrow	Wide	Int.	Narrow	Wide	Int.	Narrow
Lake Karapiro	22	14	1		6	3	6	2	11	3
Pastoral streams										
Mangahanene	5	1	4	–	–	1	–	1	–	–
Mangakara	2	–	2	–	–	–	1	1	–	1
Hakarimata (3 streams)	24	–	20	5	4	3	7	–	15	
Forested streams										
Mangakara	7	–	–	7	–	–	–	6	5	–
Hakarimata (3 streams)	14	–	–	12	–	–	2	–	10	–

Table 7 Weight-length relationships of longfinned eels in the Waikato River basin, and in Lake Matahina. *N*, sample size; weight-length relationship in the form of $\ln W = \ln a + b \ln L$; *W*, weight in g; *L*, length in mm, r^2, correlation coefficient; CF, condition factor; CL, 95% confidence limits; length ranges as for Table 3; weight ranges as for Table 4; *P* for all models < 0.001.

Habitat	*N*	*a*	$b \pm$ SE	r^2	CF ± CL
Pastoral streams					
Ahirau	33	−14.38	3.25 ± 0.07	0.99	2.74 ± 0.15
Hakarimata (3 streams)	53	−14.45	3.25 ± 0.05	0.99	2.48 ± 0.12
Mangapiko	30	−11.99	2.86 ± 0.25	0.83	2.57 ± 0.17
Forested streams					
Hakarimata (3 streams)	22	−13.93	3.17 ± 0.13	0.97	2.72 ± 0.28
Mangakara	11	−10.99	2.72 ± 0.43	0.82	2.76 ± 0.27
Hydro-electric lakes					
Lake Karapiro	65	−13.72	3.12 ± 0.17	0.85	2.51 ± 0.12
Lake Matahina	22	−13.89	3.17 ± 0.02	0.95	2.76 ± 0.10

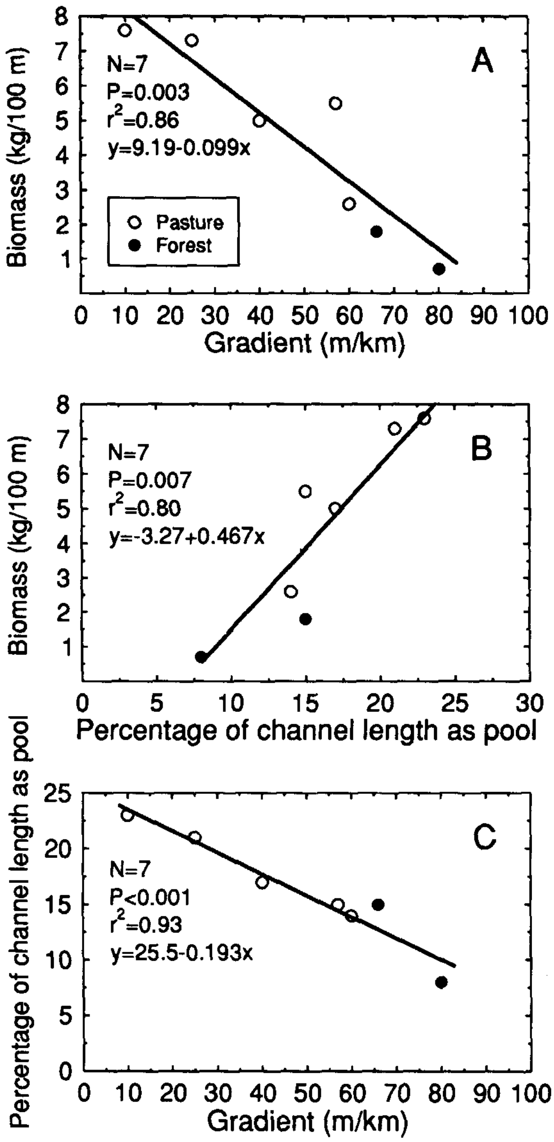

Fig. 5 Association of eel biomass with **A**, gradient; **B**, percentage of channel as pool habitat; **C**, relationship of pool habitat to channel gradient.

bands in otoliths appear to reflect this limited movement by showing uniform widths characteristic of different habitats.

Water temperature is probably the most important factor causing habitat-specific growth differences in longfinned eels. Low water temperatures are well known to reduce eel mobility and lower growth rates (e.g., Cairns 1942; Sinha & Jones 1967; Nyman 1972; Ryan 1984; Chisnall 1989). In addition, increased light available to pastoral streams, and the generally higher trophic status of lakes, may allow greater food production in these habitats than in forested streams.

Most eels examined had two or more concentric areas in their otoliths with different widths of growth bands. It is likely that growth in two or more habitats caused this variation in band width, because the majority of eels from any particular habitat had > 60% of their rings of one type (Table 2 and 6, Fig. 2). Eighteen longfinned eels from pastoral stream sites below forest in the Hakarimata Range had occasional series of narrow growth-bands on their otoliths, suggesting that some growth had occurred in forested habitat (e.g., Fig. 2D and E). Conversely, most longfinned eels from forested sections of these streams had some series of intermediate width growth-bands on their otoliths, but always < 30%, suggesting that some growth had taken place in pastoral stream or river habitat during passage through the lower catchment. Sloane (1984) also recognised this phenomenon when he found several closely spaced rings surrounded by a few broadly spaced rings on otoliths from *A. australis* in Tasmania. He interpreted the different ring series as representing slow growth in the Clyde River followed by a number of years of faster growth in headwater lakes.

Hydro-electric lakes

The greater size at age of most longfinned eels from Lake Karapiro than at other study sites is probably related to low eel densities in the lake and its eutrophic nutrient status (Livingston et al. 1986). Eels may also expend less energy in lake environments compared with eels in streams. Recruitment has been restricted to the Waikato River above Karapiro since completion of the Karapiro hydro-electric dam in 1947. Growth rates of longfinned eels are also high in Lake Matahina on the Rangitaiki River where recruitment has been restricted and the remnant eel population is small (Chisnall & Hayes 1991).

As longfinned eels grow larger, they may become mainly piscivorous, and can be voracious cannibals (Cairns 1942; Jellyman 1989). The high energy content of fish promotes fast growth (e.g., Ryan 1982). The lack of eels smaller than 500 mm in the samples from Lake Karapiro, and in two of its tributaries (Mangahanene and Mangakara Streams), may be evidence of cannibalism. Elvers are known to successfully climb the Karapiro dam and enter the lake (e.g., Jellyman & Todd 1982), yet only three eels < 500 mm were caught. Predation of small eels during trapping may have contributed to this effect but cannot explain the lack of small eels caught during exhaustive electro-fishing of the two tributaries (Mangahanene and Mangakara Streams). A similar conclusion was drawn by J. Boubée (pers. comm.) after repeated sampling of Lake Matahina in 1989, when less than 7% of his catches were eels smaller than 500 mm in length. Eels caught in Mangapiko Stream, above Lake Waikare (this study) were also greater than 500 mm in length.

Variability of longfinned eel growth in both Lakes Karapiro and Matahina was probably due to the congregation of eels from different habitats as a consequence of lake level lowering. The inclusion of some eels that had probably grown mostly in pastoral and forested streams added to growth variability.

Pastoral streams

The fast to moderate growth rates of longfinned eels in pastoral streams are likely to be influenced by several important factors which may include: water temperature, high food abundance (Taylor 1988; Quinn & Hickey 1990), low gradients that cause low water velocities and a high proportion of pool habitat, intraspecific competition, and interspecific competition with shortfinned eels.

The most important factor contributing to the faster growth of longfinned eels in the lowland Ahirau Stream compared with other pastoral streams was

Table 8 Eel density and biomass in streams of the Waikato River basin. LF, longfinned eel; SF, shortfinned eel.

		Eel density			Eel biomass					
		number (100 m)$^{-1}$			kg (100 m)$^{-1}$			kg ha^{-1}		
Habitat	% LF	LF	SF	Total	LF	SF	Total	LF	SF	Total
Lowland pasture										
Mangahanene	37	2.5	4.3	6.8	3.3	4.3	7.6	133.6	171.1	304.7
Ahirau	23	6.3	21.3	27.6	5.5	1.8	7.3	391.7	127.6	519.3
Pasture below forest										
Hakarimata (3 streams)	66	7.1	3.7	10.8	4.6	0.4	5.0	329.4	31.1	360.5
Mangapiko	81	7.8	1.8	9.6	4.6	0.9	5.5	217.0	42.3	259.3
Mangakara	100	2.5	–	2.5	2.6	–	2.6	129.0	–	129.0
Indigenous forest										
Hakarimata (3 streams)	100	2.7	–	2.7	1.8	–	1.8	107.4	–	107.4
Mangakara	100	1.1	–	1.1	1.1	–	1.1	54.3	–	54.3

Table 9 Freshwater age of longfinned eels in the Waikato River basin and in Lake Matahina at commercial threshold weights, and at 1500 g, estimated from weight-age regressions (Table 4). Age at maturity estimated from Model I length-age regressions (Table 3) (male 50–70 cm, and female > 80 cm, Todd 1980). CL, 95% confidence limits using age-weight regressions (Sokal & Rohlf 1981).

	Age in years at specific weights (CL in brackets)			Age at maturity (years)	
Habitat	220 g	250 g	1500 g	Male	Female
Pastoral streams					
Ahirau	11 (4–14)	12 (5–14)	20 (14–23)	12–18	≥ 22
Hakarimata (3 streams)	19 (8–22)	20 (9–23)	32 (21–34)	20–30	≥ 33
Mangapiko	9 (0–13)	10 (1–14)	28 (21–32)	15–21	≥ 26
Forested streams					
Hakarimata (3 streams)	26 (9–29)	28 (11–31)	50 (34–54)	30–45	≥ 48
Mangakara	7 (0–18)	10 (0–20)	49 (38–59)	22–38	≥ 48
Hydro-electric lakes					
Lake Karapiro	7 (0–15)	9 (0–16)	26 (14–34)	10–20	≥ 22
Lake Matahina	12 (0–21)	13 (0–22)	31 (20–41)	16–27	≥ 32

probably predation on the large number of small shortfinned eels present there. Ahirau Stream sustained almost twice the biomass of longfinned eels than did lowland Mangahanene Stream which had similar numbers and biomass of both eel species (Table 8), and few small eels.

Intraspecific and interspecific competition among large individuals of both eel species in Mangahanene Stream may have been responsible for the relatively lower growth rate of longfinned eels there. Territoriality and antagonistic behaviour of large eels is documented by several authors (e.g., Ford & Mercer 1986; Knights 1987), and growth rates are consequently promoted or inhibited. Both eel species (mostly large individuals) caught in Mangahanene Stream were evenly distributed throughout the stream section sampled. Conversely, in the Ahirau Stream, large longfinned eels dominated the population and occupied the pools (more productive habitat), whereas shortfinned eels (mostly small individuals) were only caught in the runs and riffles.

Pasture has been shown to provide terrestrial invertebrates to fish in streams during floods (Mitchell 1984; Rounick & Hicks 1985; Chisnall 1987; Jellyman 1991). Eels in lowland pastoral streams are more likely to have access to terrestrial invertebrates than eels in pastoral streams immediately below forest where gradients are high and the flood plain is narrower. Terrestrial invertebrates can make a significant contribution to the diet of longfinned eels (Cairns 1942; Burnet 1952; Chisnall 1987; Jellyman 1989). Longfinned eels have also been shown to consume more terrestrial prey when available than common aquatic food species (Chisnall 1987).

Slower growth of longfinned eels in pasture below forest (Hakarimata Range streams and Mangapiko Stream) than in the lowland Ahirau Stream, is also likely to be associated with reduced availability of pool habitat (Fig. 5). Limited foraging area for large eels, along with reduced productivity in fewer and smaller pools, may contribute to reduced eel growth.

The large Y-intercepts of growth models for longfinned eels in both forested and pastoral sections of Mangakara Stream, and in pastoral Mangapiko Stream (Tables 4 and 5) may be explained by the fast growth of juvenile eels en route to these streams. Fast growth of juveniles is indicated by the young ages at which longfinned eels attain the threshold commercial weight (220 g) in both streams (7 to 9 years, Table 9). Wide growth-band widths that were found in otoliths of longfinned eels from Mangakara Stream are consistent with fast growth as juveniles in Lake Karapiro (Table 2).

Annual length increments of longfinned eels estimated from otolith-determined ages in the present study (12–36 mm, Table 3) were similar to increments in tagged longfinned eels in three pastoral Canterbury streams (Burnet 1969). Burnet measured annual increments that averaged 10–20 mm for longfinned eels 350–800 mm in length. In addition, two large longfinned eels recaptured after 10 years from the same streams had grown 25 mm and 28 mm in length annually (Burnet 1969).

The reduction in catch of shortfinned eels with increased gradients (Table 1 and 8) is consistent with the known distribution of the species, which is predominantly lowland (e.g., Jellyman & Todd 1982). Longfinned eels prefer water with high dissolved oxygen concentrations, are capable climbers, and are therefore frequently found in upstream reaches (Cairns 1941; Jellyman 1977, 1989; Jellyman & Todd 1982).

Forested streams

Low growth rates and narrow growth-band widths on otoliths of longfinned eels from forested streams may be attributable to low water temperatures, low food abundance, fast water velocities associated with high gradients, limited pool habitat, and possibly interspecific competition. Water temperatures in streams in native forest in the Waikato region do not rise much above 14°C throughout the year (e.g., S. Hanchet, MAF Fisheries, Wellington, unpubl. data; J. Rutherford, NIWA Ecosystems, Hamilton, unpubl. data). The response of longfinned eels to low water temperatures in forested streams has not been studied, but slow growth is a probable consequence. Catches of both New Zealand eel species in the Waikato River have been shown to reduce when water temperatures drop below 14°C (Chisnall 1987), and longfinned eels are thought to reduce or stop feeding when water temperatures are below 7–8°C (Burnet 1955). Other studies of both shortfinned and longfinned eels indicate that cessation of feeding occurs when water temperatures fall below 5–6°C (Woods 1964; Jellyman 1991). It is also well known that narrow otolith increments are produced at lower water temperatures (e.g., Umezawa & Tsukamato 1991).

Streams in native forest have lower food availability than pastoral streams because fish and invertebrate biomass may be low (Taylor 1988; Hanchet 1990; Quinn & Hickey 1990), and vegetation inhibits overland run-off. Low abundance of fish in upper catchments probably limits piscivory by longfinned eels, and could impair growth compared with lower catchments where fish are more plentiful.

The macroinvertebrate biomass is significantly reduced with increased gradient in New Zealand streams (Quinn & Hickey 1990). Invertebrates are important food for longfinned eels (Cairns 1942; Burnet 1952; Chisnall 1987; Jellyman 1989). Freshwater crayfish (koura, *Paranephrops planifrons*) are usually the most abundant prey species present in forested streams in the Waikato region (S. Hanchet, unpubl. data). Koura are also the most common food item found in longfinned eel stomachs in forested streams (B.L.C. pers. obs.). In eel removal experiments (Hanchet & Chisnall 1991), koura densities increased markedly after eels were removed from two pastoral streams below forest.

Reduced pool habitat in higher gradients of forested streams restricts the foraging area for longfinned eels, and appears to limit density to about one eel per pool. Higher gradients may also cause longfinned eels to expend more energy to maintain their position against faster flows, further restricting growth. Galaxid species occur in forested streams, generally at low densities (Hanchet 1990), and where present together with longfinned eels must increase competition for food.

Comparative growth rates

Growth rates of longfinned eels in pastoral streams were considerably faster than growth rates for coexisting shortfinned eels. In the Ahirau Stream, annual incremental growth of longfinned eels was 36 mm, whereas for shortfinned eels it was 18 mm (length = 110.4 + 21.9 age, $r^2 = 0.63$, $N = 95$, ages 5–18 years, B.L.C. unpubl. data). Longfinned eels from Hakarimata Range streams also grew faster than shortfinned eels; incremental growth was 24 mm (this study) and 16 mm (Chisnall & Hayes 1991), respectively .

Growth of longfinned eels in unexploited streams in the present study (25–36 mm, Table 4) was generally faster than that found in an exploited population in the lower Waikato River. In the exploited population, longfinned eels smaller than 500 mm had relative annual increments of between 15 and 17 mm (ages 5–20 years, Chisnall 1989). This difference in growth is not necessarily caused by exploitation and may be entirely an effect of habitat differences. However, intensive commercial fishing, which removes large eels, is thought to cause the high densities of small eels observed in the backwaters of the Waikato River and result in slow growth (Chisnall 1989).

The relatively fast growth rates observed for eels from the hydro-electric lakes Karapiro and Matahina were considerably slower than attained by *A. nebulosa labiata* in Lake Kariba, Zambia (Balon 1975). The average annual length increment found by Balon was 77 mm. This rapid growth was similar to that attained by longfinned eels in the hydro-electric Lake Aniwhenua on the Rangitaiki River (upstream of Lake Matahina, Mitchell & Chisnall 1992).

Annual length increments determined for longfinned eels in the present study (12–36 mm) are slightly lower than those obtained for both European eels (*A. anguilla* 20–46 mm: Dekker 1986) and American eels (*A. rostrata* 34–62 mm: Hurley 1972; Helfman et al. 1984a, 1984b).

Biomass

Eel biomass in unexploited streams of the Waikato River basin has apparently changed little in 40 years. The yield from lowland pastoral Ahirau Stream (519 kg ha^{-1}, Table 8), was similar to the 578 kg ha^{-1} yield estimate of longfinned eels reported by Burnet (1952) in nearby lowland pastoral Kaniwhaniwha Stream. Biomass estimates in other pastoral streams (129–361 kg ha^{-1}) were generally similar to catches in the upper Waipa River (308 kg ha^{-1}, Burnet 1952). The yield from forested Hakarimata Range streams and Mangakara Stream (107 and 36 kg ha^{-1}) was also similar to the estimate of 62 kg ha^{-1} in the forested Ngakoaohia Stream (Burnet 1952). These similarities are surprising given the considerable commercial exploitation that eel populations have undergone during the last 4 decades. This may imply that recruitment levels have remained relatively constant.

Management implications

The relatively fast growth rates achieved by longfinned eels in Lakes Karapiro and Matahina suggest a method by which the commercial fishery and possibly potential breeding stocks could be enhanced. Improved access of eels into hydro-impoundments by construction of elver passes over dams throughout the country (e.g., Mitchell 1990; Mitchell & Boubée 1990), may provide highly productive new fisheries. In addition, if downstream passage from these lakes was provided for mature eels, longfinned eel breeding stocks may also be enhanced.

Hydro-electric impoundments in New Zealand rivers are generally considerable distances upstream from the sea, and have low population densities of land-locked eels, making them well suited for the production of female longfinned eels. Over 50% of longfinned eels caught in Lakes Karapiro and Matahina were larger than 750 mm and within the size range of mature females (Todd 1980; Jellyman & Todd 1982). There is evidence from work on *A. anguilla* that the proportion of females in an eel population increases with distance upstream (Aprahamian 1988). Occurrence of females in an eel population is also high if population density is low (Rossi & Colombo 1979; Colombo et al. 1984). The selective production of female eels in the hydro-lakes is nationally important for the fishery because commercial fishing pressure tends to selectively remove females from the population.

The considerable age of females from forested streams (≥ 48 years) has particular significance in terms of production from reserve areas. To maintain breeding stocks of longfinned eels, reserve areas (where commercial fishing is prohibited) are advocated to ultimately ensure recruitment of juveniles throughout New Zealand (Todd 1981; Todd & Dodgshun 1982). Almost all such areas are under indigenous forest (such as in national parks and scenic reserves), and are removed from the coast. Most rivers flowing from these reserve areas are likely to be exposed to commercial fishing pressure in their lowland reaches. There is clearly a need for protection of longfinned eel females as they migrate from reserve areas. This could best be accomplished by imposing an upper size restriction on the commercial fishery (e.g., 1500 g, Table 9). The particularly slow growth of eels from these areas, causing considerable time lags between generations, makes conservation of such stocks important.

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