A review of age and growth data for New Zealand freshwater eels (*Anguilla* spp.).

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1.   EXECUTIVE SUMMARY

A review of published and unpublished age and growth studies of New Zealand freshwater eels is presented, and the growth-related biology is summarised. Authors of growth studies have often postulated why growth varied between areas, but as the studies were of wild populations none of the assumed influential factors could be experimentally controlled. A growth model is presented to help determine which factors most affect growth, using the available data sets. Habitat type (which is probably an alias for food availability) appears to be the most important factor. Eel density, particularly of conspecifics, is also important. The length of the growth season is determined by water temperature. Ideally, any further studies to investigate variation in growth will collect detailed nutritional and environmental data, and provide density estimates for both eel species. Eel fishing has the potential to alter growth rates if it results in significant changes in eel densities. Apparent variations in otolith interpretation between readers can be controlled if one reader verifies all data sets, or if a detailed reading protocol is established.

2.   INTRODUCTION

Two species of freshwater eel occur in New Zealand. The longfinned eel (*Anguilla dieffenbachii*) is an endemic species. The shortfinned eel (*A. australis*) also occurs in southeast Australia, Tasmania, New Caledonia, and some South Pacific islands. Both species are widespread throughout New Zealand and frequently occur in the same habitat. However, the longfin has a preference for flowing waters and tends to penetrate further inland than the shortfin (Jellyman 1994).

The commercial fishery for eels developed in the 1960s, though annual catches were less than 100 t until 1967. Landings peaked at 2434 t in 1975, and have been relatively stable at about 1400 t annually since 1982 (Jellyman 1993). North Island landings comprise about two-thirds shortfins, whereas in the South Island the two species are landed in approximately equal quantities. Management of commercial fishing for eels is currently limited to controls on netting practices, minimum fish sizes, and a moratorium on issuing new licences (Jellyman 1993). Lake Ellesmere is the only eel fishing area for which an annual quota is specified.

Jellyman (1993) listed one of the three main areas of concern which influence the management of the eel fishery as the "slow growth rates of eels, and their consequent vulnerability to over-fishing". Some commercial fishers have opposed the conclusion that eel growth is slow, and they consider that this has led to an unduly conservative approach to eel management and conservation. Some maintain that eels grow much faster in certain areas that they fish, but no studies have demonstrated a correlation between growth rate and fishing pressure.

Cairns (1941) produced the first report on age and growth of New Zealand eels, but his study probably combines data from several sample sites. Subsequently, numerous published and unpublished age data sets have become available, and they demonstrate that growth rates for both species can vary considerably between and within catchments (e.g., Chisnall & Hicks 1993). Published studies often discuss factors that could cause growth rate variations. Jellyman (in press) examined 19 and 26 data sets for shortfins and longfins, respectively, and concluded that the factors most likely to affect growth rates are eel density, food availability, and interactions between eel species. Water temperature was a less important factor.

The intent of the current review, requested by the Inshore 2 Fishery Assessment Working Group, is to:

i.   collate all existing literature and any available unpublished data on the growth of New Zealand species of *Anguilla*;

ii.   summarise the growth-related biology of *Anguilla* spp. in New Zealand;

iii. look for trends and factors that might help explain the wide variations in growth rates, and attempt to create a growth model incorporating these factors; and

iv.   evaluate the requirements for further ageing studies and investigations of growth in different habitats.

3.   LITERATURE REVIEW

Although many of the data sets available for examination are unpublished or only in summarised form, a significant body of discussion is associated with the numerous published papers. This information has been searched to see whether it provides answers to any of the following growth-related questions.

3.1   What causes variations in growth between areas?

Chisnall & Hayes (1991) sampled shortfin eels in various habitats in the lower Waikato River catchment. They concluded that the faster growth of older (13+ years) eels in Lake Waahi, relative to Lake Whangape, was due to a greater abundance of food (mysid shrimps and common bullies). Lake Waikare eels had an even faster growth rate, and this was attributed to this lake having very low densities of eels following poor recruitment and heavy fishing. Several factors were presumed to cause the low growth rates in pastoral streams relative to lakes: lower minimum water temperatures, lower food abundance, and greater energy expenditure requirements to maintain station in moving waters. Inter-specific competition effects were also postulated; while the eel population in the sampled lakes and swamp comprised 95% shortfins, in the pastoral streams about half the eels were longfins. The Whangamarino Swamp contained two colour morphs of eels (light and dark), with the dark eels being the slowest growing of any population, while the light eels exhibited moderate growth. Chisnall & Hayes (1991) postulated that the dark morph eels were permanent residents of the swamp, and hence were subject to periods of low water levels during summer causing reduced mobility and low food availability. Summer is an important growth period

for most eels. The light morph eels were presumed to have moved into the swamp from adjacent waterways and lakes at times of high water levels, and so had growth rates comparable to eels from these habitats.

Chisnall (1993) reported on the growth of longfin and shortfin eels from the lower Waikato River, including several hydro lakes. Eels in hydro lakes (particularly Lake Arapuni) exhibited fast growth attributable to low eel densities (due to poor recruitment) and abundance of food. In the river, commercial fishing had removed most of the large eels. The remaining small eels (mostly less than 50 cm long) were abundant, but their growth was constrained due probably to inter- and intra-specific competition for food. Eel densities were also high in the Waikato River estuary, but the abundance and diversity of prey in this habitat allowed growth to remain relatively high.

The availability and energy content of food can exert both short-term and long-term influences on growth. Chisnall (1993) reported increases in growth rates when shortfin eels attained a length of about 45 cm. He postulated that at that size eels are able to change to a predominantly piscivorous, high energy, diet. Growth rates can also decrease over time, as shown by Chisnall (1994) for shortfins in the Taharoa lakes. Juveniles grew faster than at most Waikato sites, but as eels became larger growth slowed, due probably to a shortage of prey. Chisnall (1989) found seasonal variations in growth of shortfins in backwaters of the Waikato River. In autumn, growth rates of eels younger than about 10 years declined, possibly due to a reduced abundance of aquatic invertebrates. In contrast, the growth rate of older eels increased at the same time, in parallel with the renewed availability of fish and shrimp prey species.

Chisnall & Hicks (1993) examined the growth of longfin eels in streams through pasture and indigenous forest, and found that growth in pastoral streams was significantly greater. They postulated that the increased light exposure on pastoral streams produced higher water temperatures and higher trophic status. Also, more terrestrial invertebrates were washed into streams through pasture. Pastoral streams tend to have lower gradients than those through forest, producing more deep pools, and requiring eels to expend less energy to maintain their position. In a comparison of two similar pastoral streams, the growth of longfins was faster in the Ahirau Stream (where the population was dominated by large longfin eels in the productive pools) than in the Mangahanene Stream (where there were approximately equal numbers of large eels of both species evenly distributed along the stream). Inter- and intra-specific competition was likely to have been greater in the latter stream, causing a reduced growth rate.

Growth of longfins in hydro lakes was also relatively fast. As found for shortfins, the lower eel densities in these habitats, combined with the reduced need for motile energy expenditure, probably acts to enhance growth (Chisnall & Hicks 1993).

Greater eel densities in the south branch of the Waimakariri River were postulated as the reason why both species of eel at that site had slower growth than those in the Doyleston Drain or the Cust Main Drain (Burnet 1969). Harries (1974) noted a wide range of growth rates for longfins within and between sites on the Clutha and Taieri Rivers, but did not suggest causes for this variation.

Low water temperatures are known to lower shortfin growth rates (Cairns 1941, Chisnall 1989), so it can be assumed that eels in habitats with extended periods of low water temperatures will have growth rates relatively slower than eels in consistently warmer habitats. At temperatures below about 6 °C eel motility and feeding activity virtually ceases (Harries 1974, Ryan 1984, Jellyman 1991).

In summary, numerous factors have been postulated to cause variation in growth rates, but none have been tested experimentally. Factors presumed to enhance growth are an abundance of food, reduced eel densities (due either to fishing mortality or poor recruitment), higher water temperatures, and the need to expend less energy in still or slow moving waters.

3.2 Do individual eels have a consistent growth rate?

Harries (1974) and Chisnall & Hicks (1993) examined the growth of individual longfin eels over time by assuming that otolith band width was proportional to growth in body length in the year the band formed. In both studies, growth was found to be variable within the life histories of individual fish.

Chisnall & Hicks (1993) classified otolith bands into three categories, narrow, medium, and wide. They found that most otoliths showed variation in band width, but that most eels from a particular habitat had more than 60% of their bands in one category. From these results, it was assumed that eels had different growth rates in different habitats as they migrated upstream, but that there was limited movement between habitats by non-migratory adults (and hence, relatively constant growth).

The relatively sedentary nature of adult eels is supported by tagging studies. Burnet (1969) tagged longfin and shortfin eels, recovered about 20% of tags over the following 3 years, and found that recaptures were generally made in the same 180 m section of waterway where the eels had been released. Tagged eels were as short as 10 cm, but recaptures were rare below 30 cm, due probably to migration out of the study area by the smaller eels. Chisnall & Kalish (1993) tagged 22 longfin and 25 shortfin eels in a 420 m section of stream, and in the next 3 years recaptured 68% and 40% of the shortfins and longfins, respectively. Few eels had moved more than 20 m from their tagging site, with the maximum movement being 140 m. No tagged eels were caught when fishing 200 m above or 500 m below the study reach.

3.3 What is the effect of fishing on growth rate?

Only two studies present sets of age and growth data collected at the same location, but separated in time by a period of heavy fishing pressure.

Chisnall & Hayes (1991) reported on a comparison of shortfin growth in Lake Waikare. The first sample was collected in 1980–81 when fishing pressure was low to moderate, and the second in 1987 after a period of heavy fishing which had clearly lowered eel densities. Eels sampled in 1987 had a growth rate about four times faster than that calculated for the 1980–81 sample, implying that reduced eel densities due to heavy fishing pressure led to increased growth rates for those eels surviving. While the two samples were aged by different readers, it is unlikely that between-reader differences in otolith interpretation could account for the significant difference in slopes of the age-length relationship.

Jellyman *et al.* (1995) compared shortfin growth rates at two sites in the Lake Ellesmere catchment. Samples were taken at Timberyard Point in 1974–75 and 1995, and in Kaituna Lagoon in 1974–76 and 1994. Fishing pressure at both sites was low to moderate prior to the first sample, and high before the second (although the lagoon was the less fished of the two sites). Growth rates in the 1990s were higher than those in the 1970s, and most of this increase was exhibited by large females. Growth rates for the smaller males had not changed at Timberyard Point, but were higher at Kaituna Lagoon. Overall, the changes were slight, particularly when compared with the Lake Waikare data above. The Lake Ellesmere otoliths were also aged by different readers.

Chisnall (1994) sampled large shortfin eels from Lake Harihari in 1994, after a period of heavy fishing in 1992. The most recent otolith bands were distinctly wide, indicating a period of fast growth during 1993. This is consistent with reduced competition amongst larger eels following heavy fishing.

3.4 Do eels mature or migrate at a particular age?

Todd (1974, 1980) sampled migrating shortfin and longfin eels from various sites over a wide geographical range and concluded that age, rather than length, was probably the factor inducing migration to spawn. There were wide variations in the size and age at migration for both species. However, males of a species consistently migrated at a younger age (and smaller size) than females, and shortfins migrated at a younger age (and smaller size) than longfins. Average ages at migration for males and females, respectively, were 14 and 22 years for shortfins, and 25 and 36 years for longfins. The age range of shortfin eels migrating from Lake Onoke was 8–22 years for males and 12–35 years for females (Todd 1980).

Shortfin males from Lake Ellesmere showed no change in mean age at migration over the period 1975–95 (Jellyman *et al.* 1995). The mean age was between 14 and 15 years, with a range of 8–22 years. This study did indicate that males were maturing at a slightly smaller size in the 1990s than in the 1970s, but it is still likely that maturity is primarily determined by size (D. Jellyman, pers. comm.).

Burnet (1969) and Harries (1974) presented data on mean size at migration. The means and ranges were comparable to those of Todd (1974). Harries (1974) postulated that sexual maturation of longfins was more related to length than age, although this conclusion was based on the relationship between ovary size and body length rather than actual size or age at the time of spawning migration. He also concluded that faster growing eels matured at a relatively smaller body length than slow growing eels.

3.5 Is recruitment variation evident?

A variation in year class strengths is noted in only one study. Jellyman *et al.* (1995) concluded that a strong 1963 year class of male shortfins was apparent migrating from Lake Ellesmere in 1978 and 1979 (as 15- and 16-year-olds, respectively).

In a study of glass-eel migration, Jellyman (1979a) fished the same site in the Waikato River from August to November in 1972–74. There was a nine-fold difference between years in the total weight of glass-eels caught.

In other studies when raw age-length data are plotted, sample sizes are generally too small to draw sound conclusions about year class strength. Difficulties with otolith interpretation, a significant problem when ageing older fish (Todd 1974, Chisnall & Hicks 1993, Jellyman 1995), would also tend to smear a strong year class across several age groups.

Significant recruitment variation must occur, particularly in habitats that are at times cut off from the sea by natural barriers (e.g., Lake Ellesmere, Wairarapa lakes).

3.6   Can instantaneous total mortality be estimated?

Jellyman (1995) estimated instantaneous total mortality (Z) to be 0.02 for longfins in upland Lake Rotoiti, Nelson. This population produced the longest lived and some of the slowest growing eels of any New Zealand sample. As the lake has not been commercially fished, Z is also an estimate of instantaneous natural mortality (M). M was similarly estimated for unexploited stocks of eels in Lake Pounui, Wairarapa, and gave values of 0.038 for shortfins and 0.036 for longfins (D. Jellyman, unpublished data).

Estimates of Z for shortfins from Lake Ellesmere are 0.20 for the period 1974–81, and 0.25 for 1994–95 (Jellyman et al. 1995). Both values would include a component attributable to fishing mortality, and it is likely that the increase in Z between samples is entirely attributable to increased fishing pressure.

Chisnall & Stephens (unpublished results) calculated estimates of Z for numerous samples from the Waikato River, Taharoa lakes, and Rangitaiki River catchments. For longfin eels, all the estimates were from populations which had been fished lightly or not at all, and Z ranged from 0.01 to 0.05. For shortfins, the samples comprised populations that had experienced the full range of fishing pressures (nil to very high), and Z ranged from 0.02 to 0.15. There was a positive, but poor, correlation between fishing pressure and Z. It must be noted that many of these estimates were based on relatively small samples of aged fish.

4.   MODELLING METHODS

Each available set of age-length data was characterised to produce the various predictor and dependent variables outlined below. Individual data were not available; this work was done using published (or unpublished) estimates of age-length relationships. Data are presented separately for shortfin (Table 1) and longfin (Table 2) eels.

Predictor variables

Catchment
Habitat type
Fishing intensity prior to sampling
Density of the eel species being examined
Density of both eel species combined
Food availability

Otolith reader
Mean water temperature

The first seven variables above are defined in Appendix 1. Where possible, eel density values were based on experimental data which provided some measure of relative biomass. However, about 40% of these values had to be estimated by "educated guess", so all density estimates were "binned" into one of six qualitative categories ranging from zero to very high. The fishing intensity values were based largely on local knowledge, as catch records do not detail precisely where fish were caught, so it was also a qualitative index. The food availability variable was more an index of the abundance of other non-eel fish, as estimated for the Waikato and Rangitaiki catchments by Chisnall & Stephens (unpublished results), so probably underestimated food availability at sites where the invertebrate biomass was high relative to the fish biomass.

Mean annual water temperature (Temp, °C) was estimated for each sample from latitude (Lat) and altitude (Alt) data using the equation from Mosley (1982), where:

$$\text{Temp} = 95.8 - (46.5 * \log(\text{Lat})) - (3.46 * \log(\text{Alt}))$$

Dependent variables

Slope of the age-length relationship (where age is in years and length is in millimetre)
Length at age 15 years (shortfins) or 20 years (longfins)
Weight at age 15 years (shortfins) or 20 years (longfins)

Most age-length relationships were considered to be linear over the available ranges of age, but curves had been fitted to some data sets, i.e., shortfin samples 24 and 27–33 and longfin samples 17, 19, and 20. To obtain a slope for the data sets where curved relationships had been presented, a linear approximation was calculated by regressing points on the curve at 3 year intervals from age 10 years to the maximum recorded age. An example of this procedure is given in Figure 1. Length at age 15 or 20 years was derived from the original curved relationship. "Age" in all data sets was assumed to represent completed years of freshwater life.

Weight at age was estimated from an age-weight relationship (if one had been calculated), or by applying the length at age to a length-weight relationship (if one was presented). For samples where no age-weight or length-weight equations were available, weight at age was estimated using a length-weight relationship from a similar habitat type, preferably in the same catchment. Samples requiring the last procedure are noted in Tables 1 and 2.

Additional data

Items of information obtained for each data set but not used in the model were:

Location – a geographical name, e.g. "Lake Waikare", "Balclutha".
Latitude and altitude – used to estimate mean annual water temperature.
Sample date – year when all or most of the sample was collected.

Sample method – provided information on whether the sample was likely to represent all sections of the population in the survey area, e.g., a fyke net made with 12 mm mesh would allow the escapement of small eels.

Ageing method – allowed a judgement on the validity of the data.

Age range – showed whether the calculated age-length relationship could be used to derive a valid length at age 15 or 20 years.

Location, latitude, altitude, and sample data are presented in Tables 1 and 2.

The model

Data for each species were analysed separately. Preliminary data analysis tested for non-linear relationships between pairs of predictor and dependent variables. ("Catchment", "habitat type", and "otolith reader" were not included in this analysis.) All but one of the relationships appeared to be random; two examples are presented in Figure 2. The exception was the relationship between fishing pressure and the slope of the age-length equation for shortfin eels which was best described by a quadratic function (see Figure 2).

A multiple regression technique was used to examine how the eight predictor variables influenced the three dependent variables. The dependent variables were analysed separately. Initially, all predictor variables except "water temperature" were classified as categoric, but the results obtained when modelling were nonsensical from a biological perspective. They indicated that one or more of the variables eel density, food availability, and fishing pressure was a significant predictor, but that its categories influenced growth in a random way. For example, eel density categories 0, 1, and 4 might enhance growth, but categories 2, 3, and 5 retarded it. To be useful predictors, these variables would have to influence growth in a regular manner. Classifying them as continuous variables showed whether they had any regular significant effect. Consequently, in the modelling results presented below, all variables except "catchment", "habitat type", and "otolith reader" were classified as continuous. The general form of the model was, therefore:

$\log_e$(dependent variable) = intercept + k_1(water temperature) + k_2(food abundance) + k_3(specific eel density) + k_4(total eel density) + k_5(fishing pressure) + catchment + habitat type + otolith reader

where intercept and k_n are constants, and catchment, habitat type, and otolith reader are constants related to a particular category of those variables. [In the shortfin model with slope as the dependent variable, fishing pressure (FP) was modelled as a quadratic, i.e., k_5(FP) + k_6(FP*FP).]

The number of fish aged in each sample was used as a weighting factor for that sample in the model. It was assumed that confidence in the slope or the length at a particular age was proportional to the number of data points in the sample. Ideally, the standard errors of the regression coefficients would be used to obtain sample weightings, but these were unavailable for virtually all samples.

The logarithms of the dependent variables were modelled to ensure that positive dependent variables were predicted. When modelling untransformed dependents it was found that

negative values could be predicted from logical sets of predictor variables. The transformed data models also explained more variance.

For each model, the natural logarithm of the chosen dependent variable was regressed against each of the predictor variables to determine which explained the most variability in the dependent variable. This predictor variable was then included in the model and the regression was repeated against the selected variable and each of the other predictor variables to determine the next most powerful variable. The stepwise regression procedure was continued until an F test showed that the increase in the sum of squares of regression (SSR) from an extra variable was not significant at the 5% level, i.e., the probability of obtaining a larger value of $F_{1,N-k}$ was less than 0.05, where

$$F_{1,N-k} = \frac{\Delta SSR}{SSE/(N-k-1)}$$

and where N is the number of records in the sample, k is the number of variables already used in the regression, ΔSSR is the increase in SSR due to the addition of the extra variable, and SSE is the sum of squares of the error (before adding the extra variable). At each iteration, the predictor variable with the most explaining power was chosen using the SSR as a measure of the amount of variability in the data explained by the variables included in the model.

5.   RESULTS

5.1   Data set comparability

The sampled sites are plotted, by species, in Figure 3. Samples had been collected over the period 1956 to 1995, generally using one or more of the following capture methods: electric fishing, line fishing, baited traps, and fyke nets with mesh sizes ranging from 1 to 12 mm. Multiple capture methods were sometimes used to attempt to sample the full size range of the population (e.g., Jellyman 1995). The samples of large eels from hydro-electric Lake Aniwhenua were collected from the intake screens.

It appears that all methods poorly sample very small eels owing either to technical or behavioural reasons. Electric fishing is the method best able to sample small eels (Chisnall & Stephens, unpublished results), but even with this technique, stunned elvers are harder to detect and collect than larger eels. However, the poor representation of small eels was not considered a problem in the current analysis. The eels not sampled would generally be less than 7 years old, so would have no effect on the calculated mean length at age 15 or 20 years. Also, removing the juvenile data allowed the age-length relationship for the remaining eels to be treated as linear rather than a curve, enabling a comparison of slopes (i.e., growth rates) within the model.

Counts of rings in otoliths formed the basis for all the age data sets. Burnet (1969) used growth increments of tagged and recaptured eels to define adult growth, but relied on ages from otolith ring counts to determine juvenile growth, and, hence, confirm the calculated adult growth curve. An examination of seasonal changes in otolith margins (Jellyman 1979b) and the tagging and recapture of eels injected with oxytetracycline (Chisnall & Kalish 1993) have

shown that zones in otoliths form annually in both *Anguilla australis* and *A. dieffenbachii*. Counting zones in scales results in underestimates of age (Todd 1974, Jellyman 1979b).

Although all the data sets examined here were based on otolith ring counts, the counts were derived by numerous workers, and it is not known whether they all used a similar interpretation. Eel otoliths can be difficult to read. They are small, band width can vary considerably within an otolith (Chisnall & Hicks 1993), and bands on otoliths from old fish are narrow and difficult to differentiate (Todd 1980, Jellyman 1995). Current workers (i.e., B. Chisnall, D. Jellyman, and co-workers) agree on how otolith bands should be interpreted. Otoliths from most earlier studies are not available, so it is not possible to independently determine whether otoliths from all studies were interpreted similarly. Todd (1974, p. 160) noted that "the general spacing of rings was important and any irregularly spaced black rings were called false rings and not counted", which appears to contrast with the findings of Chisnall & Hicks (1993) that annual band width was variable throughout the fish's life. The model presented below tested for a reader effect on growth.

5.2 Growth model

Otolith sample size varied considerably, with ranges of 10–1437 for shortfins and 7–344 for longfins. It was assumed in the final analysis presented here that the accuracy of an age-length relationship was proportional to the number of points used to derive it. However, other runs of the model using either no weighting factor, or weighting by log(sample size), changed only the order of importance of the non-significant variables.

For shortfin eels, the slope of the age-length relationship was not well described by the available variables (Table 3). "Catchment" was the most important variable, and the inclusion of "otolith reader" produced a significant improvement in the model fit, although the R^2 value was only 0.36. "Habitat type" was the next most influential variable, but its inclusion did not improve the fit using the significance criteria adopted here. The addition of the next most influential variable (fishing pressure) did improve the model significantly. The length and weight at age 15 years for shortfins were much better described, with the variables "catchment", "habitat type", and "otolith reader" being the significant predictors (R^2: 0.82 for length, 0.86 for weight). Hence, all dependent variables were influenced most by the same set of three predictor variables.

For longfin eels, the slope of the age-length relationship was quite well described ($R^2 = 0.78$) by the same set of three predictor variables (Table 4). "Catchment" had the most explaining power, followed by "habitat type", then "abundance of longfin eels". For the length- and weight-at-age models, the same three predictor variables explained the bulk of the variance, but the addition of "water temperature" and "total eel abundance" was found to significantly improve the explaining power of the models. R^2 values for the length-at-age and the weight-at-age models (after all significant predictor variables had been included) were both 0.90.

The first iteration of the longfin model indicated that "otolith reader" would be a significant predictor for both the dependent variables (*see* Table 4). However, subsequent iterations indicated that all the variation attributable to "otolith reader" was explained by "catchment". This was different to the result obtained for shortfins, where "catchment" and "otolith reader" were both important predictor variables and appeared to explain different sections of the total

variation within the model.

Values for the constants and variables in the six models are given in Table 5. For shortfinned eels, the Waimakariri catchment appeared to be related to slow growth, while Himitangi, Makara Stream, and the Rangitaiki River appeared to promote growth. The habitat effect indicated that hydro-electric lakes clearly promoted growth, eels from lowland lakes and estuaries had moderate growth, and growth was slowest in swamps, pastoral streams, and lowland rivers. The otolith reader effect implied that Burnet (1969) estimated a greater age at length relative to all other readers, and that variation between the more recent readers was less marked but still significant.

For longfin eels, the Makara, Rotoiti, and Waimakariri catchments appeared to promote slow growth, and the south Wairarapa and Taharoa catchments were associated with fast growth. However, as noted above, much of the catchment effect in these models was explained by otolith reader differences. Growth was slow in swamp, lowland lake, and upland lake habitats, moderate in lowland river and forested streams, and fastest in estuaries, pastoral streams, and hydro lakes.

6. DISCUSSION

It is immediately apparent from the literature review and the modelling exercise that the determinants of eel growth are very complicated. Growth rates of individual fish of both species vary significantly between catchments, within a catchment, and even within small sections of a catchment. Growth can also vary within the life history of an individual fish. Also, the true determinants of growth are confounded by apparent difficulties with otolith interpretation, by sexual differences in growth which were generally not examined, and by an undefined "catchment" factor which is important in the model.

6.1 Otolith interpretation

Numerous authors noted a difficulty in interpreting bands in otoliths, particularly when the fish are old and the bands are narrow. Although most studies conducted since 1980 used the same otolith preparation technique (Hu & Todd 1981), the predictor variable "otolith reader" explained a significant proportion of the variation in all growth models (although for longfins it became incorporated in the "catchment" effect). Much of this variation was attributable to Burnet's (1969) growth curves calculated from growth increments after tagging, and it is known that age data calculated from this technique may not be strictly comparable to otolith data (Francis 1988). However, significant variation was also apparent between otolith readers. Jellyman et al. (1995) reported a between-reader comparison (for readers L. Hu and P. Todd) which demonstrates the interpretation problem. Of 296 shortfin otoliths examined, only 56% (166) were considered readable by both readers. Of those 166 otoliths with an age range of 6–25 years, 51% were aged identically, and another 34% differed by 1 year. There did not appear to be any bias between readers. An examination of within-reader variance by B. Chisnall, who was the primary reader for most of the age-length data sets, indicated that 80% of second readings were within ± 1 year of the first (B. Chisnall, pers. comm.). Between-reader data for B. Chisnall and D. Jellyman found 95% of readings were within ± 3 years.

Differences between readers may not produce growth relationships that are significantly different biologically, and these relationships are probably satisfactory for stock assessment purposes. However, in any programme examining the causes of variation in eel growth, it would be important that one worker reads, or at least validates the readings of, all otoliths used in the study.

6.2   Sexual differences in growth

Sexual differences in growth have been widely reported for *Anguilla* species around the world (Jellyman, in press), and have been noted for both New Zealand species (Harries 1974, Todd 1974). However, this aspect has seldom been incorporated into growth studies, presumably because of the difficulty of determining the sex of a non-migrating eel (Harries 1974). (Eels spawn only once, after they migrate to sea, so for most of their lives in fresh water they have small, poorly developed gonads which are difficult to sex macroscopically.) Todd (1974) noted that in the Makara Stream, shortfin females were 2–10 cm longer than males at equivalent ages, but that the difference between longfins was less pronounced. He also noted that eels for which sex could not be determined macroscopically had an even slower rate of growth than that for males. Jellyman *et al.* (1995) reported female shortfins from Lake Ellesmere to be only about 6 mm longer than males at age 15 years, but about 23 mm longer by age 20. Harries (1974) examined sexual differences in growth of longfins at four sites on the Taieri River, and found that growth rates diverged only after about 15 years, but that females could be 5–18 cm longer than males at age 30.

The differences in growth rates between sexes could appear as between-area variations if sex ratios differ between sites. Harries (1974) found sex ratios at sites on the Taieri River to vary from 100% females to two males per female. Ratios could vary significantly over small distances; at Meggat Burn the ratio of females to males was 43 : 1, yet it was 1.6 : 1 only 5 km away at Waihola. Todd (1974) found the ratio of shortfin females to males in Lake Ellesmere to be 1 : 59 over the period 1972–80, which contrasts sharply with a ratio of 14 : 1 calculated for the same habitat in 1942.

Clearly, sex ratios could influence the calculated growth rate for a sample. This factor could not be examined in this review because there is little information linking length, age, and sex. Such information will be difficult to collect. Harries (1974) noted that macroscopic sex differentiation of non-mature eels is difficult and can be erroneous. Of the eels that Harries attempted to sex, 36% were indeterminate, although most fish longer than 60 cm could be sexed.

Fishing could also change the apparent growth rate at a site if it altered the sex ratio of the resident population. This would most likely show up as a reduction in growth rate due to the removal of many of the larger (and faster growing) females.

6.3   The catchment effect

The catchment variable explained the most variation in both models for both species. However, of all the variables examined in the model, this was the least well understood. It was apparent that catchment described different effects for the two species. For longfins, much of the catchment effect was explained by between-reader ageing variation, as might be

expected where different workers have tended to investigate eels in different catchments. But for shortfins, the catchment effect appeared to be independent of between-reader variation.

Aspects which may combine to produce a catchment effect are water temperature, sex ratio, and nutrition. Low temperatures are known to retard eel growth. Water temperatures were measured in few of the studies, so mean annual temperatures were estimated from latitude and altitude data. However, the generalised equation of Mosley (1982) would not account for individual peculiarities of a sample site, e.g., spring-fed waters may be relatively cool, while shallow unshaded waterways may be relatively warm. The possible effect on apparent growth rates of sex ratio differences between populations has been described above. Nutrition levels and the availability of preferred food items could vary significantly between catchments. The food abundance variable examined in the model described only the abundance of other fish species (not invertebrates) and was only roughly estimated for many of the samples. Growth is certainly influenced by food availability and this aspect was poorly examined in the model presented here. It is possible that much of the catchment effect could be explained if more comprehensive nutritional data were available.

6.4   Summary and requirements for future investigations

Although a significant body of age and growth data exists, most of the studies were of eels from the Waikato River catchment. The geographical distribution of the remaining data is sparse. No age data exist for eels from the Northland, Hawkes Bay, Manawatu, and Southland eel return areas; these areas combine to produce about a third of the annual eel landings. Some data are now quite old (e.g., Harries 1974) and may not be applicable to contemporary eel populations in the same areas because of, for example, habitat modifications or changes in eel densities.

The numerous published growth studies suggest that growth is influenced by a number of factors, with food availability and abundance of conspecifics being most influential, and interspecific competition and water temperature being secondary factors. These conclusions are based on the information from the available studies. However, all these studies were of wild populations, with no opportunity to control any factors and thereby test their influence.

The modelling exercise examined the influence on growth of several variables. The quality of the data was variable. The food abundance variable was the least reliable as it did not incorporate invertebrates or terrestrial derived food items. The eel abundance and fishing pressure variables were generally well known, but were sometimes based on educated guesses. All other variables were reliable. However, two of the most important variables in all the significant models (catchment and habitat type) often had only one or two data points in particular categories (see Tables 1 and 2). For both species, only three catchments had more than two data points. Conclusions drawn from models using such sparse data should be treated with caution.

Habitat type appeared to be an important variable for both species. It is probably a measure of food availability, and indicates that growth was fast in high productivity habitats (e.g., estuaries, pastoral streams) and slow where productivity is low (e.g., swamps, upland lakes). The abundance of conspecifics is an important factor affecting the growth of longfin eels. The catchment effect would probably decline in importance if more comprehensive productivity

and environmental data were available for individual study sites. The otolith reader effect can be controlled by having one reader verify all data sets, or by establishing a detailed reading protocol.

In conclusion, the major determinant of eel growth appears to be habitat type, which is probably an alias for the nutritional status of the sampled area. Eel density is also important. Conspecific interactions appear to be more influential than any interaction between species, suggesting that dietary separation, habitat preferences, or behavioural mechanisms act to reduce interspecific competition. The length of the growing season is probably strongly influenced by water temperature (Jellyman, in press).

Growth of New Zealand eels in natural habitats does appear to be slow relative to other temperate *Anguilla* species (Tesch 1977, Jellyman, in press). Of the samples examined in this review, 84% exhibited growth rates of 1–3 cm per year. Thus, the contention by some commercial fishers that New Zealand eels are not slow growing is not supported here. However, aquaculture trials have shown that both species have the potential to grow to 40–45 cm within a year (Jones *et al.* 1983), so it is unlikely that New Zealand eels are genetically predisposed to slow growth.

The contention by some commercial fishers that eels grow faster in areas that are fished could not be clarified here. Fishing pressure was not a significant variable in any of the growth models; the relationship between growth rate and fishing pressure appears to be random (*see* Figure 2). Comparisons of samples taken several years apart from the same site indicate that increased fishing activity can cause an increase in growth rate (Lake Waikare) or no change in growth rate (Lake Ellesmere). Thus, the lack of sufficient data precluded any conclusions on the effect of fishing on growth rates. This is an area where future work could be useful for eel management.

Any experimental investigation of the determinants of eel growth must control levels of nutrition, eel density, and water temperature. However, it is uncertain how such a study could be used to better manage wild stocks. As individual eels migrate through a catchment they will probably be exposed to differing, and generally unknown, regimes of nutrition, eel density, and temperature. Hence, an individual's growth could be variable, and variation of size at age within a population at a single site could also be substantial. It is possible to sample eels in a localised area and calculate a growth curve that fits the raw data well, but the applicability of this growth curve to the management of the rest of the stock is limited. Age data from throughout a catchment (or from an even wider area) could be combined to produce a growth relationship that is probably more applicable to stock assessment involving population modelling, even though variation of individual points around this curve will be great.

It may be possible to enhance the model presented above by obtaining more age-length data sets from some of the under-represented habitat types and geographical areas. This model could then be used to estimate mean growth of eels from areas where no growth data exist, based on the main habitat type of the area and some indices of eel abundance and water temperature. Ultimately, the degree of sophistication of any future ageing studies for stock assessment purposes will be dictated by the type of stock assessment method chosen.

7. ACKNOWLEDGMENTS

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Table 1: Summary of available data for shortfin eels. Lat, latitude; Alt, altitude (m asl); n, number of fish aged; Cat, catchment; Hab, habitat; FP, fishing pressure; Ab1, shortfin abundance; Ab2, total eel abundance; Food, food abundance; Reader, otolith reader; Temp, estimated mean water temperature (°C); Slope, slope of the age-length relationship; Leng, length at age 15 years (cm); Wght, weight at age 15 years (g); –, no data; *, indicates weight was estimated using a length-weight relationship from another sample

No.	Location	Lat	Alt	Year	n	Cat	Hab	FP	Ab1	Ab2	Food	Reader	Temp	Slope	Leng	Wght	Reference
1	Whangamarino swamp	37.32	20	1988	47	1	2	3	2	2	1	1	18.2	10.6	47	122	Chisnall & Hayes 1991
2	Whangamarino swamp	37.32	20	1988	16	1	2	4	4	4	1	1	18.2	23.3	51	311	Chisnall & Hayes 1991
3	Waikato River estuary	37.33	1	1992	92	1	1	5	2	2	5	1	22.7	19.7	49	367	Chisnall 1993
4	Lake Waikare	37.42	25	1979	50	1	6	2	4	4	5	2	17.8	10.6	46	181*	Todd unpublished in Chisnall 1989
5	Lake Waikare	37.42	25	1987	47	1	6	5	3	3	5	1	17.8	46.8	69	889	Chisnall & Hayes 1991
6	Huntly – Meremere	37.45	25	1984	76	1	5	5	2	2	5	1	17.8	12.6	44	171	Chisnall 1993
7	Lake Whangape	37.45	25	1987	96	1	6	5	5	5	3	1	17.8	23.3	48	178	Chisnall & Hayes 1991
8	Lake Rotongaroiti	37.47	25	1992	102	1	6	2	5	5	3	1	17.8	6.2	41	122*	Chisnall & Stephens unpublished data
9	Lake Rotongaro	37.48	25	1992	116	1	6	2	4	4	3	1	17.8	18.4	52	260*	Chisnall & Stephens unpublished data
10	Lake Waahi	37.53	25	1987	79	1	6	5	5	5	3	1	17.8	28.0	48	200	Chisnall & Hayes 1991
11	Huntly	37.55	22	1985	624	1	2	5	5	5	5	1	17.9	14.1	39	119	Chisnall 1993
12	Hakarimata	37.62	95	1987	103	1	3	2	1	2	2	1	15.7	15.9	40	114	Chisnall & Hayes 1991
13	Ahirau Stream	37.67	95	1989	85	1	3	1	2	3	4	1	15.7	21.9	44	162*	Chisnall & Kalish 1993
14	Lake Kainui	37.68	30	1992	74	1	6	3	1	1	1	1	17.4	12.6	43	174	Chisnall & Stephens unpublished data
15	Lake Okowhaeo	37.68	30	1992	82	1	6	2	1	1	1	1	17.4	15.5	48	223	Chisnall & Stephens unpublished data
16	Lake Ngaroto	37.95	30	1992	99	1	6	3	4	4	1	1	17.3	12.5	42	137	Chisnall & Stephens unpublished data
17	Lake Karapiro	37.98	60	1989	18	1	8	4	1	2	2	1	16.2	17.5	64	539	Chisnall 1993
18	Lake Arapuni	38.07	113	1992	10	1	8	1	1	1	2	1	15.2	43.5	103	2540	Chisnall 1993
19	Lake Harihari	38.15	5	1994	66	2	6	2	2	2	1	1	19.8	14.1	38	180	Chisnall 1994
20	Lake Taharoa	38.17	5	1993	113	2	6	1	2	2	1	1	19.8	16.0	52	231	Chisnall & Stephens unpublished data
21	Lake Numiti	38.18	5	1994	18	2	6	0	1	1	1	1	19.8	22.3	–	–	Chisnall 1994
22	Lake Matahina	38.15	30	1988	35	3	8	0	2	2	2	1	17.1	21.9	62	1315	Chisnall 1993
23	Lake Aniwhenua	38.25	100	1991	15	3	8	0	1	1	1	1	15.3	89.1	120	4419*	Mitchell & Chisnall 1992
24	Pukepuke lagoon	40.33	5	1972	127	4	6	1	5	5	4	3	18.7	27.1	68	694*	Jellyman 1979b
25	Makara Stream	41.22	15	1972	318	6	3	1	2	3	2	2	16.6	20.8	50	246	Todd 1974
26	Lake Wairarapa	41.25	1	1991	58	5	2	4	2	2	3	1	20.7	18.2	47	171*	Chisnall unpublished data
27	Lake Pounui	41.35	1	1978	513	5	6	0	1	1	4	3	20.7	15.2	38	88*	Jellyman unpublished data
28	South Branch	43.47	20	1957	50	8	3	0	2	3	3	4	15.1	12.7	22	18*	Burnet 1969
29	Doyleston Drain	43.77	10	1956	77	9	3	0	1	2	4	4	16.0	32.0	64	533	Burnet 1969
30	Kaituna lagoon	43.80	8	1976	611	9	6	1	5	5	4	2	16.3	15.6	45	169	Jellyman et al. 1995
31	Kaituna lagoon	43.80	8	1994	264	9	6	4	3	3	4	1	16.3	19.1	52	270	Jellyman et al. 1995
32	Timberyard Point	43.80	8	1975	1437	9	6	2	5	5	4	2	16.3	13.6	44	157	Jellyman et al. 1995
33	Timberyard Point	43.80	8	1995	208	9	6	5	3	3	4	1	16.3	13.4	46	181	Jellyman et al. 1995

Table 2: Summary of available data for longfin eels. Lat, latitude; Alt, altitude (m asl); *n*, number of fish aged; Cat, catchment; Hab, habitat; FP, fishing pressure; Ab1, longfin abundance; Ab2, total eel abundance; Food, food abundance; Reader, otolith reader; Temp, estimated mean water temperature (°C); Slope, slope of the age-length relationship; Leng, length at age 20 years (cm); Wght, weight at age 20 years (g); –, no data; *, indicates weight was estimated using a length-weight relationship from another sample

No.	Location	Lat	Alt	Year	*n*	Cat	Hab	FP	Ab1	Ab2	Food	Reader	Temp	Slope	Leng	Wght	Reference
1	Mangapiko Stream	37.43	160	1990	30	1	3	0	1	1	3	1	15.0	25.1	65	679	Chisnall & Hicks 1993
2	Lake Rotongaro	37.48	25	1992	28	1	6	2	2	5	3	1	17.8	10.8	50	254*	Chisnall & Stephens unpublished data
3	Huntly	37.55	25	1984	86	1	5	5	1	2	5	1	17.7	19.2	56	472	Chisnall 1993
4	Huntly	37.55	25	1985	217	1	2	5	2	5	5	1	17.7	13.7	46	310	Chisnall 1989
5	Hakarimata	37.62	95	1989	22	1	4	0	1	1	1	1	15.7	14.7	36	134	Chisnall & Hicks 1993
6	Hakarimata	37.62	95	1987	53	1	3	2	2	2	2	1	15.7	24.1	51	268	Chisnall & Hicks 1993
7	Ahirau Stream	37.67	95	1989	29	1	3	1	2	3	4	1	15.7	35.8	78	1408	Chisnall & Hicks 1993
8	Mangahanene Stream	37.95	100	1989	10	1	3	0	4	5	1	1	15.4	19.4	–	–	Chisnall & Hicks 1993
9	Lake Karapiro	37.98	60	1989	62	1	8	4	2	2	2	1	16.2	19.4	71	757	Chisnall & Hicks 1993
10	Mangakara	38.03	290	1990	11	1	4	0	1	1	1	1	13.8	11.9	49	433	Chisnall & Hicks 1993
11	Lake Arapuni	38.07	113	1992	10	1	8	1	1	1	2	1	15.2	23.4	107	3715	Chisnall 1993
12	Lake Taharoa	38.17	5	1993	19	2	6	1	1	2	1	1	19.8	24.8	67	708	Chisnall & Stephens unpublished data
13	Lake Waipapa	38.32	130	1992	7	1	8	0	1	1	2	1	14.9	15.8	–	–	Chisnall 1993
14	Lake Matahina	38.15	30	1988	22	3	8	0	2	2	2	1	17.1	18.8	57	483	Chisnall & Hicks 1993
15	Lake Aniwhenua	38.25	100	1991	13	3	8	0	1	1	1	1	15.3	31.0	82	1601*	Mitchell & Chisnall 1992
16	Makara Stream	41.22	15	1972	220	6	3	1	2	3	2	2	16.6	21.2	57	446	Todd 1974
17	Lake Pounui	41.35	1	1978	344	5	6	0	1	1	4	3	20.6	16.1	50	309	Jellyman unpublished data
18	Lake Rotoiti	41.80	610	1991	114	7	7	0	1	1	2	4	10.8	8.9	42	183	Jellyman 1995
19	Cust Main Drain	43.35	50	1956	104	8	3	0	1	2	4	4	13.8	17.0	47	208	Burnet 1969
20	South Branch	43.47	20	1957	123	8	3	0	2	3	3	4	15.1	8.5	30	48	Burnet 1969
21	Lee Stream	45.03	450	1974	50	10	3	1	4	4	3	5	9.7	15.2	45	181*	Harries 1974
22	McGregor's Drain	45.20	300	1974	49	10	3	1	4	4	3	5	10.3	26.3	66	629*	Harries 1974
23	Sutton Creek	45.57	180	1974	63	10	3	1	4	4	3	5	10.9	18.5	51	272*	Harries 1974
24	Silverstream	45.88	30	1974	42	10	3	1	3	3	3	5	13.4	25.0	68	694*	Harries 1974
25	Meggat Burn	45.95	20	1974	49	10	3	1	3	3	4	5	14.0	15.2	43	156*	Harries 1974
26	Henley	45.97	1	1974	23	10	1	1	1	1	5	5	18.5	25.7	74	914*	Harries 1974
27	Waihola Channel	46.02	1	1974	44	10	1	1	2	2	5	5	18.5	16.8	53	308*	Harries 1974
28	Alexandra	45.57	135	1974	36	11	5	1	2	2	3	5	11.4	5.2	72	836*	Harries 1974
29	Balclutha	46.25	9	1974	17	11	5	1	2	2	3	5	15.1	17.4	51	272*	Harries 1974
30	Puerua	46.37	1	1974	40	11	1	1	3	3	5	5	18.3	10.0	52	289*	Harries 1974

Table 3: Choice of variables in order of importance for shortfin eels in the stepwise regression of [A] $\log_e$(slope of the age-length relationship), [B] $\log_e$(length at age 15 years), and [C] $\log_e$(weight at age 15 years). Numbers in the table are the sums of squares of the regression, SSR. Significance levels for an F test showing whether the addition of the new variable improved the describing power of the model: **, P<0.01; *, P<0.05; NS, not significant. R^2, multiple regression coefficient of the best fit at each iteration

A. Slope of the age-length relationship

Variable	1	2	3	4	5	6	7	8
							SSR at iteration	
Catchment	102							
Otolith reader	27	162						
Habitat type	95	154	189					
Fishing pressure	46	151	189	249				
Water temperature	1	100	164	190	257			
Total eel abundance	23	127	168	202	256	261		
Shortfin abundance	33	136	167	205	255	260	264	
Food abundance	5	102	163	194	249	257	262	265
Significance of ΔSSR		*	NS	*	NS	NS	NS	NS
R^2	0.22	0.36	0.42	0.55	0.57	0.58	0.58	0.58

B. Length at age 15 years

Variable	1	2	3	4	5	6	7	8
							SSR at iteration	
Catchment	78							
Habitat type	33	96						
Otolith reader	3	94	117					
Food abundance	4	81	95	118				
Water temperature	3	78	98	117	120			
Total eel abundance	0	92	101	117	120	121		
Shortfin abundance	0	93	100	116	119	121	122	
Fishing pressure	0	78	98	116	119	120	121	124
Significance of ΔSSR		*	**	NS	NS	NS	NS	NS
R^2	0.55	0.67	0.82	0.83	0.84	0.85	0.86	0.87

C. Weight at age 15 years

Variable	1	2	3	4	5	6	7	8
							SSR at iteration	
Catchment	1011							
Habitat type	488	1246						
Otolith reader	67	1196	1452					
Food abundance	52	1061	1248	1470				
Total eel abundance	3	1230	1313	1464	1515			
Shortfin abundance	2	1213	1311	1463	1511	1527		
Water temperature	22	1078	1281	1452	1474	1516	1527	
Fishing pressure	4	1044	1273	1452	1470	1513	1527	1528
Significance of ΔSSR		**	**	NS	NS	NS	NS	NS
R^2	0.62	0.74	0.86	0.87	0.90	0.91	0.91	0.91

Table 4: Choice of variables in order of importance for longfin eels in the stepwise regression of [A] $\log_e$(slope of the age-length relationship), [B] $\log_e$(length at age 20 years), and [C] $\log_e$(weight at age 20 years). Numbers in the table are the sums of squares of the regression, SSR. Significance levels for an F test showing whether the addition of the new variable improved the describing power of the model: **, $P<0.01$; *, $P<0.05$; NS, not significant. R^2, multiple regression coefficient of the best fit at each iteration

A. Slope of the age-length relationship

Variable	1	2	3	4	5	6	7	8
							SSR at iteration	
Catchment	142							
Habitat type	71	186						
Longfin abundance	3	147	198					
Total eel abundance	0	165	194	206				
Fishing pressure	2	150	186	201	208			
Water temperature	8	143	185	198	206	211		
Food abundance	3	142	193	200	206	209	211	
Otolith reader	51	145	186	198	205	208	210	311
Significance of ΔSSR		**	*	NS	NS	NS	NS	NS
R^2	0.56	0.73	0.78	0.81	0.82	0.83	0.83	0.83

B. Length at age 20 years

Variable	1	2	3	4	5	6	7	8
							SSR at iteration	
Catchment	39							
Habitat type	26	57						
Longfin abundance	0	46	67					
Water temperature	0	41	61	74				
Total eel abundance	2	51	64	72	80			
Food abundance	1	40	58	68	76	81		
Fishing pressure	2	41	62	68	74	81	81	
Otolith reader	34	39	57	67	74	80	81	81
Significance of ΔSSR		**	**	*	**	NS	NS	NS
R^2	0.44	0.64	0.76	0.84	0.90	0.91	0.91	0.91

C. Weight at age 20 years

Variable	1	2	3	4	5	6	7	8
							SSR at iteration	
Catchment	480							
Habitat type	216	583						
Longfin abundance	1	556	696					
Water temperature	18	499	630	772				
Total eel abundance	10	551	649	753	845			
Food abundance	2	481	602	706	791	853		
Fishing pressure	56	490	640	698	775	846	855	
Otolith reader	433	477	584	695	772	846	853	855
Significance of ΔSSR		*	**	*	**	NS	NS	NS
R^2	0.51	0.62	0.74	0.82	0.90	0.91	0.91	0.91

Table 5: Values of constants and variables for the three growth models (slope, length at age, and weight at age) for the two species. For each categorical variable, the model selects one of the categories as a base case (indicated by variable = 0) and relates the other categories to it. nd, no data for that variable; –, variable not included in the final model

| Variable	Longfins			Shortfins		
	Slope	Length	Weight	Slope	Length	Weight
Intercept	2.761	6.755	14.986	3.466	4.756	8.227
Catchment						
Waikato River	0.577	–0.447	–1.465	–0.076	–0.030	–0.088
Taharoa lakes	1.203	0.664	2.723	–0.055	–0.054	–0.050
Rangitaiki River	0.694	–0.622	–1.803	0.692	–0.034	0.614
Himatangi	nd	nd	nd	0.664	0.730	2.316
Sth. Wairarapa	0.771	0.910	3.908	0.086	0.148	0.251
Makara Stream	0.343	–0.678	–2.352	0.389	0.248	0.804
Lake Rotoiti	–0.392	–1.757	–5.548	nd	nd	nd
Waimakariri River	–0.354	–1.439	–5.000	–0.924	–1.068	–3.388
Lake Ellesmere	nd	nd	nd	0.000	0.000	0.000
Taieri River	0.567	–0.249	–0.828	nd	nd	nd
Clutha River	0.000	0.000	0.000	nd	nd	nd
Habitat				–		
Estuary	0.047	–0.277	–0.852		–0.437	–0.938
Swamp	–0.309	–1.699	–5.791		–0.657	–2.040
Pastoral stream	0.362	–0.420	–1.327		–0.597	–1.948
Forested stream	–0.515	–0.978	–2.718		nd	nd
Lowland river	–0.229	–0.867	–2.830		–0.545	–1.702
Lowland lake	–0.547	–1.612	–5.979		–0.469	–1.530
Upland lake	–0.392	–1.757	–5.548		nd	nd
Hydro lake	0.000	0.000	0.000		0.000	0.000
Reader	–	–	–			
B. Chisnall				–0.650	–0.397	–1.296
P. Todd				–0.820	–0.494	–1.613
D. Jellyman				–0.830	–0.798	–2.470
A. Burnet				0.000	0.000	0.000
D. Harries				nd	nd	nd
Eel abundance (1 sp.)	–0.206	–0.764	–2.772	–	–	–
Eel abundance (2 sp.)	–	0.467	1.773	–	–	–
Water temperature	–	–0.089	–0.300	–	–	–
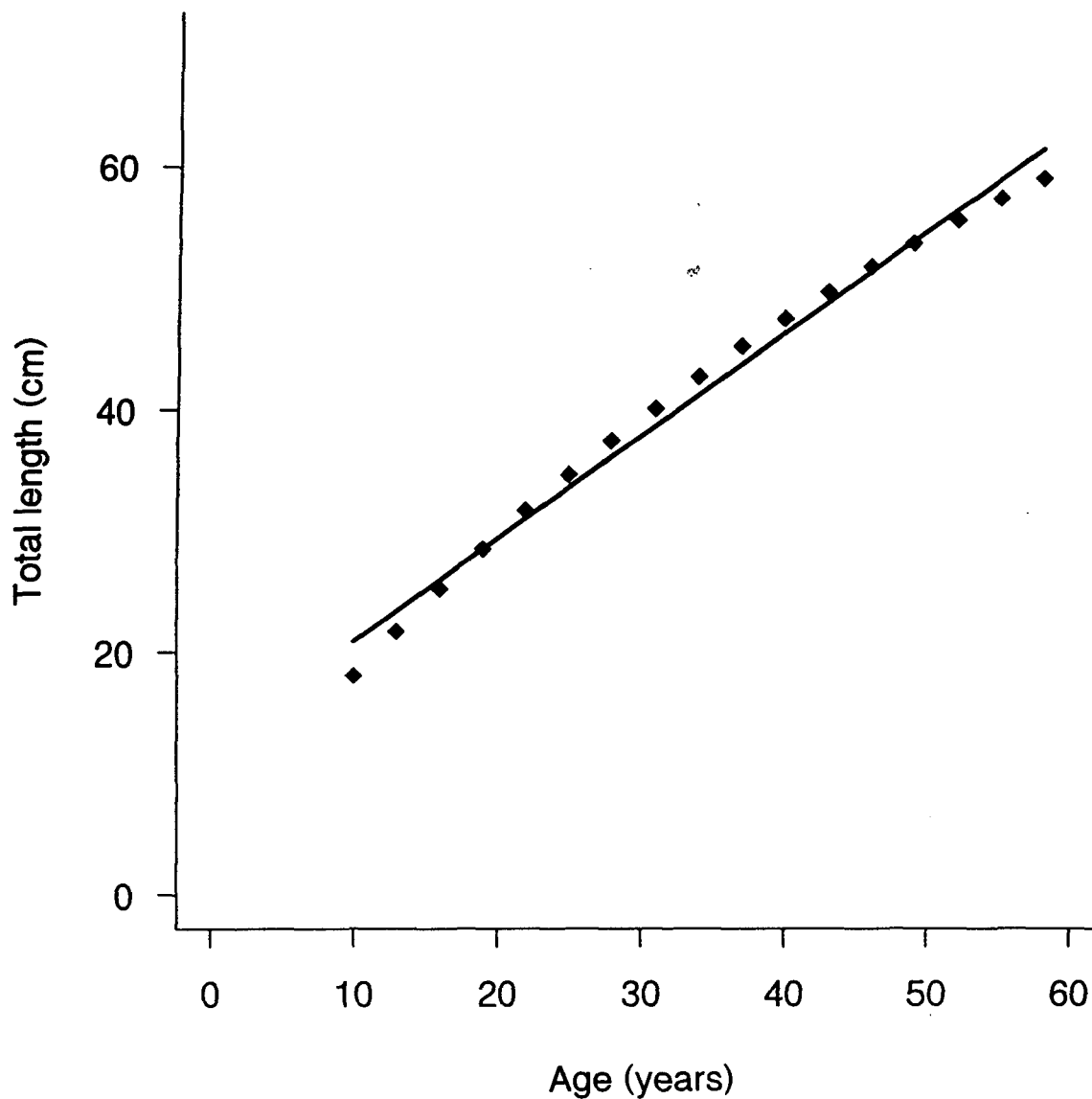
Figure 1. Example of the procedure used to calculate a linear age-length relationship when only a curved relationship had been presented. A linear regression (solid line) was fitted to the set of points calculated every 3 years from age 10 from the reported curve equation. The example given is for longfin eels from the Waimakariri South Branch (sample 20 in Table 2).
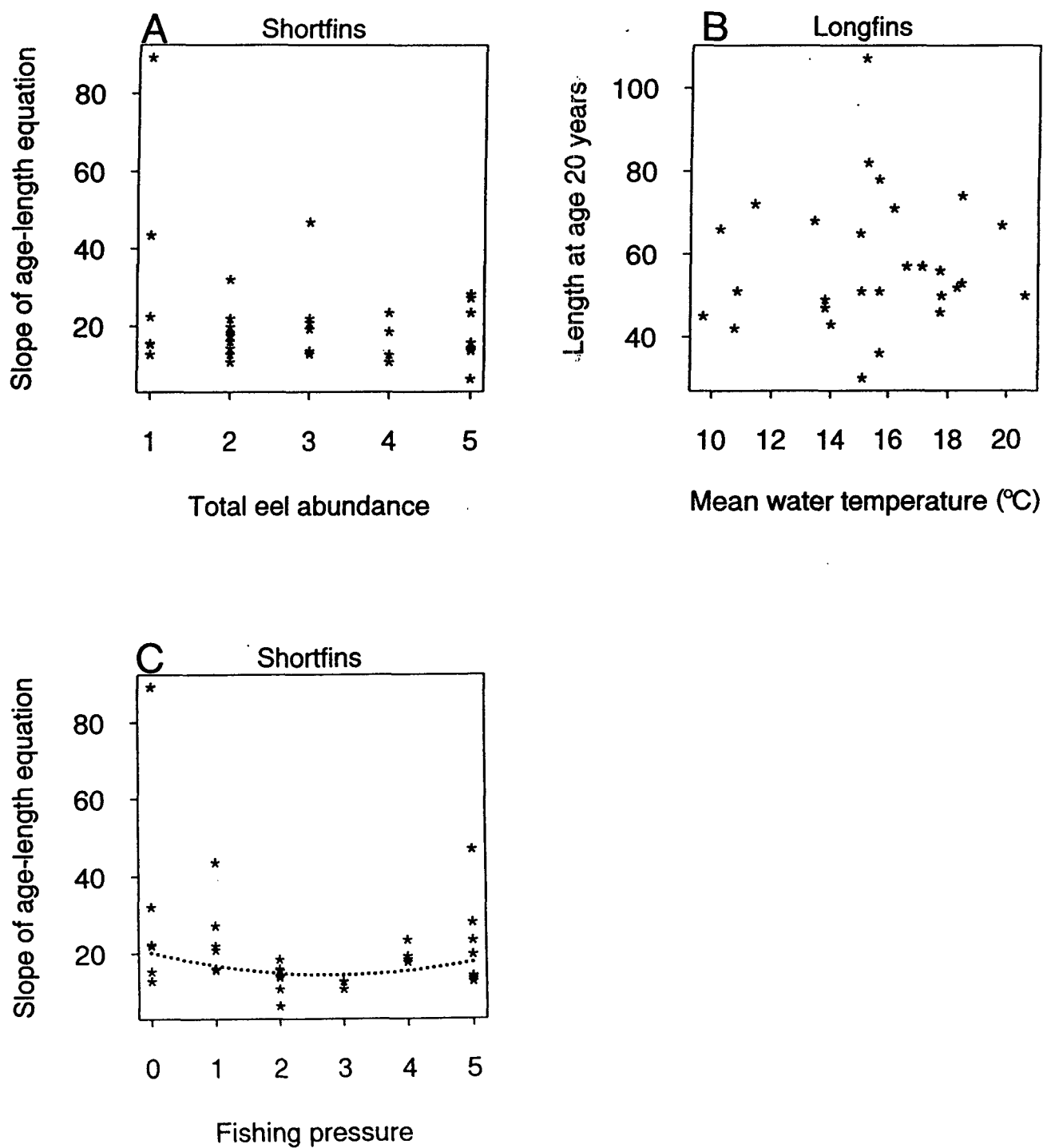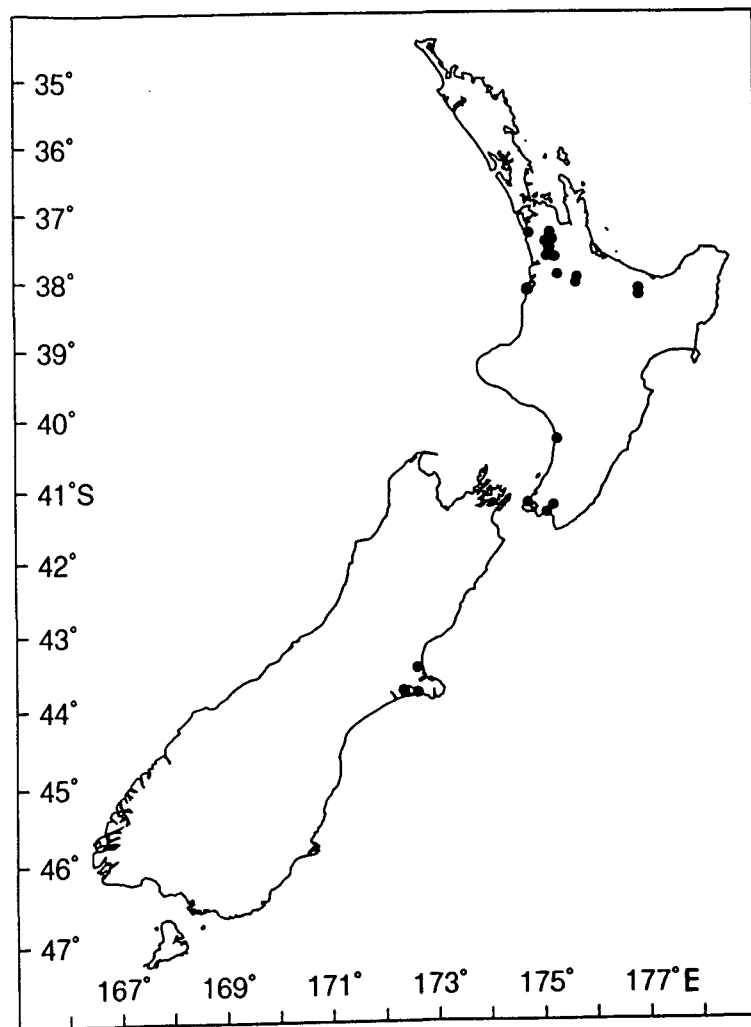
Figure 2. Example plots of exploratory data analysis showing the relationship between pairs of predictor and dependent variables. All plots appeared random (examples A and B) except for the relationship between slope and fishing pressure for shortfins which was best described by a quadratic function (shown as a broken line in C).
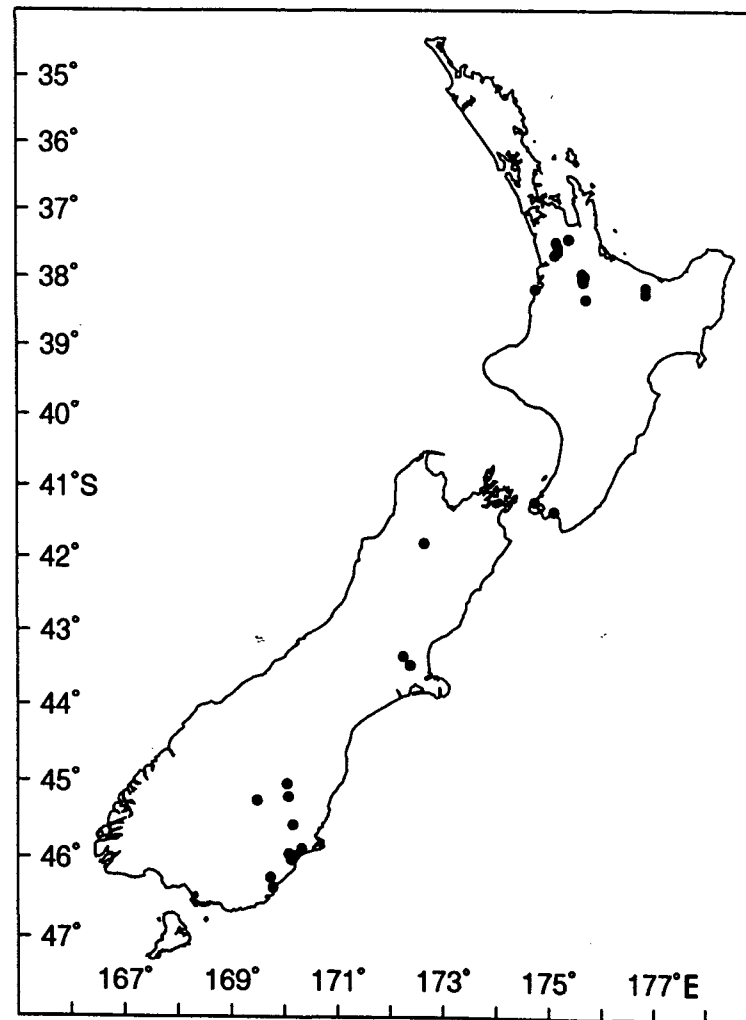
Shortfins

Longfins

Figure 3. Positions of sites for which eel age-length data are available, by species.

Appendix 1. Definition of variables.

Catchment

1   Waikato River, Waikato
2   Taharoa lakes complex, Waikato
3   Rangitaiki River, Bay of Plenty
4   Himatangi, Manawatu
5   Southern Wairarapa
6   Makara Stream, Wellington
7   Lake Rotoiti, Nelson Lakes
8   Waimakariri River, Canterbury
9   Lake Ellesmere, Canterbury
10 Taieri River, Otago
11 Clutha River, Otago

Habitat type

1   Estuary
2   Swamp
3   Pastoral stream
4   Forested stream
5   Lowland river
6   Lowland lake
7   Upland lake
8   Hydro lake

Reader

1   B. Chisnall
2   P. Todd
3   D. Jellyman
4   A. Burnet
5   D. Harries

Fishing intensity, eel densities, and food availability

0   Nil
1   Low
2   Low–moderate
3   Moderate
4   Moderate–high
5   High

Eel densities (kg/ha, where biomass data available)

0
1–100
101–200
201–300
301–500
≥ 501