

**Evaluation of the 1998 transfer of juvenile longfin eels into
Lake Hawea from recaptures, and ageing validation based on
otolith annual ring deposition**

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EXECUTIVE SUMMARY

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In this report we evaluate the success of the 1998 transfer of juvenile longfin eels (*Anguilla dieffenbachii*) into Lake Hawea in terms of growth, survival, and movement from recaptures in 2001 and 2008. We also attempt to validate ageing by comparing otolith annual growth ring deposition with known age at recapture of tagged eels.

In February 1998, Lake Hawea was stocked with about 9500 juvenile longfin eels sourced from the lower Clutha River. A sub-sample of transferred eels ($n = 2010$) was tagged with coded wire tags. In February 2001 and February 2008 the eel population in Lake Hawea was sampled.

2001 sampling

A total of 228 longfin eels was caught in Lake Hawea in February 2001, of which 12 were deemed to be resident (over 84 cm) and 216 to be recaptures of juvenile eels released into the lake in February 1998. Of the recaptures, 19.4% (42) had tags (tag-recaptures) compared with 21.3% at release indicating good tag retention and/or low mortality due to tagging. Tags had no adverse effect on growth since length and weight of tag-recaptures were not different to those of untagged recaptures ($p > 0.05$). Only recaptures with tags were killed, and all were found to be female.

Mean length and weight at recapture were 56 cm and 498 g, and during the three years at liberty eels grew on average about 14 cm and 325 g (all recaptures). There was no difference between length or weight at recapture of tag-recaptures and recaptures without tags ($p > 0.05$) indicating that tagging did not affect growth. Growth rate from tag-recaptures (mean annual length increment) was 4.1 cm.yr^{-1} , linear, and faster than at release when it was 2.4 cm.yr^{-1} ($p < 0.01$). Mean eel condition (k) for all recaptures improved from 2.24 at release to 2.75 and was significantly different ($p < 0.001$).

Eels dispersed throughout the lake but density was highest in The Neck, the point of release. Eels caught outside The Neck were larger (length and weight) and in better condition ($p < 0.001$) than inside The Neck. This was unrelated to length, weight, and condition at tagging indicating that the difference in growth occurred as a result of location within the lake.

2008 sampling

A total of 410 longfin eels was caught in Lake Hawea in February 2008, of which 11 were assumed to be resident and the remainder ($n = 399$) were recaptures of juvenile eels released into the lake in February 1998. Of the 399 recaptures, 19.2% (79) had tags (tag-recaptures) compared with 21.3% at release indicating good tag retention and/or low mortality due to tagging. Only tag-recaptures were examined for sex, and all were found to be female.

Mean length and weight were 80 cm and 1450 g and during the 10 years at liberty, eels grew on average about 38 cm and 1277 g (all-recaptures). Growth rate from tag-recaptures (mean annual length increment) was 3.6 cm.yr^{-1} , linear, and was significantly greater than at release ($P < 0.01$), but less than in 2001 ($P < 0.05$). Mean eel condition (k) for all recaptures improved from 2.24 at release to 2.72 and was significantly different ($p < 0.001$). Eel condition between 2008 and 2001 was not significantly different.

Generic comments

Eels transferred into Lake Hawea experienced accelerated growth and mean annual increment in length almost doubled. Growth was one of the highest on record for the New Zealand longfin and suggests that eels released in 1998 into Lake Hawea are thriving. The fast growth was ascribed to low density and abundant food. Recaptured eels were all females, indicating that either eels differentiated into females because density was low, or that males moved out of the lake to more preferred habitat downstream (juvenile eels were observed below Hawea Gates 17 months after release).

Based on the results of Lake Hawea enhancement, stocking of recruitment limited lakes in the Clutha River catchment is a viable option, and eels, at least from initial releases, will experience rapid and accelerated growth.

Ageing validation

From the recaptures of tagged eels, it was possible to determine actual growth rates of individual eels, and these showed significant differences pre- and post-transfer. Otoliths from the 2008 recaptured eels were then examined to see whether any similar enhanced growth was consistently present, which would correspond to the transfer of eels into Lake Hawea, and thus act as a “date stamp” on the otoliths. Enhanced growth (indicated by otolith ring radii) was present on most otoliths, and as there were 9 years of completed growth beyond the start of this enhanced growth (the period that tagged eels were at large in Lake Hawea), this confirmed that the hyaline rings were annual in formation and that our ageing techniques were relatively accurate.

1. INTRODUCTION

In 1998, as part of a larger Ministry of Fisheries programme to enhance Maori customary eel fisheries, over 9000 juvenile sub-commercial longfin eels (*Anguilla dieffenbachii*) were caught in the lower Clutha River and transported upstream where they were released in Lake Hawea (Otago southern lakes district), in a shallow bay known as ‘The Neck’ (Beentjes 1998) (Figure 1). The Neck is a Nohoanga¹ site which is recognised by the Crown as being of historical customary importance to Maori for mahinga kai. Before transfer, a sub-sample of about 2000 eels was tagged (coded wire tags, CWT) and individual length and weight recorded. This work was carried out under Ministry of Fisheries project EEL9702.

The total commercial catch taken from Lake Hawea over 38 years (1960 to 1998) is estimated at about 450 t. Although some commercial fishing is still permitted in the headwater lakes (Lakes Dunstan, Wanaka, Wakatipu, and Hawea), longfin eel numbers have declined markedly and only a small fraction of the virgin biomass remains. While commercial fishing has contributed to the decline in biomass, construction of Roxburgh and Clyde Dams (completed in 1958 and 1992, respectively) has accelerated the net loss by blocking recruitment of young eels (Figure 2). Indeed, even without the impact of fishing, the population is ageing and numbers declining as mature eels migrate to sea to spawn, but are not replaced by young recruits. Before stocking with juvenile longfin eels in 1998, eel abundance in Lake Hawea was very low and the remaining eels were large old longfin females (Beentjes et al. 1997). Hence, we expect all eels transferred to the lake, whether tagged or not, to be distinguishable from the much larger and older residents by size alone.

In February 2001, three years after the 1998 transfer, the eel population in Lake Hawea was sampled to evaluate growth, survival, and movement since transfer (Beentjes & Jellyman 2001, 2003) (Ministry of Fisheries project EEL2000/02). A total of 228 longfin eels was caught, of which 12 were deemed to be resident (over 84 cm) and 216 to be recaptures of juvenile eels released into the lake in February 1998. Of the recaptures, 19.4% (42) had tags (tag-recaptures) compared with 21.3% at release indicating good retention of the CWTs and/or low mortality due to tagging. Further, all tag recaptures were females, consistent with sex structure of high country lake longfin populations (Beentjes et al. 1997). During the intervening three years, these eels experienced nearly twice the growth rate of those from the lower Clutha River where they were initially captured, and their condition was also markedly improved. These eels had also dispersed out from The Neck throughout the entire lake (Figure 2). Indications were that the transplantation had been successful with good survival and enhanced growth (Beentjes & Jellyman 2001, 2003).

In February 2008, 10 years after the 1998 transfer, a commercial landing of eels from Lake Hawea was opportunistically scanned for the presence of tagged eels by Mossburn Enterprises, Invercargill. Of the 410 longfin eels in the landing, 76 had coded wire tags and these were provided to NIWA for further examination. In this report we evaluate the success of the 1998 transfer in terms of age, growth, and condition of eels from release through to 2001 and 2008 recaptures, and also attempt to validate ageing through otolith annual ring deposition. Validation works on the assumption that enhanced growth following transfer should show as an inflexion in the distance between annual growth increments.

1.1 Description of Lake Hawea

Lake Hawea is a glacial, oligotrophic lake with an estimated littoral area of 46.5 km² (Beentjes et al. 1997) which is 34% of the total lake area (138 km²). It lies at an altitude of 347 m, and has a mean and maximum depth of 192 and 384 m respectively. The catchment is largely tussock grassland growing on poor soils derived from schist (Flint 1975). The main water sources are the Hunter River

¹ Ngai Tahu settlement Act 1998, Schedule 95, site no. 28, Lake Hawea western shore, NM 447

and Dingle Burn, and the lake drains via the Hawea Gates (weir structure) into the Hawea River (Figure 2). “The Neck” is a shallow narrow bay on the west side mid-way up the lake (see Figure 1). The littoral zone of The Neck is about 1.9 km² at average lake level and 4% of the total lake littoral area. Most of the bay is less than 20 m deep.

Lake level fluctuates by 10 m as a result of hydro-storage, and a drop of this amount reduces the area of The Neck by about half. The submerged aquatic vegetation has been shown to be impoverished compared to nearby Lake Wanaka, probably because of these fluctuations (Clayton et al. 1986). No surface water temperature data were available for Lake Hawea, but the mean temperature in nearby Lake Wakatipu ranges seasonally from 9 to 16 °C (Irwin & Jolly 1970).

Koaro (*Galaxias brevipinnis*), common bully (*Gobiomorphus cotidianus*), brown trout (*Salmo trutta*), rainbow trout (*Onchyrhynchus mykiss*), and Chinook salmon (*Onchyrhynchus tshawytscha*) are common throughout the lake (Jellyman 1984), with upland bullies (*Gobiomorphus breviceps*) found only in a few tributaries (Allibone 1997). Invertebrates of Lake Hawea have not been studied.

Overall objective

1. To evaluate the 1998 eel enhancement of Lake Hawea

Specific objectives

1. To determine the 2008 population size/age structure, growth, condition, and sex of longfin eels (including tagged eels) in Lake Hawea, and compare to 2001 and 1998 (year of transfer) data.
2. To validate ageing based on otolith ring deposition following transplantation into Lake Hawea.

2. METHODS

The 2001 recaptures were documented by Beentjes & Jellyman (2001, 2003), but where necessary results and analyses are included in this report to allow comparison of population growth characteristics at release in 1998 and in 2008.

Terminology

<i>tag-recaptures</i>	recaptures with coded wire tags.
<i>untagged-recaptures</i>	recaptures without coded wire tags. Assumption of recapture based on length, distinguishing these from resident eels.
<i>all-recaptures</i>	tagged and untagged recaptures.

2.1 Transfer and re-sampling

2.1.1 Transfer (1998)

In February 1998, 1630 kg of juvenile, predominantly longfin, eels (an estimated number of 9421 eels) were caught by commercial eel fishers in the Matau and Koau branches of the lower Clutha River (see Figure 1) using baited fyke nets with 12 mm mesh and escape tubes blocked to retain small eels. A subsample of 2010 longfin eels (21.3%) was tagged with sequentially coded wire tags inserted in the top of the head, and individual lengths and weights were recorded. Each stainless steel tag (1.25 x 0.25 mm) was etched with a unique 6-bit binary code. Two shortfin eels were found during tagging and therefore the total number of shortfin eels in our captured eels was estimated at seven (0.07%). No shortfin eels were tagged. With the exception of 96 longfin eels retained for ageing, eels were transported 200 km by commercial eel tanker to Lake Hawea and released at The Neck (see Figure 1).

The stocking rate estimates were 8 kg. ha⁻¹ for the littoral area of The Neck, equivalent to 0.35 kg. ha⁻¹ for the littoral area of Lake Hawea. Hereafter, unless specified, “eels” refers to longfin eels.

2.1.2 Re-sampling (2001)

Between 18 and 23 February 2001, Lake Hawea was surveyed to recapture a sample of eels from the 1998 release. The lake was arbitrarily divided into three areas: Neck, South, and North (Figure 2). A total of 150 fyke net lifts (30 in South, 30 in North and 90 in The Neck) were made using commercial baited fyke nets (12 mm mesh), left overnight with escape tubes blocked to retain small eels. Nets were placed in locations considered to be favoured eel habitat such as weed beds, log jams, and overhanging willows, at depths ranging from about 3 to 10 m. Nets were checked each morning, and all captured eels were taken ashore, anaesthetised with 2-phenoxyethanol, species identified, and length and weight recorded. Eels were also checked for the presence of coded wire tags using a hand-held tag detector wand. Eels with tags were killed, and the heads retained for tag retrieval. Gonads of all tagged eels were examined macroscopically and sex was assigned using the descriptions of Beentjes & Chisnall (1998). All other eels were retained in holding bags in the water and returned alive to The Neck at the end of the last day’s sampling to avoid re-catching the same eels. Tags were removed from heads in the laboratory and read using a binocular microscope so as to match individual weights and lengths at recapture with those at release.

Annual length (cm.yr⁻¹) and weight increments (g.yr⁻¹) were determined from:

all-recaptures:

$$L_{incr} = (mean_{lgth_recap} - mean_{lgth_tag})/yr_{lib}$$

$$W_{incr} = (mean_{wt_recap} - mean_{wt_tag})/yr_{lib}$$

where $mean_{lgth_recap}$ = mean length at recapture, $mean_{lgth_tag}$ = mean length at tagging, yr_{lib} = years at liberty, $mean_{wt_recap}$ = mean weight at recapture, $mean_{wt_tag}$ = mean weight at tagging.

tag-recaptures:

$$L_{incr} = (lgth_{recap} - lgth_{tag})/yr_{lib}$$

$$W_{incr} = (wt_{recap} - wt_{tag})/yr_{lib}$$

where $lgth_{recap}$ = length at recapture, $lgth_{tag}$ = length at tagging, wt_{recap} = weight at recapture, wt_{tag} = weight at tagging.

2.1.3 Re-sampling (2008)

Unlike the fishery independent directed re-sampling of Lake Hawea carried out by NIWA in 2001, the 2008 sample was taken by a commercial eel fisher during the course of a routine fishing trip in Lake Hawea. Commercial fyke nets (12 mm mesh) with 25 mm escape tubes were baited and left overnight. All captured eels were landed into Mossburn Enterprises (Invercargill) where the processor (Vic Thompson) identified species, and recorded length and weight for each eel. In addition, all eels were checked for the presence of CWTs using a hand-held tag detector wand (provided by NIWA) and those found to have tags were flagged on the datasheet, frozen whole, and sent to NIWA for tag retrieval. Individual lengths and weights of these tagged eels, as recorded by the processor, were not provided with the frozen sample and hence, we were unable to positively match length and weight of putative tag recaptures at the factory with those in the laboratory. Several months later the sample of tagged eels was thawed, length and weight measured, and checked for CWTs using the hand-held

wand. CWTs were dissected out and read under a binocular microscope. The individual weights and lengths at recapture and release were then matched. The gonads were examined macroscopically and sex was assigned; maximum width (dorso-ventral plain) of the gonad was recorded.

An adjustment was made for the length of tag-recaptures to allow for a 2.5% reduction in length following freezing. The conversion was estimated from the difference between length of tag-recaptures measured at the factory and those in the laboratory.

Annual length (cm.yr^{-1}) and weight increments (g.yr^{-1}) were determined as for 2001 re-sampling (Section 2.1.2).

2.2 Ageing

2.2.1 Transfer (1998)

Sagittal otoliths from a length stratified sub-sample of 96 transferred eels (4 otoliths per centimetre length class) were removed for ageing and prepared using the crack-and-burn method (Hu & Todd 1981). Otolith halves were mounted in silicone rubber sealant on microscope slides and observed under X10–100 magnification using a compound microscope with side illumination. The central area of oceanic larval growth was ignored (Jellyman 1979) and age (expressed as years spent in fresh water) determined by counting the number of complete hyaline zones or winter rings in the otolith. Otoliths were assigned a readability score (1–5) where 1 = unreadable, 5 = excellent readability. For subsequent analyses, only otoliths that scored 3 or more were included.

Annual length (cm.yr^{-1}) and weight increments (g.yr^{-1}) were estimated as follows:

$$L_{incr} = (lgt h - 6)/age$$

Where $lgt h$ = total fish length (cm) and 6 is the length at recruitment into fresh water, and age (years) = the number of hyaline rings counted.

$$W_{incr} = wt/age$$

Where wt = fish weight (g). As glass eels weigh only 0.2 g, within the limits of weighing accuracy, no adjustments for this weight were made.

2.2.2 Re-sampling (2008)

Otoliths were also removed from the 2008 tag-recaptures, prepared and aged as above. Annual length (cm.yr^{-1}) and weight increments (g.yr^{-1}) over the lifetime of eels, and at release were estimated as follows:

$$L_{incr_life} = (lgt h_{recap} - 6)/age$$

$$L_{incr_release} = (lgt h_{tag} - 6)/age - 10$$

$$W_{incr_life} = wt_{recap}/age$$

$$W_{incr_release} = wt_{tag}/age - 10$$

where 6 is total length (cm) at recruitment into fresh water and 10 is the number of years since release.

2.3 Lake Hawea resident eel population before transfer

Before the transfer, Lake Hawea was surveyed using baited commercial fyke nets (12 mm net mesh) set overnight in December 1995 (Beentjes et al. 1997) and February 1998 (Beentjes 1998), when lengths and weights of all captured eels were recorded, and otoliths removed for ageing; otoliths were prepared using the same techniques described for the transferred juvenile eels. Sampling of Lake Hawea in 2001 (eels over 84 cm) and 2008 (eels over 109 cm) also resulted in captures of resident eels, distinguishable from stocked eels by size.

2.4 Descriptive and statistical analysis

The length–weight relationship was determined from the linear regression model:

$$\log W = b(\log L) + \log(a),$$

where W = weight (g), L = length (cm), b and a are regression coefficients, and logs are natural logarithms.

Eel condition (k) was calculated as follows:

$$k = W \times 10^6 / L^3,$$

Descriptive and statistical analyses were conducted to compare growth characteristics of juvenile eels at time of release into Lake Hawea with those at recapture in 2001 and 2008 (StatSoft 2007). The parametric t -test (dependent and independent samples) was used where all tested variables conformed closely to a normal distribution. The following questions were addressed.

Did tagging affect growth ?

To determine if tagging affected growth, length, weight, and condition of the 2001 tag-recaptures and 2001 untagged-recaptures were compared (t -test independent samples). This could not be done for 2008 because we could not, with any certainty, identify the tag-recaptures from the untagged recaptures in the all-recaptures dataset provided by Mossburn Enterprises.

Did eel annual growth rate change after release into Lake Hawea ?

To determine if annual growth rates at release (= growth in the lower Clutha River where these eels were captured) were significantly different from those at recapture in 2001 and 2008, annual length increments (cm.yr^{-1}) at release and recapture were compared (t -test independent samples); annual length increments at release were determined from length at age from a sub-sample of transferred eels as well as 2008 aged tag-recaptures, and those at recapture from tag-recaptures.

Did condition (k) change after release into Lake Hawea ?

To determine if eel condition (k) at release and recapture was significantly different, a t -test (dependent samples) was used to test between condition at release and condition of tag-recaptures. A t -test for independent samples was also used to test condition between release and all-recaptures. To determine if condition had changed between 2001 and 2008, a t -test (independent samples) was used to compare condition of all-recaptures.

Was growth and condition of recaptures variable within Lake Hawea ?

To determine if eel growth varied within the lake, length, weight, and condition (k) of all-recaptures at The Neck were compared (Mann-Whitney U test) with those in areas outside The Neck (South and North combined). The same test was used to compare the length, weight and condition of tag-recaptures.

Was growth linear ?

Linear regression analysis was used to test the assumption of linear growth by plotting length at tagging (independent variable) against growth increment (mm.yr^{-1}) (dependent variable) for tag-recaptures. A slope of zero indicates that growth is linear.

2.5 Age validation

Age validation is based on the precept that since somatic growth rate increased markedly after transfer into Lake Hawea, this should also be expressed in the growth of the otolith radius which has been shown to be related to length (Jellyman 1979, Graynoth 1999).

The 79 otoliths removed from the 2008 tag-recaptures were aged, and the otolith half that best showed the nucleus and a full complement of rings was chosen for measuring the putative annuli. Otoliths were viewed at $\times 40$ magnification using a Leica compound microscope, and photographed using a Zeiss AxioCam camera with reflected light from a cold light source. Photographs were viewed and measured using ImageJ software. Hyaline rings on the photographed image were annotated with a cross, and distance (mm) between consecutive crosses was measured along the ventral axis where the radius of the otoliths is greatest, starting at the nucleus (Figure 3). Photographs were examined by two experienced readers and ages assigned to the rings. Age of 1 year old was taken as the first year in fresh water, ignoring the growth check that forms when eels move from marine to freshwater. Because the 2008 recaptures were taken in the summer of 2008, there was no 2008 winter hyaline ring, only the summer growth margin, and the last complete ring was assumed to correspond to the winter of 2007. Likewise the time and year of release (February 1998) meant that the 1999 year was the first full year of growth in Lake Hawea. As hyaline rings are laid down in winter, 1 October was assumed to be the birth date (Jellyman 1979).

The cumulative distance between the rings was calculated from the individual distances and this is equivalent to the otolith radius (minus the width from the nucleus to the check corresponding to arrival in fresh water). Preliminary examination of the data indicated that initial growth of the otolith radius in the first few years after entry to fresh water was fast, after which growth slowed. Analysis and presentation of the otolith ring data was therefore carried out for three groups with an implicit assumption that the assignment of ages to the rings was correct, i.e., post transfer – rings laid down in the 10 years after the 1998 transfer into Lake Hawea; pre transfer– rings laid down in the 10 years before transfer; juvenile– rings laid down more than 10 years before transfer. These data were examined for evidence of a change in growth rate following transfer into Lake Hawea. A Kolmogorov-Smirnov test was first used to find whether variables were normally distributed; as they were not, an $(x + 1)$ transform was applied. Repeated measures ANOVA was then used to determine if the widths of otolith rings differed over all years using total fish length as a covariate. A Bonferroni post-hoc test was then used to see which pair-wise comparisons between years were different, and whether any significant changes corresponded to the time of transfer.

3. RESULTS

3.1 Release (1998)

The length frequency distribution representative of the longfin juvenile eels released into Lake Hawea in 1998 is shown in Figure 4. Eels at release were too small to determine sex since longfin eels do not differentiate until about 50 cm (Beentjes & Chisnall 1998). The length distribution was unimodal, size ranging from 30 to 55 cm with a mean length of 42 cm (Table 1). Weight ranged from 55 to 380 g with a mean of 173 g. Most (77%) of these eels were less than the commercial minimum legal size of

220 g. At release, the mean age was 15 years and mean annual growth was 2.38 cm.yr^{-1} and 10.9 g.yr^{-1} (Table 2). Estimates of mean annual growth at release from the 2008 aged tag-recaptures were similar at 2.53 cm.yr^{-1} and 12.1 g.yr^{-1} (Table 2) and there was no significant difference between these estimates (*t*-test independent samples, $P = 0.17$). The lengths at age of the 1998 and 2008 aged eels are shown in Figure 5.

3.2 Resident eels in Lake Hawea

Before release

The two surveys (1995 and 1998) (Beentjes et al. 1997, Beentjes 1998) of the resident eel population of Lake Hawea before stocking yielded only three longfin eels on each survey and these data were combined because they were few and three years is not long relative to the size and age of these eels. The mean length of eels from both surveys combined was 112 cm and mean weight 4880 g (Table 3). There was no overlap in size and age of resident eels in Lake Hawea and those juveniles that were released into the lake (see Figure 4). All eels had well developed ovaries. The mean age of resident eels was 56 years although most otoliths were difficult to read and confidence in these ages is low. The width between annuli did not indicate accelerated growth in recent years despite the low eel density in the lake. The mean growth rate was 1.89 cm.yr^{-1} .

2001 and 2008 sampling

Twelve of the eels sampled in February 2001 were over 84 cm and were deemed to be resident eels, clearly distinguishable from the recaptures based on size alone (see Figure 4). Similarly, 11 of the eels in the 2008 sample were deemed to be residents (length over 109 cm, see Figure 4). The descriptive statistics of these eels are shown in Table 3.

3.3 Recaptures

2001 sampling

A total of 228 longfin eels was caught in Lake Hawea in February 2001, of which 12 were assumed to be resident and the remainder ($n=216$) were recaptures of juvenile eels released into the lake in February 1998 (Tables 1 and 4, see Figure 4). No shortfin eels were caught. Of the 216 recaptures, 19.4% (42) had tags (tag-recaptures) compared with 21.3% at release. One tagged eel could not be included in the analyses because details of weight at tagging did not match.

Macroscopic examination of the gonads of the 42 tag-recaptures showed that they were all females at an early stage of development (not illustrated).

2008 sampling

A total of 410 longfin eels was caught in Lake Hawea in February 2008, of which 11 were assumed to be resident and the remainder ($n = 399$) were recaptures of juvenile eels released into the lake in February 1998 (Tables 1 and 4, see Figure 4). No shortfin eels were caught. Of the 399 recaptures, 19.2% (79) had tags (tag-recaptures) compared with 21.3% at release. Three tagged eels could not be included in the analyses because details of weight at tagging did not match or the tags could not be located.

Macroscopic examination of the gonads of the 79 tag-recaptures showed that they were all females. A summary of ovary width statistics is given in Table 4 and width of the ovaries plotted against eel length is shown in Figure 6. Ovary width increased with eel length although there was considerable variability. Although these ovaries were not staged, the width would indicate that they are predominantly stages 2 and 3, as defined by Beentjes & Chisnall (1998).

3.4 Size and growth

2001 recaptures

The length distribution of the 2001 all-recaptures has remained unimodal but the range of lengths increased due to variable growth rates (see Figure 4). Mean length and weight of all recaptures was 56 cm and 498 g ($n = 216$) (see Table 1) and for tag-recaptures 56 cm and 485 g ($n = 41$) (Table 4). During the three years at liberty, eels grew on average about 14 cm and 325 g (all-recaptures) (Figure 7). For the tag-recaptures, length and weight increase was comparable to that of all-recaptures (13 cm and 300 g) (see Tables 1 and 6). Lengths at tagging and recapture are plotted for the tag-recaptures (see Figure 4). There was no difference (significance level of $P < 0.05$) between length and weight at recapture of tag-recaptures ($n = 41$) and recaptures without tags ($n = 175$) (t -test independent samples).

Mean annual length increment over the three years since release was 4.1 cm.yr^{-1} ($n = 41$ tag-recaptures) compared to 2.38 cm.yr^{-1} at release ($n = 96$) (Table 4, see Table 1) and was significantly different (t -test independent samples, $P < 0.001$) (Figure 8). Length at tagging plotted against annual growth increment (Figure 9) indicated that the slope was not significantly different from zero (linear regression, $P = 0.26$) – residual analysis indicated that there was no increase in variability in annual length increment with size suggesting that growth in length was linear and unrelated to length at tagging.

2008 recaptures

The length distribution of the 2008 all-recaptures has remained unimodal, but compared to 1998 and 2001 is less well defined and the range of lengths has increased due to variable growth rates over time (see Figure 4). There is no overlap in size range between the eels released in 1998 and those recaptured in 2008. Mean length and weight of 2008 all-recaptures was 80 cm and 1450 g ($n = 399$) (Table 1) and for tag-recaptures 79 cm and 1462 g ($n = 79$) (Table 4). During the 10 years at liberty, eels grew on average about 38 cm and 1277 g (all-recaptures) (see Figure 7). For the tag-recaptures, length and weight increase was comparable to that of all-recaptures (37 cm and 1281 g) (see Tables 1 and 4). Lengths at tagging and recapture are plotted for the tag-recaptures (see Figure 4). Length and weight of tag-recaptures ($N=41$) and untagged-recaptures ($N=175$) could not be tested because it was not possible to separate the tagged from the untagged eels in the all-recaptures database (see Methods).

Mean annual length increment over the 10 years since release was 3.6 cm.yr^{-1} ($n = 76$ tag-recaptures) (Table 4) and was significantly greater than at release ($n = 96$) (t -test independent samples, $P < 0.001$), but less than in 2001 (t -test independent samples, $P < 0.05$) (see Figure 8). Length at tagging plotted against annual growth increment (Figure 9) indicated that the slope was not significantly different from zero (linear regression, $P = 0.27$) – residual analysis indicated that there was no increase in variability in annual length increment with size suggesting that growth in length was linear and unrelated to length at tagging. Indeed, the plot of time and mean size confirms that length increases linearly, and weight exponentially (see Figure 7).

3.5 Condition

2001 recaptures

Eel condition (k) of all-recaptures improved from a mean of 2.24 at release ($n = 2010$) to 2.75 in 2001 ($n = 216$) (see Table 1, Figure 10) and the difference was statistically significant (t -test independent samples $P < 0.001$). For the 41 tag-recaptures, condition also improved at recapture (2.26 at tagging and 2.70 at recapture) (Table 4) and the difference was significantly different (t -test dependent

samples $P < 0.001$). Condition of tag-recaptures ($n = 41$) and untagged-recaptures ($n = 175$) was not significantly different ($P > 0.05$; t -test independent) (Table 4).

2008 recaptures

Eel condition (k) of the all-recaptures improved from a mean of 2.24 at release ($n = 2010$) to 2.72 in 2008 ($n = 216$) (Table 1, Figure 10) and the difference was statistically significant (t -test independent samples, $P < 0.001$). There was no difference, however, between all-recapture condition in 2001 and that in 2008 (t -test dependent samples, $P = 0.17$). For the 76 tag-recaptures, condition also improved at recapture (2.28 at tagging and 2.90 at recapture) (Table 4) and the difference was significantly different (t -test dependent samples $P < 0.001$). The condition of tag-recaptures ($n=41$) and untagged-recaptures ($n=175$) could not be tested because it was not possible to separate the tagged from the untagged eels in the all-recaptures database (see Methods).

3.6 Within-lake growth variation (2001)

All eels were released into The Neck in February 1998 and after three years at liberty had dispersed throughout the lake. Comparison of recapture length, weight, and condition of eels caught in The Neck ($n=178$) and outside The Neck ($n=38$) (Table 5) indicated that eels from outside The Neck were significantly larger (length and weight) and in better condition (t -test independent samples, $P < 0.01$ for all three variables). The difference in growth inside ($n = 34$) and outside ($n = 7$) The Neck was supported by tag-recapture data where recaptured length and weight, annual length and weight increments, and condition were all significantly greater outside The Neck ($P < 0.05$ for all variables, Mann-Whitney U non-parametric test). Length, weight, and condition at tagging of eels caught inside and outside The Neck were not significantly different ($P > 0.05$, for all three variables) indicating that the difference in growth occurred as a result of location within the lake and not size at release.

A similar analysis could not be carried out for 2008 recaptures because we had no information on the specific locations where individual eels were caught.

3.7 Length-weight and length-age relationship

The length-weight (cm and g) relationships at release and recapture were:

Release 1998	weight = 0.001087(length) ^{3.1926}	(n=2010, R ² =0.93)
Recapture 2001	weight = 0.000886(length) ^{3.2809}	(n=216, R ² =0.92)
Recapture 2008	weight = 0.000686(length) ^{3.3146}	(n=399, R ² =0.92)

The length-age (cm and years) relationships at release and recapture were:

At release	length = 1.1852(age) + 23.08	(n=96, R ² =0.45)
Recapture 2008	length = 0.3286(age) + 70.7	(n=96, R ² =0.02)

3.8 Distribution and abundance (2001)

Recaptures in 2001, including tag-recaptures, were caught in all three areas (Neck, North, South) indicating that some eels had moved from The Neck to the extreme north and south ends of the lake as well as across to the east side of the lake. Catch per unit effort for the entire lake, and for The Neck and outside The Neck separately, is shown in Table 6. Eels were nearly twice as abundant (kg/net) in The Neck than outside and the contrast may have been greater had we not repeat fished The Neck causing some local depletion over the sampling period.

For comparison, CPUE is also shown for the lower Clutha River where juvenile eels were caught in 1998. The relative abundance of eels (kg/net) in Lake Hawea post stocking is less than the lower Clutha River by a factor of about four by weight and 17 by number.

3.9 Age validation results

Of the 79 otoliths that were examined and photographed, seven had poor readability and we were unable to assign rings with confidence for age validation, leaving 72 otoliths. The mean distances between annual growth rings for the juvenile stage, the 10 year period before transfer, and the 10 year period after transfer, are shown in Figure 11. The means are significantly different among the three data sets (*t*-test independent samples, $P < 0.001$). The mean distance and the cumulative mean distance (= otolith radius) between rings by year for the 20 year period before recapture are shown in Figure 12. There was some variation among the 72 otoliths, with four main types of growth pattern recognised: 1) “up” – marked increase in growth corresponding to time of transfer (43%); 2) “inflexion” – a sharp increase in growth for a few years following transfer, followed by resumption of growth rate similar to that before transfer (24%); 3) “flat” – no change in growth after transfer (24%); 4) “down” – a decline in growth after transfer (8%). The pattern of growth of one otolith (1%) was too variable to discern any trend. Overall, the pooled data set indicate that growth increased dramatically in the year that corresponds with 1999, i.e., the growth period from the winter 1998 to winter 1999, the first full year in Lake Hawea (Figure 12, see Figure 4). Subsequently, growth remained accelerated for four years before declining in 2003 and returned to levels similar to, but slightly above, pre-transfer growth. This growth pattern is also evident in the cumulative distance plot where there is an inflexion in the curve that occurs in the year corresponding to 1999. The levelling off of growth after 2002 is also evident. The composite growth curve falls between that category of “up” and “inflexion”.

Total length was significantly related to annual growth (untransformed data) across all fish ($DF=19$, $F=2.423$, $P=0.001$), and annual growth differed significantly among years ($DF=19$, $F=1.816$, $P=0.017$). For the transformed data the respective results were similar (i.e., $DF=19$, $F=1.801$, $P=0.018$, and $DF=19$, $F=2.395$, $P=0.001$). Table 7 shows the results of the pair-wise comparisons of otolith ring widths, with the highlighted area representing growth since transfer. The largest number of significant pair-wise comparisons is for 1999, which is the first full year of growth in Lake Hawea.

4. DISCUSSION

In this report we present the results of a stocking experiment where juvenile longfin eels from the lower Clutha River were released into Lake Hawea in 1998. Historically, Lake Hawea contained a healthy population of longfin eels, but recruitment has been restricted since 1958 and density was very low at the time of stocking. Subsequent sampling of the lake in 2001 and 2008 yielded 216 and 399 recaptures respectively, and provided a unique opportunity to study the effects of stocking in terms of growth, movement, and potential survival. In addition, the utility of deploying coded wire tags on eels was assessed.

Validation of ageing was also attempted by examining the distance between annuli on the otoliths of the 2008 tag-recaptures. The expectation was that we would record an increase in the distance between growth rings following transfer, reflecting accelerated somatic growth – provided the intervening years equalled 9 (being complete years of growth in Lake Hawea), this would provide an independent measure of age validation.

4.1 Movement

Tagging studies on both shortfin and longfin eels in New Zealand have shown that movement of non-migratory eels is limited and tagged eels were often recaptured near or at the tagging site (Burnet 1969b, Chisnall & Kalish 1993, Jellyman et al. 1996, Jellyman & Sykes 2003). Tagging studies on the American eel (*Anguilla rostrata*) also indicate that movement is restricted within a home range of about 1 ha (Bozeman et al. 1985) and 100 m (Ford & Mercer 1986), and *A. australis* in Australia to about 400 m (Beumer 1979). By 2001, three years after release, eels had dispersed throughout Lake Hawea, but density was highest in The Neck, the point of release. It is not possible to know the time frame over which dispersal occurred, but it was probably not as a result of competition from Lake Hawea resident eels as these were present in only very low numbers. Eels probably migrated out of The Neck and around the lake to avoid overcrowding and to exploit under-utilised food resources. Periodic low water levels as a result of hydro storage demands may also have encouraged eels to move out of The Neck. This finding indicates that longfin eels placed into a largely eel-free environment will eventually occupy all suitable habitat. In 2008, the sample provided by the fisher was captured from around The Neck and the northwest head of the lake (Hunter River mouth), but other parts of the lake were not fished (see Figure 2). Hence, we have little new information about the movement and distribution of eels after the 2001 recaptures.

Although eels have remained in Lake Hawea after being captured and moved 200 km upstream, the proportion remaining cannot be determined since eels can exit the lake via the Hawea Gates (see Figure 2). Indeed, there was an anecdotal report of large numbers of juvenile eels observed below Hawea Gates in an irrigation canal about 17 months after release in July 1999. Unlike the American eel (*Anguilla rostrata*) (Helfman et al. 1987) New Zealand longfin males are not restricted to coastal and estuarine areas; however, the proportion of longfin males in the Clutha River tends to decline slightly from the coast to inland areas, indicating a preference for coastal areas (Beentjes 1999). It is likely that, if there was any credence in the observation of juvenile eels below Hawea Gates, these eels were probably males attempting to return to preferred downstream habitat. The 17 month delay between release and departure may represent the time between immaturity and sexual differentiation. Homing behaviour of displaced eels is known to occur in some Anguillids, for example, *A. australis* (New Zealand shortfin) (Jellyman et al. 1996) and *A. rostrata* (Lamothe et al. 2000). The observation that some eels departed Lake Hawea is not convincing evidence of homing as males may simply be moving in response to a preference for downstream habitat.

4.2 Size and growth

In 2008 the length distribution of eels still conformed to a normal distribution, but the variability had increased over time (range = 25 cm in 1998, 34 cm in 2001, and 41 cm in 2008) (see Table 1 and Figure 4). This is typical of fish populations where the different intrinsic growth rates of individuals are amplified over time and this tends to obscure the cohort modes which eventually accumulate and merge together; this is particularly the case for long-lived species such as eels. The tag-recapture experiment in Lake Hawea has provided a unique opportunity in fisheries research to observe temporal growth of both individuals and the population as a whole, in the absence of recruitment or a pre-existing population of similar size range.

Because eel growth in length is generally linear, assuming no significant changes in density and food availability (Jellyman 1995, 1997, Beentjes & Chisnall 1998), annual growth increment is adequately expressed in centimetres per year. Weight increases exponentially and is strongly correlated with size as larger eels accrue more weight annually than smaller eels. Annual weight increments were also estimated, as weight is the parameter of more importance to the eel industry. The results from both the 2001 and 2008 tag-recaptures indicate that growth increments were not related to size at transfer, confirming that growth in eel body length is linear (see Figure 9). This is strong evidence that the

increase in annual growth since transfer to Lake Hawea is not a function of length (i.e., larger eels growing faster than smaller eels), but is a result of the transfer to more favourable habitat. This study has provided one of the few opportunities to verify that longfin eels have constant annual length increments based on tag-recapture data, rather than the relationship between length and putative age (based on otolith rings counts).

Eels transferred into Lake Hawea in 1998 experienced accelerated growth to the extent that the annual increment in length almost doubled from 2.38 cm.yr⁻¹ at release² to around 4.1 cm.yr⁻¹ (tag-recaptures) over the first three years after transfer. In 2008 the annual length increment of tag-recaptures since transfer (3.6 cm.yr⁻¹) was similar to that in 2001 (4.1 cm.yr⁻¹) and was not statistically different, indicating that growth in length, overall, was constant since transfer into the lake (see Table 1). This statistic is perhaps not surprising given that the 2008 data also include growth for the first three years after transfer, as it was not possible to estimate growth specifically from 2001 to 2008. Analysis of the distance between annuli of the 2008 tag-recaptures, however, indicate that after an initial growth spurt soon after transfer lasting 4 to 5 years, growth declined again, but on average was greater than that before transfer (see Figure 12).

The cumulative mean distance between growth rings plot is very similar to that for the mean lengths of eels over time (see Figures 7 and 12) indicating that the otolith marginal increment deposition is strongly related to somatic growth in length. While the relationship between eel otolith radius and length has been found to be linear (Ryan 1978, Jellyman 1979), Graynoth (1999) reported a slight curvilinear relationship for both *A. australis* and *A. dieffenbachii*, the difference ascribed to the inclusion of a greater size range, including small eels. Indeed, we found juvenile ring distance to be greater than that of larger eels, more consistent with a curvilinear relationship.

Of the 72 longfin eels, 67% showed an increase in the otolith radius (i.e., categories “up” or “inflexion”) following transfer into Lake Hawea. Some eels showed no indications of a change to growth (“flat”), and a few even showed a decline in growth (“down”). This variability in growth is to be expected in a population and is reflected in the length frequency distribution in 2008 in which the range of lengths has increased over time (see Figure 4). Jellyman (2001) demonstrated similar growth inflexions in the otolith radii of migrating shortfin female eels in Te Waihora which he ascribed to a change in diet from invertebrate to fish. This conclusion was based on the finding that shortfin eels over about 50 cm are almost exclusively piscivorous (Ryan 1986) and abundance of common bullies (*Gobiomorphus cotidianus*) in Te Waihora had increased in recent years resulting from a reduction in large eels, key predators of bullies (Jellyman & Todd 1998).

Growth rates of longfin eels elsewhere in New Zealand

High growth rate is often a feature of eels in hydro lakes where density is very low because of barriers to recruitment. For example, longfins released into Lake Arapuni, the second hydro impoundment on the Waikato River, achieved annual growth of 21 cm.yr⁻¹ (Beentjes et al. 1997). Similarly, in Lake Matahina on the Rangitaiki River, growth was 5.7 cm.yr⁻¹; in both cases the exceptionally high growth was considered to be due to very low density and an abundant food source (Beentjes et al. 1997). Length and age were determined for commercial catches of longfin from more than 21 major rivers in the South Island, including the lower Clutha River (Beentjes & Chisnall 1998, Beentjes 1999). The mean annual length increment from these rivers was 2.3 cm.yr⁻¹ (s.e. = 0.13, range 1.6–3.1), similar to the value of 2.38 cm.yr⁻¹ estimated for the juvenile eels taken from the lower Clutha River to stock Lake Hawea in 1998 (Beentjes 1998). In comparison, eels released into Lake Hawea grew faster than longfins from South Island rivers as well as longfins from 13 other South Island locations (Jellyman 1997). In addition, from a review of longfin growth throughout New Zealand, apart from the extremely fast growth of longfins from North Island hydro lakes described above, growth of eels

² The growth rate at release was reported as 2.45 cm.yr⁻¹ in the initial analysis (Beentjes & Jellyman 2001, 2002), but this was revised in the study to 2.38 cm.yr⁻¹ because size at entry to freshwater was assumed to be 60 mm, and not 50 mm.

introduced into Lake Hawea was one of the highest on record for the New Zealand longfin (Cairns 1941, Burnet 1969a, Chisnall 1989, Chisnall & Hicks 1993, Chisnall & Kalish 1993, Jellyman 1995, Beentjes et al. 1997, Jellyman 1997).

Why have eels transferred into Lake Hawea grown faster than elsewhere?

As discussed, longfins greater than about 40 cm are partly piscivorous (Jellyman 1989) which would indicate that diet of eels probably changed from exclusively invertebrates to include fish, some time after transfer into Lake Hawea (mean length at transfer = 42 cm). Although stomachs were not examined, common bullies (*Gobiomorphus cotidianus*) were present in large numbers and were frequently caught in the fyke nets in 2001. Fish provide a high energy diet (Ryan 1982) and the change to piscivory may partly explain the accelerated growth of eels after transfer. Aside from these comments, anecdotal information suggests that eels commercially harvested from Lake Hawea have historically been in good condition, indicating good growth rates (Vic Thompson, eel processor, pers. comm.).

Along with density and food, water temperature has been shown to be one of the most important variables affecting growth, with warm temperatures enhancing growth (Jellyman 1991, Chisnall & Hicks 1993, Horn 1996, Jellyman 1997). Given the relatively cool water temperatures characteristic of glacial oligotrophic lakes such as Hawea, the fast growth rates of eels in Lake Hawea were unexpected, and indicate that historic growth rates of resident eels in the lake (about 2 cm.yr⁻¹, see Table 3) were not constrained by water temperature and were probably density dependent. A significant reduction in the density of eels in Lake Hawea would have occurred over time given the limited recruitment of juvenile eels beyond Roxburgh Dam (Pack & Jellyman 1988) and the commercial harvest of eels from Lakes Wakatipu, Hawea, and Wanaka where annual catches were estimated at 40 t per annum (Jellyman 1984). Why growth of eels declined a few years after transfer into Lake Hawea is uncertain, but growth rates of transferred eels became similar to those of resident eels. The diet of larger eels would be expected to contain a high proportion of fish if available, and Lake Hawea had some of the highest densities of common bullies of the five alpine lakes studied by Rowe et al. (2003). These results suggest that it was not the absolute abundance of forage fish species that affected growth rates, but perhaps it was associated with their deeper distribution resulting from fluctuations in water level and associated lack of tall vascular plants (Clayton et al. 1986, Rowe et al. 2003).

4.3 Age validation

Results from the mean lengths of tagged and recaptured eels (Figure 7) and subsequent growth rates (Figure 8) indicated that post-transfer growth significantly exceeded pre-transfer growth. From the otolith ageing of the 2008 recaptures, we were able to reconstruct their average annual growth rates (expressed as mean otolith ring widths, Figure 12). As pre- and post-transfer growth were significantly different, we assumed that the marked inflexion in ring widths corresponded to the time of transfer into Lake Hawea. The average number of post-transfer years at large was 9, consistent with transfer into the lake 10 years previously. This confirmed that our interpretation of otolith hyaline rings as annual rings was correct, and also provided an independent measure of the validity of ageing eels from otoliths. Previous validation techniques used to confirm otolith ageing have been the variations in the widths of the outer ring throughout the year (Jellyman 1979), and the use of tetracycline to provide a reference mark on otoliths (Chisnall & Kalish 1993). The present study is the first to correlate known age (from recaptures of tagged fish) with putative age derived from otolith readings, and the results confirm that the hyaline rings are annual in formation and that our ageing methods are accurate.

4.4 CPUE

CPUE analyses for the 2001 recaptures indicated that density of eels in Lake Hawea was substantially less than in the lower Clutha River where eels were sourced (see Table 6). Growth in eels is often density dependent (Tesch 1977, Horn 1996, Jellyman 1997) and high density in the lower Clutha River was probably a constraint on growth. In contrast, in the low-density environment of Lake Hawea, growth has been enhanced. Slower growth rates of eels in The Neck compared to the north and south of the lake in 2001 is further evidence of the density dependent growth. Eels caught outside The Neck were larger and in better condition, and statistical analyses confirmed that the difference in growth occurred as a result of location within the lake and not size at release.

4.5 Sex ratio

The sex of eels could not be determined at the time of transfer into Lake Hawea in 1998 because eels were immature or undifferentiated. In 2001 all tag-recaptures were found to be immature females, and in 2008 all recaptures were also exclusively female but gonad development was more advanced with some close to that seen in pre-spawning migrating eels. Male longfins migrate to sea to spawn at about 65 cm and 0.7 kg, and females at 94 cm and 2.5 kg (Todd 1980, Jellyman & Todd 1982, Beentjes & Chisnall 1998, Beentjes 1999). The sex ratio of commercial sized eels in the most heavily commercially fished South Island rivers, including lower Clutha River, is dominated by males (Beentjes 1999, Beentjes et al. 2006), so we assume, a priori, that there were at least equal numbers of potential males and females in the 1998 eel transfers. Given the size of the 2001 recaptures (see Table 1, Figure 4), only a small proportion of male eels at this time would have been large enough to have migrated (see Figure 4), and hence we would expect to have found some males in the 2001 tag-recaptures. By 2008, had there been males present, most would have migrated so we would not have expected to find many males in our sample of tag-recaptures, and indeed we found none.

Why are there no males in Lake Hawea and other high country lakes?

Eel populations of low density tend to be largely female and dense populations tend to be predominantly male, indicating that expression of sex in eels is largely dependent on the environment (Davey & Jellyman 2005). The reasons for this may involve more intense competition for resources under high density conditions. For example, densities of the American eel (*A. rostrata*) in lake environments tend to be low and eel populations are mainly females, whereas rivers tend to have high densities of mainly males (Krueger & Oliveira 1999, Oliveira et al. 2001). Similarly, continued annual stocking of an inland lake in Ireland (Lough Neagh) with elvers over many years resulted in the sex ratio becoming increasingly skewed toward males – this was ascribed to the effect of overcrowding, and in response eels differentiated into males. In New Zealand we see a similar situation with males dominating in rivers (Beentjes 1999, McCleave & Jellyman 2004, Beentjes et al. 2006) and females in high country lakes (Beentjes et al. 1997). Unlike female eels where larger size confers benefits of increased fecundity, the “pressure” on male eels is to grow rapidly and mature at the minimum possible size (Helfman et al. 1987). Hence many males could be expected to emigrate from the lake within a few years of stocking.

The strategy of sexual development for male and female eels is fundamentally different, with immature males having both male and female gonad cells. Females, however develop from undifferentiated primordial gonad tissue, and cannot develop into males (see review by Davey & Jellyman 2005). Hence, in Lake Hawea the absence of males is consistent with the concept that transferred eels that were potentially male, differentiated into females in response to low density. Further, although recruitment into Lakes Wanaka and Wakatipu has been greatly reduced since Roxburgh Dam was built in 1958, analysis of ages of eels from these lakes indicates that limited recruitment has occurred since this time, but only females are present (Beentjes et al. 1997). Given the size range of longfinned eels in these lakes we would also have expected to have found some males.

In this regard the absence of males in Lake Hawea is consistent with that in the high country lakes that are the source of the Clutha River (Beentjes et al. 1997).

Alternatively, but less likely in our view, as juvenile eels were reported below Hawea Gates about 17 months after release, we cannot rule out the possibility that these were potential males attempting to move downstream to preferred male habitat.

4.6 Tagging

Of the eels released into Lake Hawea, 21.3% were tagged and about the same proportion of recaptures (19.4%) was found to have tags in both 2001 (19.4%) and 2008 (19.2%). This suggests that even after 10 years at liberty, tag loss and/or mortality due to tagging is inconsequential, a similar conclusion to that of Thomassen et al. (2000). Tags had no adverse effect on growth since length and weight at recapture of the 2001 tag-recaptures and recaptures without tags were not significantly different. Condition was significantly different, but the level of significance was low ($P \leq 0.05$) and this result seems questionable given that weight and length were unaffected by tagging. Coded wire tagging has proven to be a useful tool for monitoring enhanced eel populations. The tag can be easily detected in the factory before processing, and tagged eels retained for later removal of tags.

4.7 Survival and mortality

Without a regular long-term monitoring programme it will not be possible to quantify survival of eels released into Lake Hawea, particularly as the lake is open to emigration. There are few estimates available of long-term survival post-stocking and most are based on elvers or glass eels as seed stock and are not directly comparable. Pedersen (2000), however, estimated survival using wild juvenile eels (*A. anguilla*, mean length 25 cm) as seed stock released into a productive lake in Denmark at 55–75% over eight years. The lake was closed to immigration and all migrating eels exiting the lake were caught in traps at the outlet.

Mortality estimates (M) of unexploited populations of the New Zealand longfin are very low (0.042) (Jellyman 1994). Based on M of 0.042, assuming no emigration out of the lake, and no fishing mortality, the population trajectory of the introduced eels would decline exponentially (Figure 13). After three years (2001) we estimate that the original population would have declined to 8305 eels (12% decline) and after 10 years (2008) to 6190 eels (34% decline). However, we know that some commercial fishing has occurred in the lake after 1998, but have no data on catches (weights or numbers). Anecdotal reports suggest that as much as 5 t could have been harvested over the last 10 years. In the absence of fishing mortality, the weight of surviving transplanted eels in 2008 would be about 9 tonnes (6190 eels \times 1450 g (mean weight in 2008)). If fishing has indeed removed 5 t, and much of this when eels were smaller, the population could now be less than 3000 eels.

4.8 Stocking

Given the very high initial growth rates experienced by longfin eels released into Lake Hawea, it seems reasonable to conclude that the stocking rate of 0.35 kg.ha⁻¹ (juveniles) for the littoral area of Lake Hawea was conservative. The projected population decline through natural mortality (Figure 13) together with the accrual of biomass through growth, resulted in an estimated 2008 biomass of about 9000 kg which equates to a density for the littoral area of the lake of 1.93 kg.ha⁻¹; this estimate does not take into account the possible emigration of eels and any fishing mortality. Nonetheless, this is only a fraction of the biomass density estimates from 12 riverine locations in New Zealand, which range from 66 to 965 kg.ha⁻¹ (see review by Jellyman 1997) and probably indicates that the stocking

potential of Lake Hawea has not been optimised. Density and growth are inversely related and therefore it might be more sensible to base future stocking rates on the desired growth of eels rather than density. Any subsequent stockings should also incorporate a tagged sub-sample in order to monitor annual growth after transfer. Tagging will assume more importance in future stockings because it may not be possible to distinguish eels from different releases, as we were able to do in the present study.

4.9 Potential for future enhancement

Based on the results of Lake Hawea enhancement, stocking of recruitment-limited lakes in the Clutha River catchment with juvenile longfins is a viable option. Lake Wanaka has only a third of the littoral area of Lake Hawea but is likely to be more productive than Lake Hawea as it has minimal lake level fluctuations, warmer water temperatures, and more diverse aquatic vegetation (Clayton et al. 1986, Rowe et al. 2003). There is concern for long-term sustainability of the longfin eel fishery which is based predominantly in rivers (Jellyman et al. 2000, Beentjes & Dunn 2008, 2010). Further, a recent length structured population model of the New Zealand wide longfin eel population indicates that female spawning stock biomass is very low in the fished areas (4%), but increases to 20–25% if protected areas are included (Dunn et al. 2009). Alternative fisheries for longfin in stocked lakes such as Hawea, Wanaka, Wakatipu, and Dunstan would relieve fishing pressure on downstream stocks. Lake Hawea could be expected to yield about 23 t of longfin landings annually, under an ongoing stocking programme (Beentjes et al. 1997). However, female and, to a lesser extent, male longfins are unlikely to contribute to future spawning stock because of the high mortality incurred during turbine passage through Clyde and Roxburgh Hydro Dams as they attempt to migrate to sea. All future transfers of immature juvenile longfins should consider the implications of males moving out of the lake and downstream after sexual differentiation has occurred.

Stocking of Lake Hawea with elvers or glass eels has not been attempted, but this may not be successful given what we know about the enhancement of Waikato River hydro lakes. Since the early 1990s 1 to 2 million elvers have been trapped below Karapiro Dam annually, and transferred to the recruitment limited upstream lakes including Karapiro and Arapuni (Martin et al. 2009). Monitoring of commercial eel fisheries from these lakes indicates that catches are poor to modest (Beentjes 2008) and these lakes are considerably less productive than expected given both the magnitude and long-term nature of the stocking programme. Reasons for this disparity between stocking rates and harvest are uncertain, but might be associated with quality of the seedstock, high initial mortality rates, overstocking, or lack of sufficient suitable habitat for juvenile eels.

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Table 1: Descriptive statistics for juvenile longfin eels tagged and released into Lake Hawea in 1998, and all-recaptures (tag-recaptures and untagged-recaptures) in 2001 and 2008. Recaptures include 41 tagged eels in 2001 and 79 tagged eels in 2008. * from Table 2; **, annual growth in 2001 and 2008 estimated from mean length or weight at recapture minus that at tagging, divided by years at liberty.

Survey	Variable	<i>N</i>	Mean	Minimum	Maximum	Standard error
1998	Release length (cm)	2010	42.0	30.0	55.0	0.10
	Annual growth (cm.yr ⁻¹)*	96	2.38	1.43	4.33	0.05
2001	Recapture length (cm)	216	55.8	40.0	74.0	0.39
	Annual growth (cm.yr ⁻¹)**	216	4.6	–	–	–
2008	Recapture length (cm)	399	79.9	60.0	101.5	0.44
	Annual growth (cm.yr ⁻¹)**	399	3.8	–	–	–
1998	Release weight (g)	2010	173	55	380	1.33
2001	Recapture weight (g)	216	498	136	1040	11.8
2008	Recapture weight (g)	399	1450	500	3240	27.4
1998	Release condition (<i>k</i>)	2010	2.24	1.37	3.55	0.005
2001	Recapture condition (<i>k</i>)	216	2.75	1.98	3.62	0.02
2008	Recapture condition (<i>k</i>)	399	2.72	1.56	4.65	0.02

Table 2: Age and annual growth estimates for longfin eels released into Lake Hawea in 1998, and also for the 2008 tag-recaptures over the lifetime of the eel and at the time of release. Annual growth was estimated from the length (or weight) at release/age. Annual growth for the 2008 eels at release was estimated from length (or weight) at tagging/age-10.

Survey	Variable	<i>N</i>	Mean	Minimum	Maximum	Standard error
1998	Age (yr)	96	15.4	6.0	32.0	0.42
	Length (cm)	96	41.3	29.0	57.0	0.74
	Weight (g)	96	172	45	455	9.57
	Annual growth at release (g.y ⁻¹)	96	10.9	3.6	23.6	0.48
	Annual growth at release (cm.y ⁻¹)	96	2.38	1.43	4.33	0.05
2008	Age (yr)	74	25.1	14	32	0.41
	Length (cm)	74	78.9	62.5	98.0	0.98
	Weight (g)	74	1486	678	2879	60.0
	Annual growth over lifetime (g.y ⁻¹)	74	60.3	29.2	148.1	2.7
	Annual growth over lifetime (cm.y ⁻¹)	74	2.97	2.01	5.58	0.07
	Annual growth at release (g.y ⁻¹)	71	12.2	4.0	38.8	0.62
	Annual growth at release (cm.y ⁻¹)	71	2.53	1.33	8.50	0.11

Table 3: Descriptive statistics for longfin eels resident in Lake Hawea before stocking (three eels were sampled in 1995 and three in 1998), and after stocking in 2001, and 2008. Eels were deemed to be residents if over 84 cm in 2001 and over 109 cm in 2008.

Survey	Variable	<i>N</i>	Mean	Minimum	Maximum	Standard error
1998 and 1995	Length (cm)	6	112	101	124	3.8
	Weight (g)	6	4880	3260	7640	705
	Age (y)	5	56	42	61	3.6
	Annual growth (cm.yr ⁻¹)	5	1.89	1.65	2.38	0.13
	Condition (<i>k</i>)	6	3.35	2.91	4.01	0.15
2001	Length (cm)	12	109	85	130	4.1
	Weight (g)	12	4253	1770	6506	432
	Condition (<i>k</i>)	12	3.15	2.05	3.77	0.13
2008	Length (cm)	11	125	110	142	2.8
	Weight (g)	11	6213	4740	8960	342
	Condition (<i>k</i>)	11	3.19	2.77	3.88	0.03

Table 4: Descriptive statistics for the 2001 and 2008 longfin tag-recaptures from Lake Hawea. The 2008 recapture length was adjusted by 2.5% to allow for shrinkage during freezing. The tagged length, weight, and condition at release in 1998 are also shown.

Survey	Variable	<i>N</i>	Mean	Minimum	Maximum	Standard error	
2001 tag-recaptures							
1998	Tagged length (cm)	41	43.1	34.0	50.0	0.56	
2001	Recapture length (cm)	41	55.7	47.0	67.0	0.80	
	Length increment (cm)	41	12.5	2.0	22.0	0.67	
	Annual growth (cm.yr ⁻¹)	41	4.1	0.7	7.3	0.22	
1998	Tagged weight (g)	41	185	90	315	7.5	
	2001	Recapture weight (g)	41	485	214	906	27.6
		Weight increment (g)	41	300	47	706	24.9
		Annual growth (g.yr ⁻¹)	41	99.1	15.5	232.6	8.2
1998	Tagged condition (<i>k</i>)	41	2.26	1.70	2.85	0.03	
	2001	Recapture condition (<i>k</i>)	41	2.70	2.06	3.46	0.05
2001 untagged-recaptures							
2001	Recapture length (cm)	175	55.9	40.0	74.0	0.44	
	Recapture weight (g)	175	500	136	1040	13.09	
	Recapture condition (<i>k</i>)	175	2.77	1.98	3.62	0.02	
2008 tag-recaptures							
1998	Tagged length	76	42.0	32.0	52.0	0.56	
2008	Recapture length (cm)	79	78.6	62.5	98.0	0.94	
	Length increment (cm)	76	36.5	20.6	55.5	0.86	
	Annual growth (cm.yr ⁻¹)	76	3.6	2.0	5.5	0.08	
	1998	Tagged weight	76	177	60	355	7.4
2008	Recapture weight (g)	79	1462	678	2879	57.3	
	Weight increment (g)	76	1281	504	2603	56.1	

Table 4—continued

Survey	Variable	N	Mean	Minimum	Maximum	Standard error
	Annual growth (g.yr ⁻¹)	76	126.9	49.9	257.8	5.56
1998	Tagged condition (<i>k</i>)	79	2.28	1.75	2.76	0.02
2008	Recapture condition (<i>k</i>)	79	2.90	2.30	3.48	0.03
2008	Gonad width (mm)	78	11.9	2.6	29.6	0.7

Table 5: Descriptive statistics for 2001 all-recaptures (N=216) from inside and outside The Neck in Lake Hawea.

Variable	N	Mean	Minimum	Maximum	Standard error
Recapture length (cm) inside Neck	178	54.9	40.0	74.0	0.42
Recapture length (cm) outside Neck	38	59.7	53.0	68.0	0.73
Recapture weight (g) inside Neck	178	464	136	1040	11.86
Recapture weight (g) outside Neck	38	653	410	956	25.49
Recapture condition (<i>k</i>) inside Neck	178	2.70	1.98	3.62	0.02
Recapture condition (<i>k</i>) outside Neck	38	3.02	2.59	3.61	0.05

Table 6: Catch per unit effort for Lake Hawea in 2001 (including all 216 recaptures and 12 residents), and from the lower Clutha River in 1998.

Location	No. nets	Catch (kg)	No. eels	CPUE	
				kg/net	No.eels/net
Lake Hawea (2001)	150	159	228	1.06	1.5
The Neck (2001)	90	118	187	1.31	2.1
Outside Neck (2001)	60	41	41	0.68	0.7
Lower Clutha River (1998)	380	1682	9722	4.43	25.6

Table 7: Results of pair-wise comparisons of the past 20 years of growth (expressed as width of annual otolith bands) of recaptured longfin eels from Lake Hawea. The columns in grey indicate post-transfer growth. X = a significant pair-wise correlation ($P < 0.05$). Note that 2008 was excluded from this plot as it did not represent a full year's growth.

	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007
1988			X					X		X		X	X	X			X	X		
1989												X								
1990																				
1991																				
1992								X		X		X	X	X		X	X	X		
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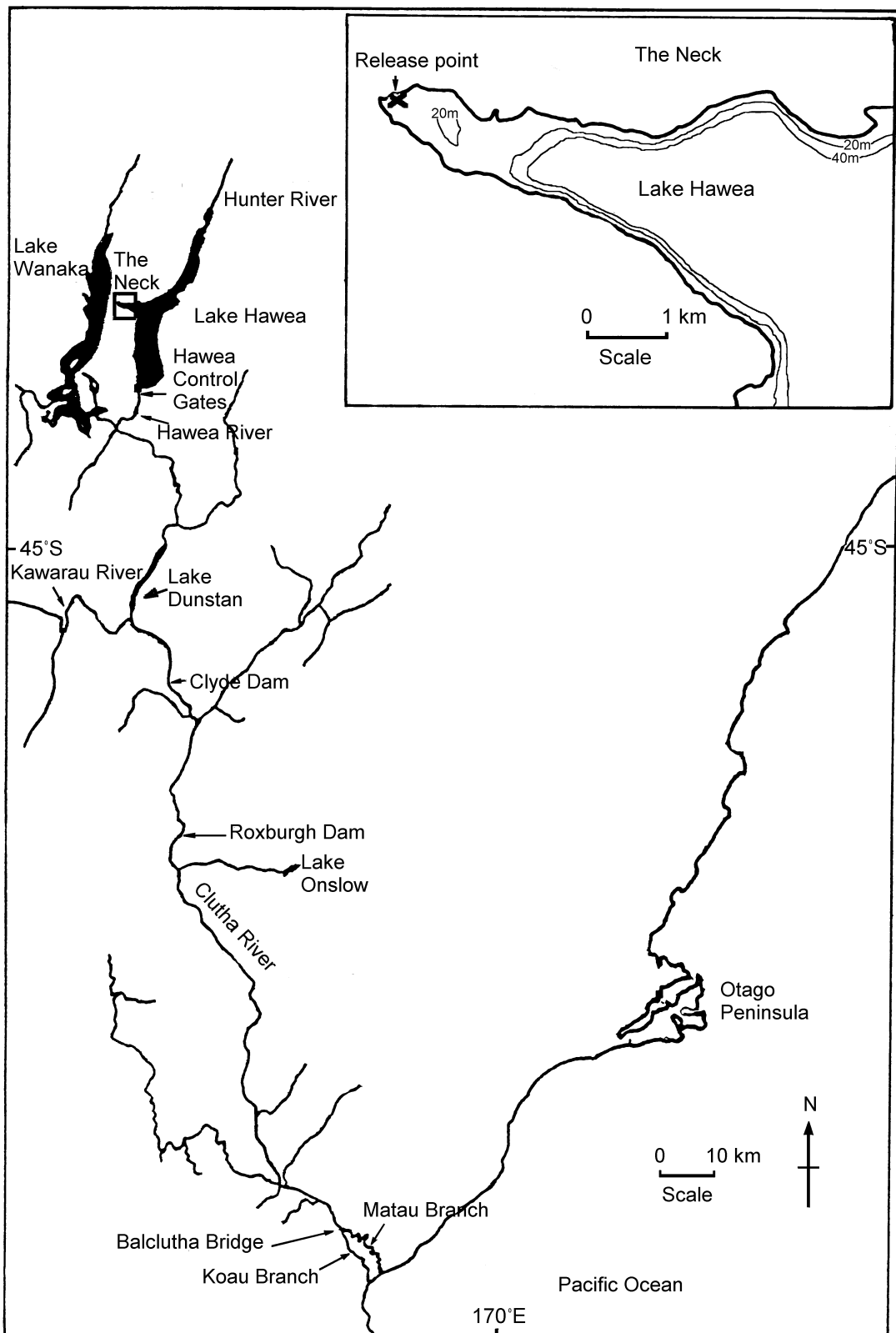


Figure 1: Map of Clutha River and Lake Hawea. Locations of juvenile eel capture from Matau and Koau branches of the lower Clutha River, and the enhancement site, The Neck at Lake Hawea, are shown.

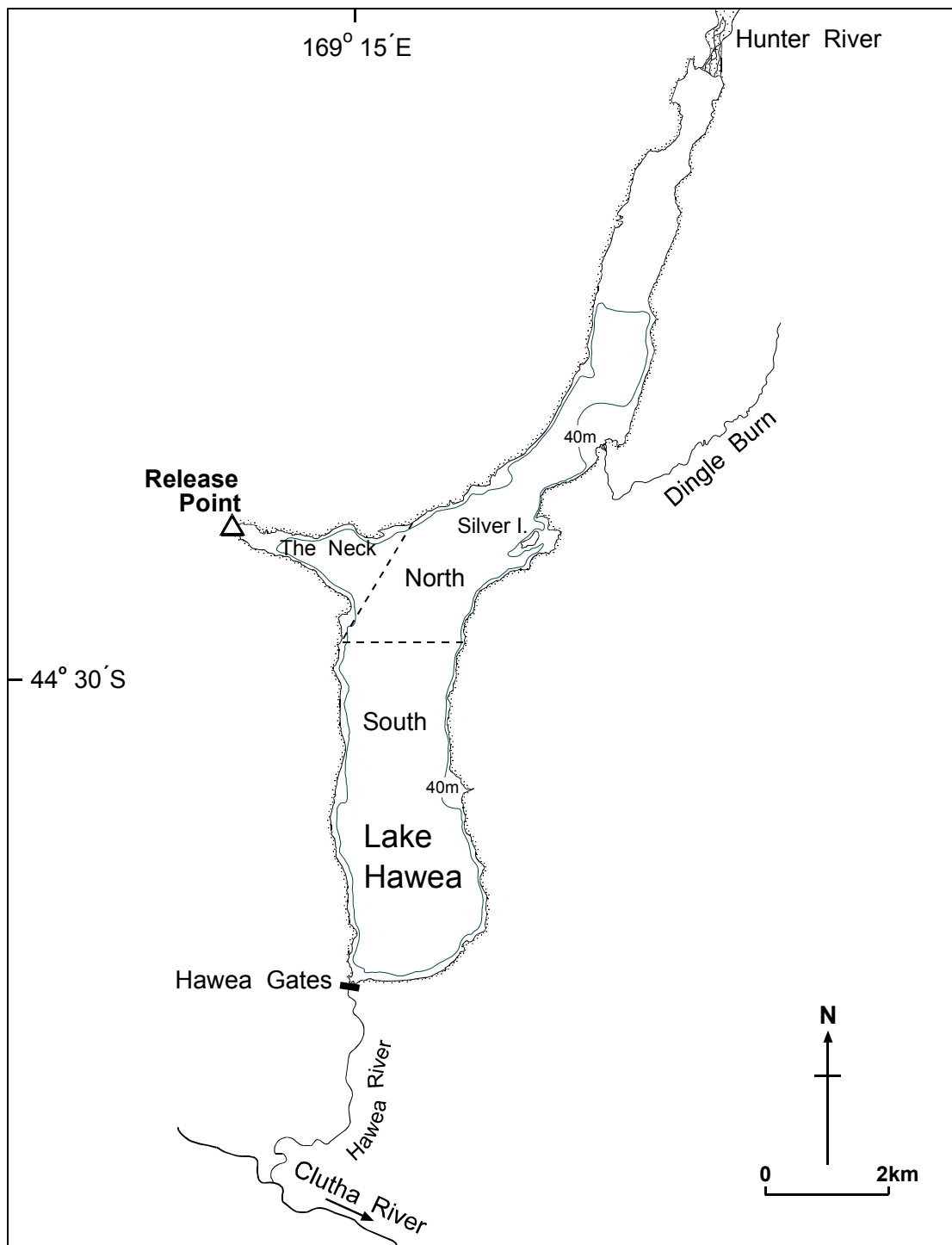


Figure 2: Map of Lake Hawea showing release point in 1998 and the three areas (The Neck, South, and North) surveyed in 2001. There is no information on location of the 2008 recaptures sample.

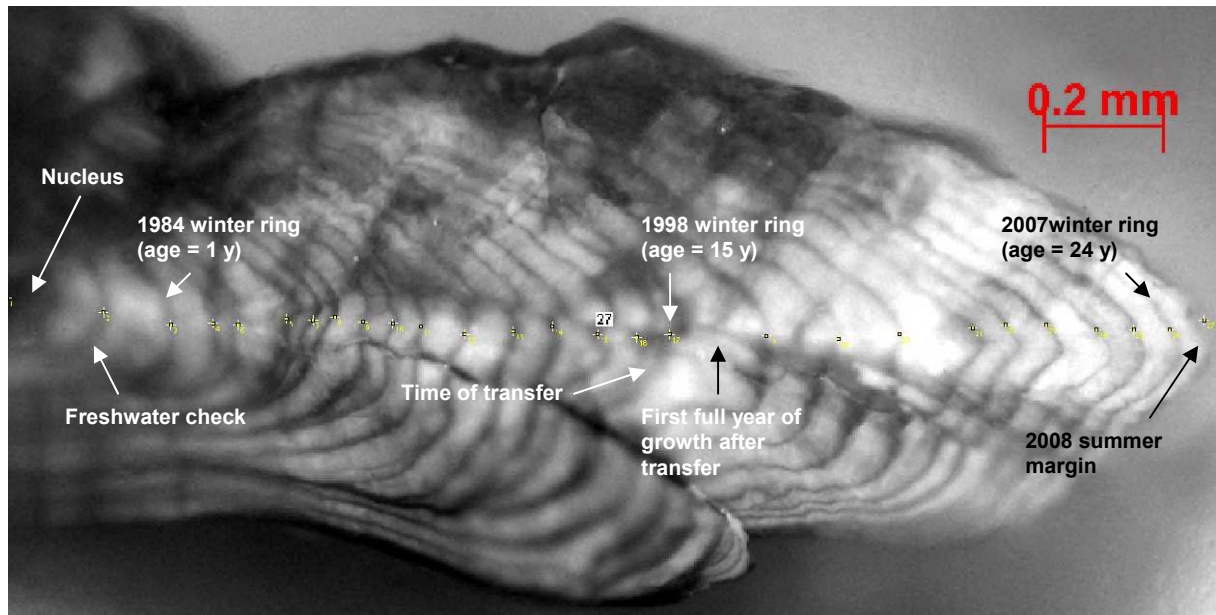


Figure 3; Photograph of sagittal otolith from a longfin eel tag-recapture from Lake Hawea in 2008 (eel recapture number 42). Eel length = 78.4 cm, age = 24 years in 2007. There are 27 annual rings identified with crosses, but the age of the eels is estimated at 24 years, because the first two correspond to the nucleus and freshwater check and the last ring to the outside of the 2008 summer marginal growth.

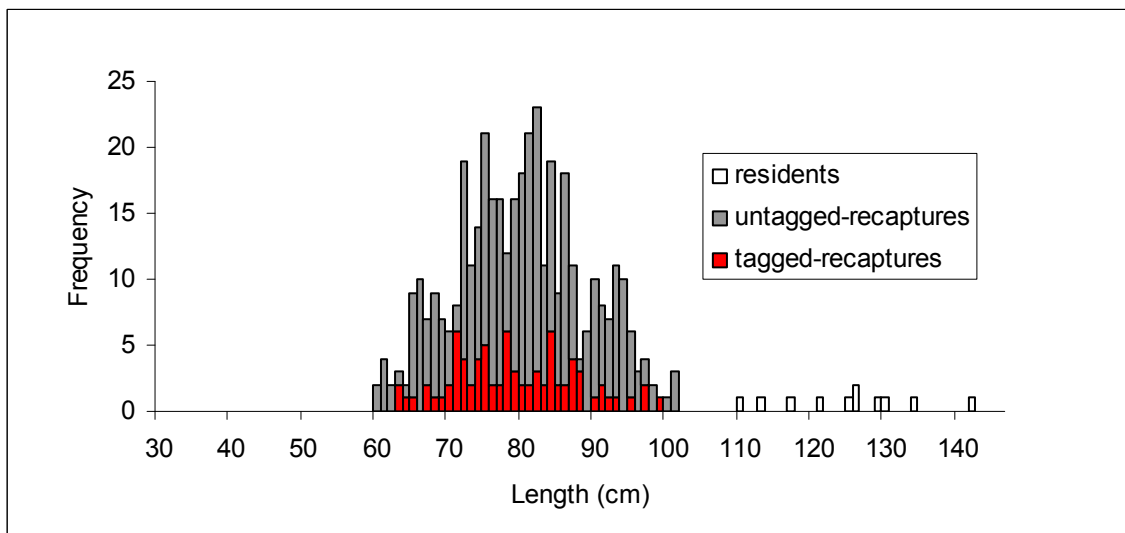
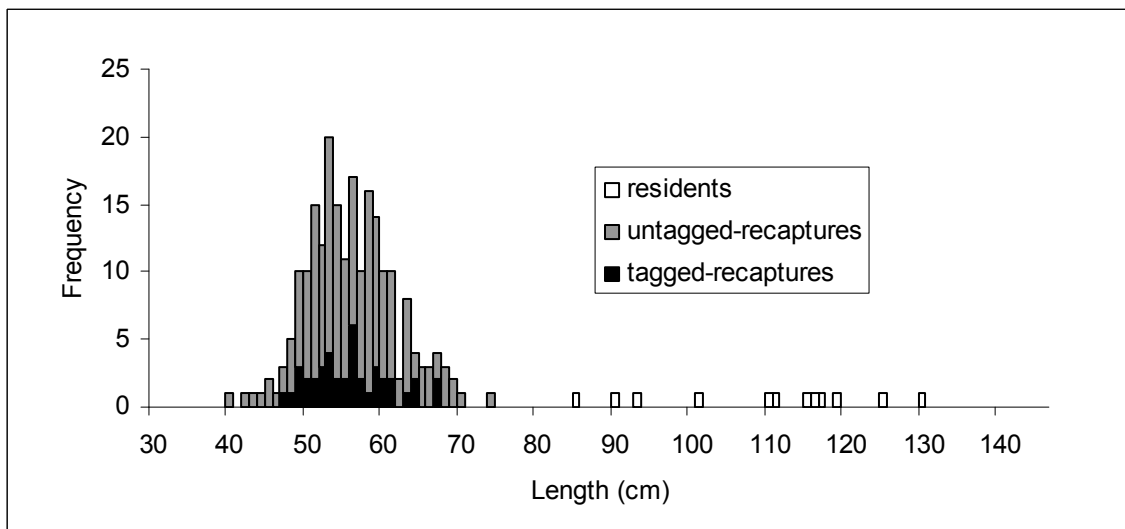
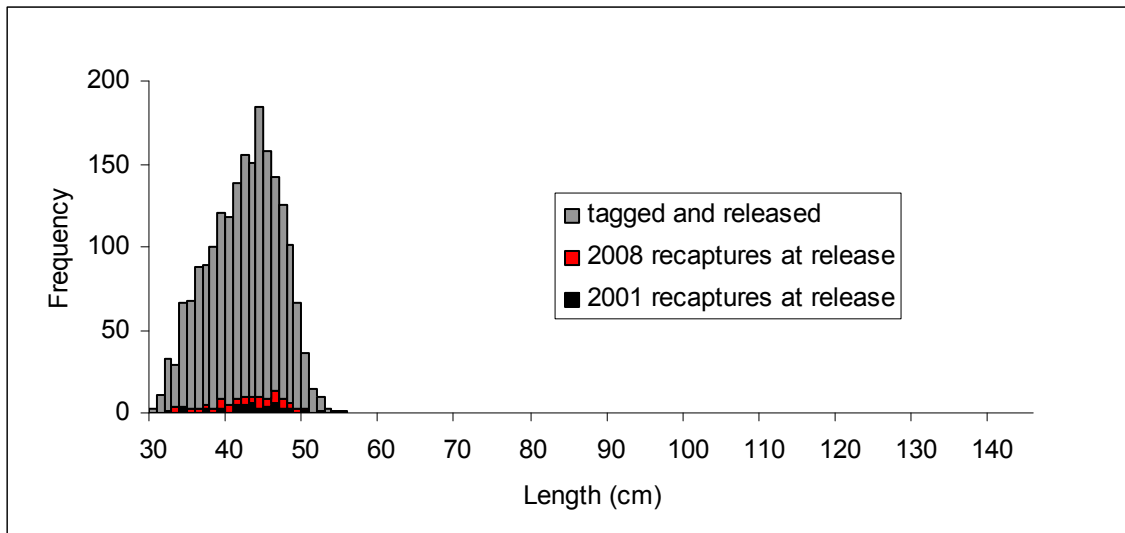


Figure 4: Length distribution of longfin eels released into Lake Hawea in 1998 (n = 210) showing size distribution of 2001 (n = 41) and 2008 (n = 76) tagged-recaptures at release (top). Length distribution of longfin eels recaptured in 2001 (n = 228, including 41 tag-recaptures and 175 untagged-recaptures) and 12 assumed residents (middle). Length distribution of longfin eels recaptured in 2008 (n = 410, including 76 tag-recaptures and 323 untagged-recaptures) and 11 assumed residents (bottom).

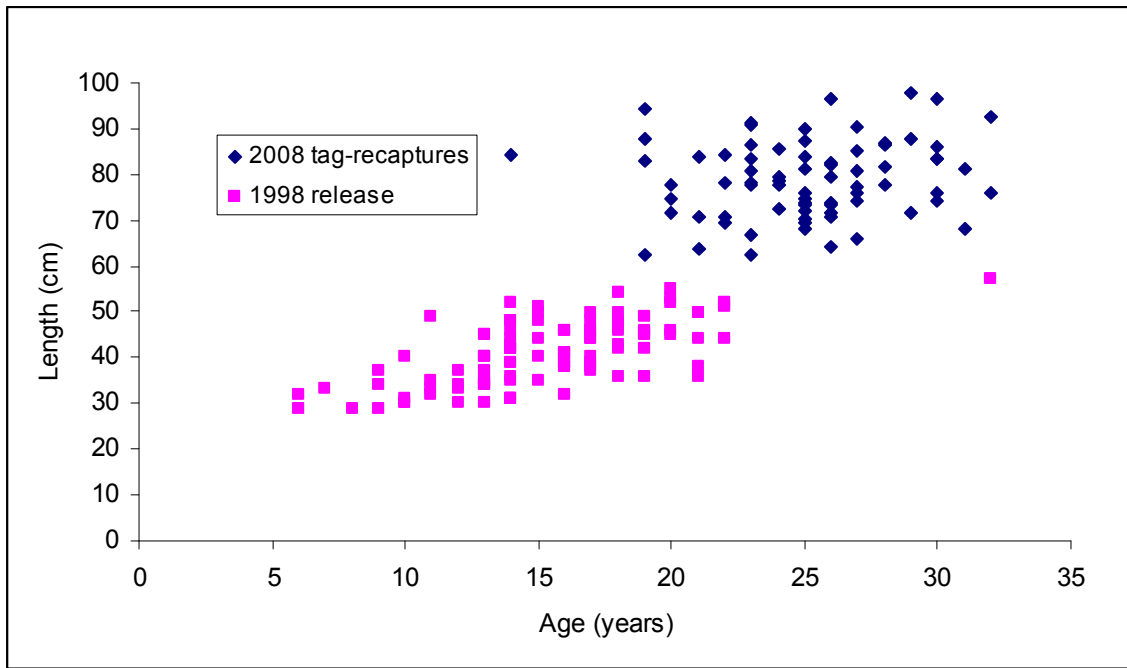


Figure 5: Length at age at release in 1998 (n = 96) and for the 2008 tag-recaptures (N=74).

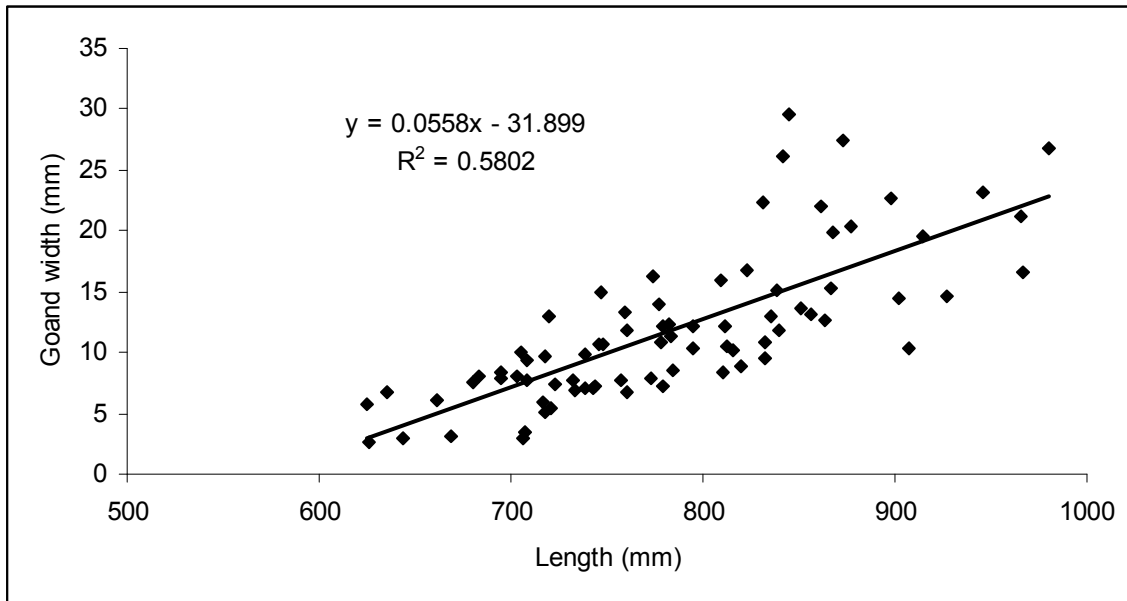


Figure 6: Gonad width plotted against eel length for longfin eels recaptured in 2008 (n = 78). A linear regression model has been fitted to the data.

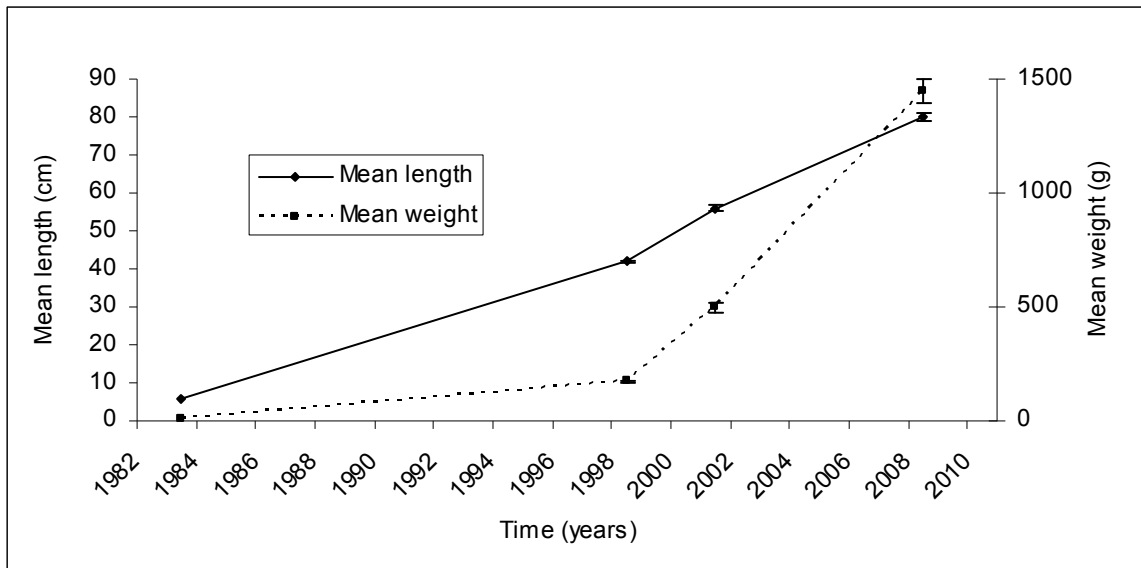


Figure 7: Mean length and weight of longfin eels at entry to freshwater (assumed to be 1983 based on mean age in 1998 of 15 years), at release into Lake Hawea in 1998 ($n = 2010$), and at recapture in 2001 ($n = 216$) and 2008 ($n = 399$). Mean length for 1983 assumed to be 6 cm (length at entry to FW), and mean weight estimated from mean weight divided by mean age in 1998 (15 years, $n = 96$). Error bars are 95% confidence intervals.

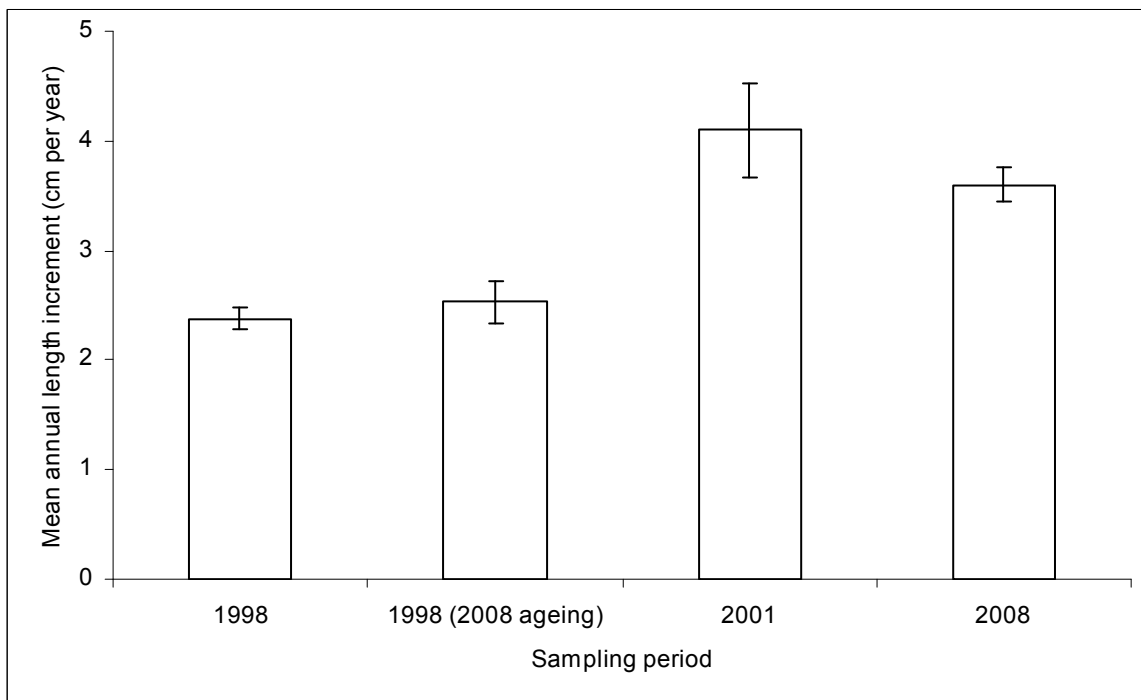


Figure 8: Mean annual length increment of longfin eels before release (1998) and at recapture in 2001 and 2008. The 1998 estimates were calculated from length-6/age of the subsample of eels released in 1998 ($n = 96$), and also from the length at age of the 2008 tag-recaptures ($n = 71$) (i.e., length at tagging /age-10). Error bars are 95% confidence intervals around the means.

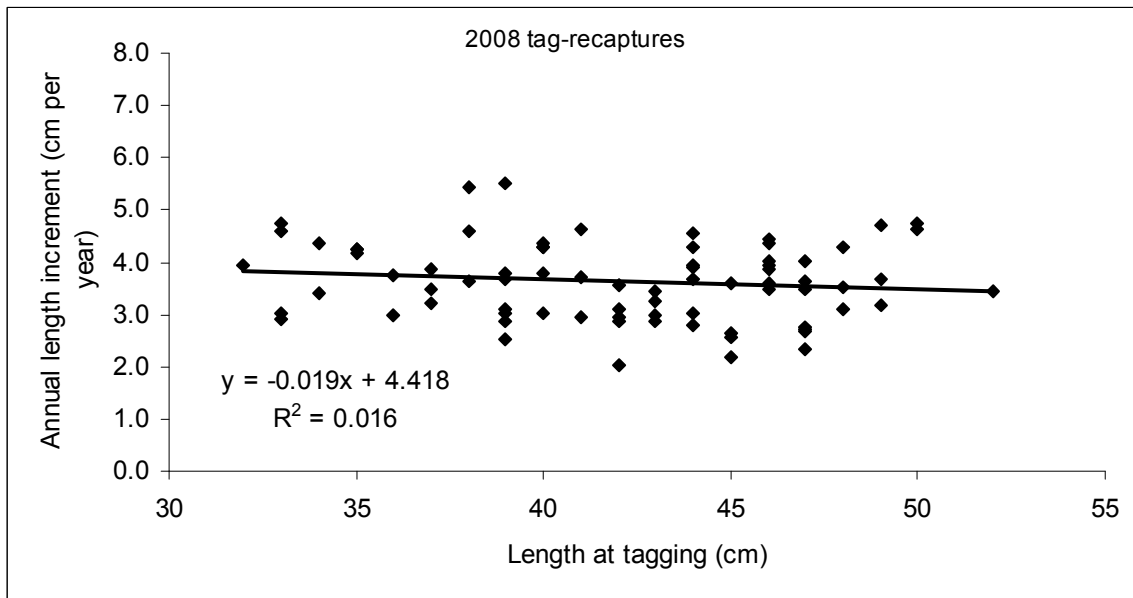
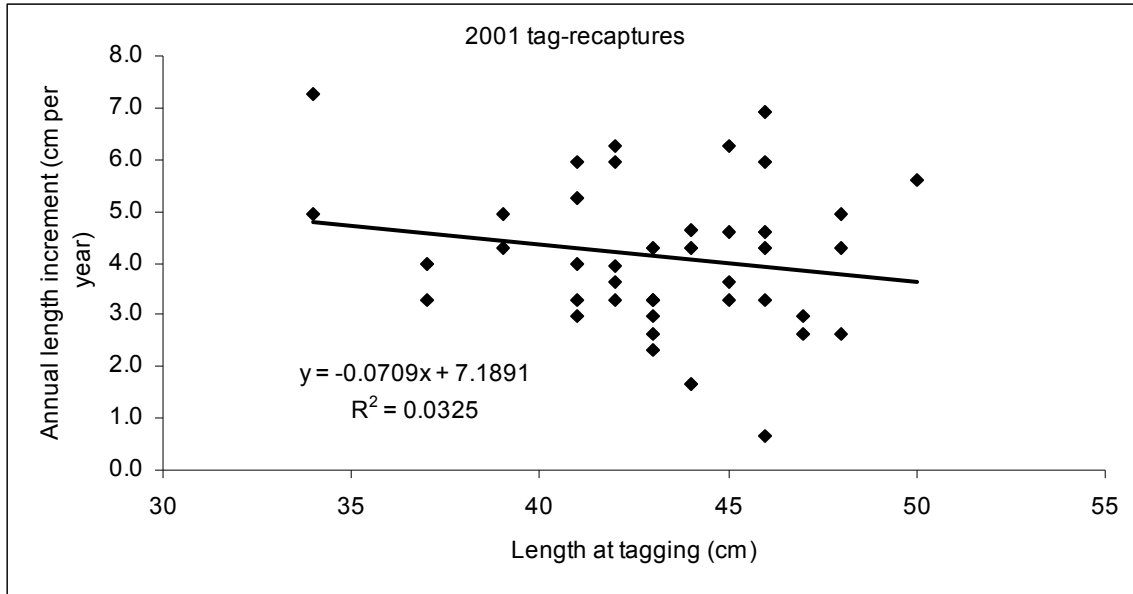


Figure 9: Length at tagging of longfin eels plotted against length increment for 2001 and 2008 tag-recaptures (2001, n = 41; 2008, n = 76).

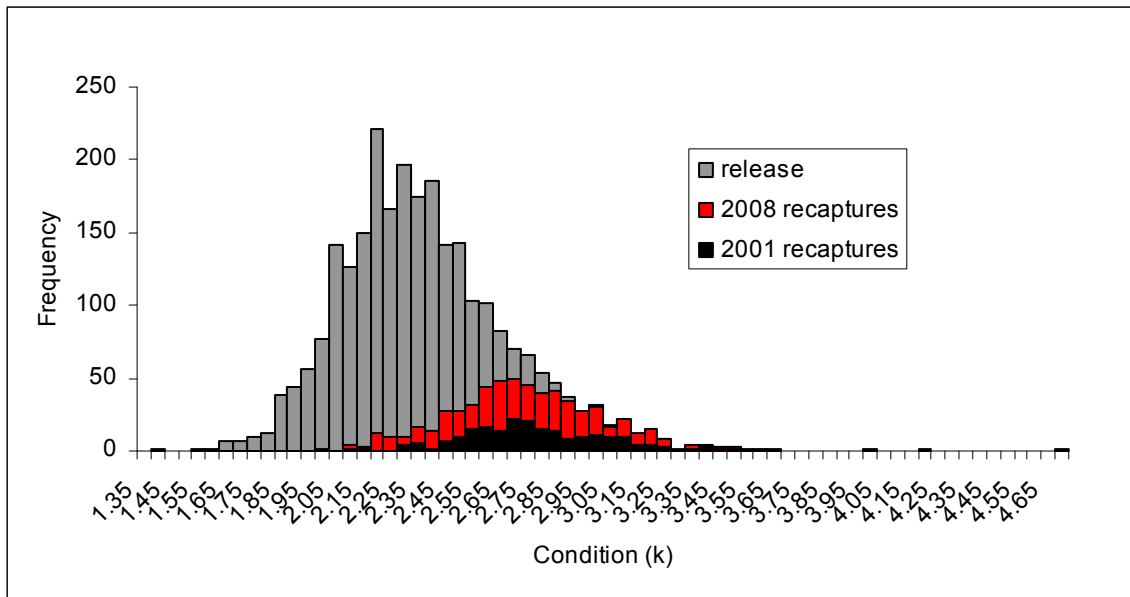


Figure 10: Condition (*k*) of all eels at release in 1998 (*n* = 210), all-recaptures in 2001 (*n* = 216) and all recaptures in 2008 (*n* = 399).

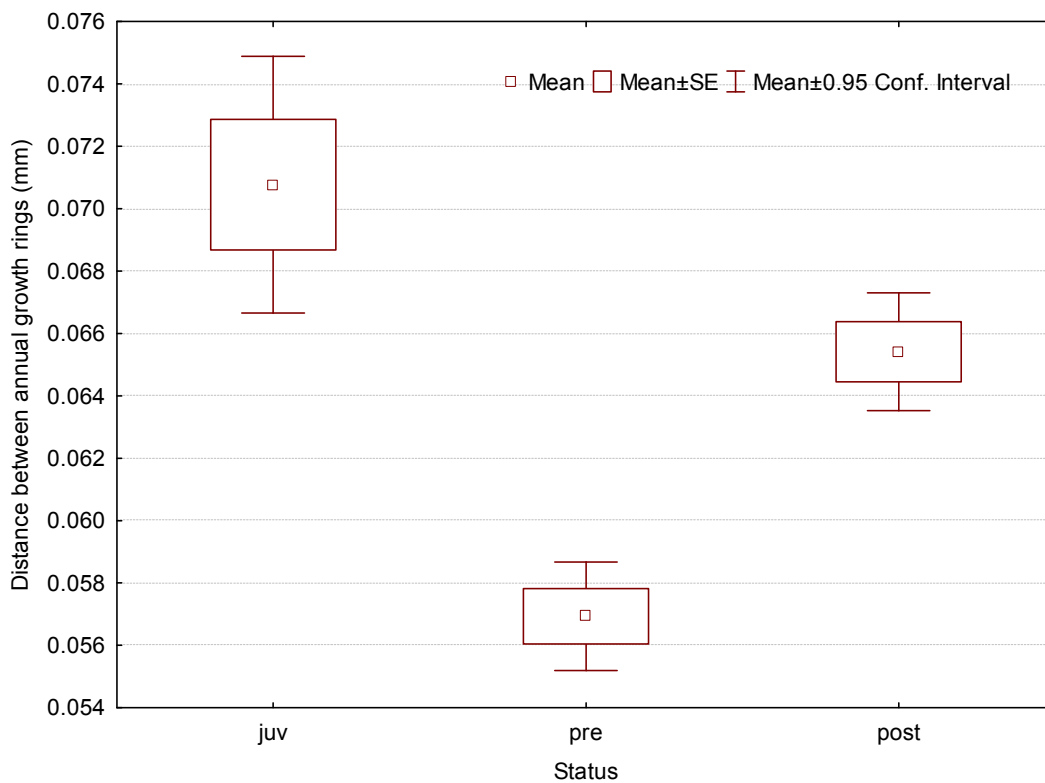


Figure 11: Box and whisker plots of mean distance between annual growth rings of otoliths from the 2008 tag-recaptures (*n* = 72 aged eels). post, rings laid down in the 10 years after the 1998 transfer into Lake Hawea; pre, rings laid down in the 10 years before transfer; juv (= juvenile), rings laid down more than 10 years before transfer.). *n* = 383 juv rings, 710 pre rings, and 720 post rings.

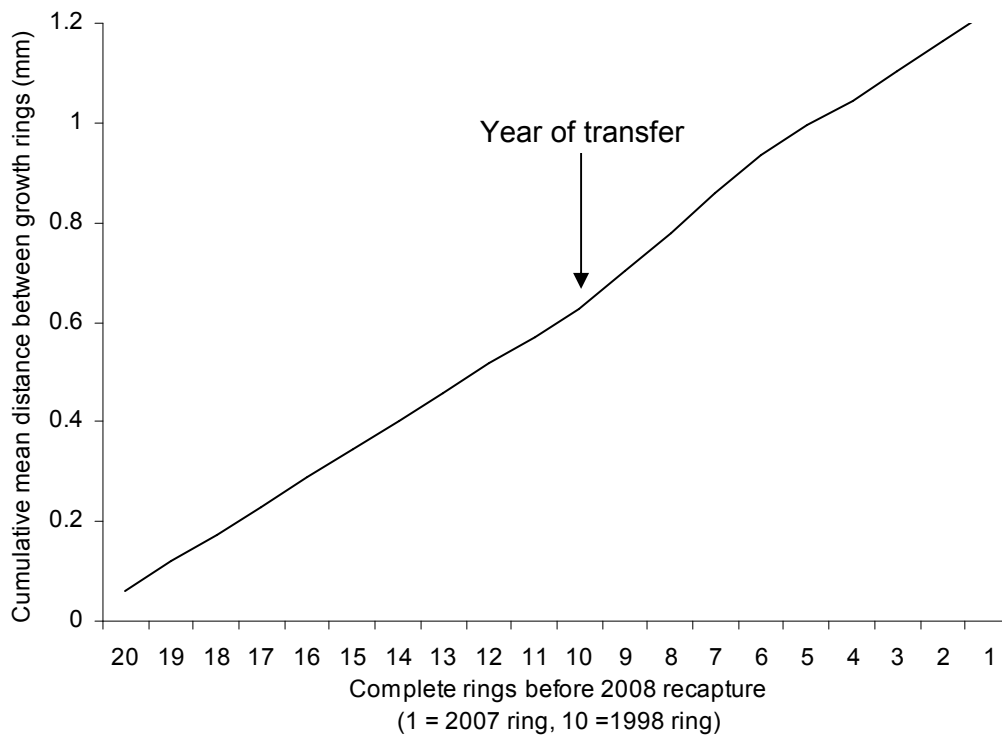
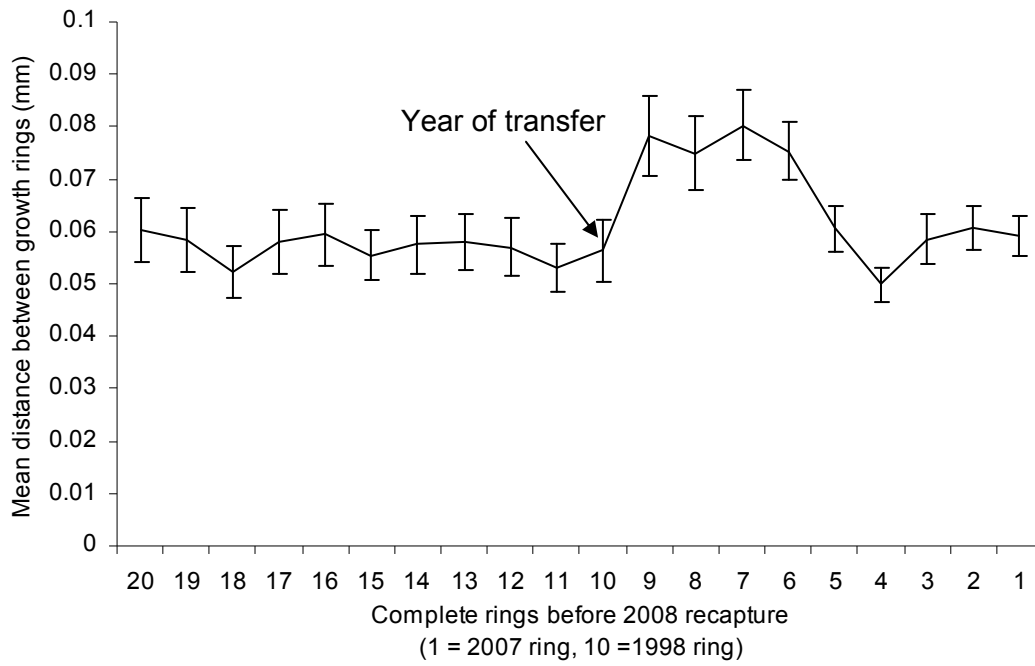


Figure 12: Top panel, mean distance between annual growth rings of otoliths from the 2008 tag-recaptures (N = 72 aged eels) for 20 years before recapture. The error bars represent 95% confidence intervals. Bottom panel, cumulative plot of mean distance between annual growth rings of otoliths from the 2008 tag-recaptures with years of transfer shown.

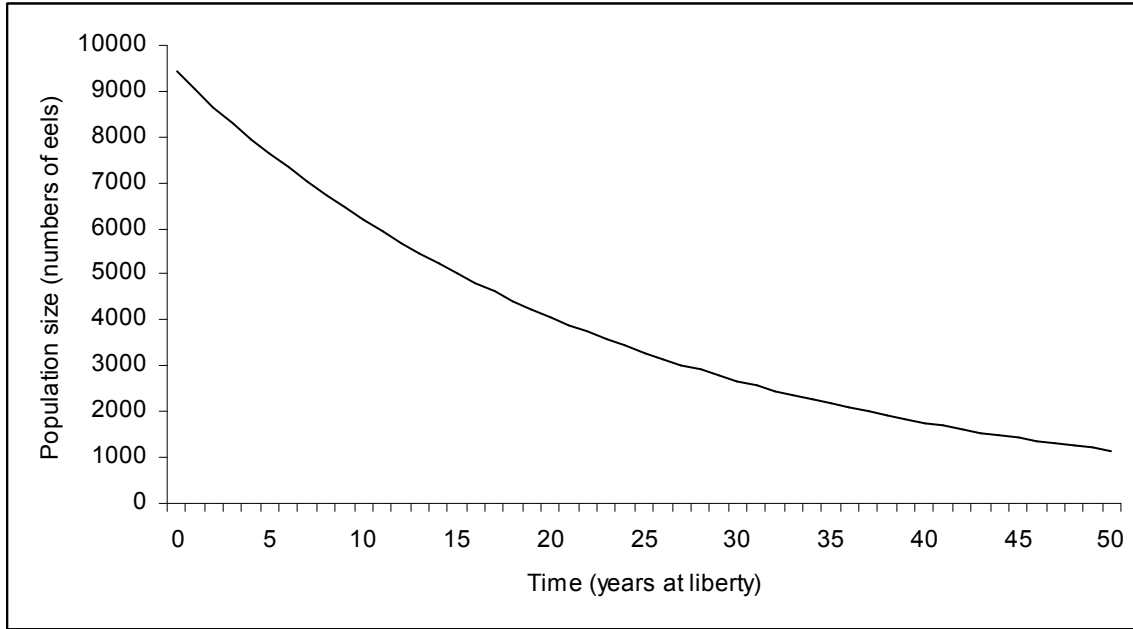


Figure 13: The projected population decline of eels transferred into Lake Hawea in 1998 through natural mortality (M). $M = 0.042$.