Age and growth estimates for New Zealand hapuku, *Polyprion oxygeneios*

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Abstract.—*Polyprion oxygeneios* (family Polyprionidae) is fished commercially and recreationally in the southern Indian and Pacific Oceans. Estimates of growth rate, age at maturity and recruitment, and longevity are required for fishery management. We used thin otolith sections to age *P. oxygeneios* from New Zealand, where it is known as hapuku. Growth bands were difficult to count, leading to low counting precision and, for some age groups, to a small between- and within-reader ageing bias. These problems, however, had little effect on the shape of growth curves fitted to length-at-age data. An oxytetracycline injection experiment supported our hypothesis of annual deposition of an opaque-hyaline band pair, but further validation is required. Independently derived von Bertalanffy growth curves (from length-frequency data) and growth-rate estimates (from tag-recapture data) for young hapuku agreed well with estimates from length-at-age data.

Juvenile hapuku are pelagic and most switch to a demersal habitat at around 50 cm total length and at an estimated age of 3–4 years. They probably recruit to commercial trawl catches at about the same age. Female hapuku appear to grow slightly faster than males. Both sexes mature at about 10–13 years. The longevity of hapuku is uncertain, but some individuals probably live longer than 60 years.

Polyprion oxygeneios (Schneider, 1801) (family Polyprionidae) is a large demersal fish that inhabits temperate and subtropical waters of the southern Indian and Pacific Oceans (Roberts, 1986; Fig. 1). It supports significant fisheries off the Juan Fernández Islands, Chile, and off New Zealand and is an important bycatch in south-east Australian longline fisheries (Johnston, 1983; Pavez and Oyarzún, 1985; Pizzaro and Yáñez, 1985; Kailola et al., 1993; Annala and Sullivan, 1997). The closely related wreckfish, *P. americanus* (Bloch and Schneider, 1801) is found in the North and South Atlantic Oceans, Mediterranean Sea, southern Indian Ocean, and south-west Pacific Ocean (Roberts, 1986; Sedberry et al., 1994) and supports fisheries throughout its range (Sedberry et al., 1994, 1996).

The ability to age *Polyprion* species is essential for proper management of their widespread fisheries, because it will enable determination of growth rates, ages at maturity and recruitment, longevity, and natural mortality rates. Previous attempts to age the two species have had limited success. Age and growth of *P. oxygeneios* have been estimated from otolith band counts in New Zealand (McDougall, 1975) and from scale annuli counts in Juan Fernández Island (Pavez and Oyarzún, 1985). A study on the age and

growth of *P. americanus* from the north-west Atlantic is currently underway (Sedberry et al., 1994, 1996; Manooch and Potts[1]). However, otolith bands have proven difficult to count in both species, scale annuli are unreliable for older fish, and the ageing techniques have not been validated.

In New Zealand, *P. oxygeneios* and *P. americanus* are managed as a single species-unit in the Quota Management System (QMS) (Paul and Davies, 1988; Annala and Sullivan, 1997). Both species are fished commercially and recreationally throughout New Zealand. They are highly sought after, but catches are relatively low. Commercial landings of both species combined peaked at 2700 t in 1983–84, but since the introduction of the QMS, they have been constrained by quotas to less than 1500 t per year (Annala and Sullivan, 1997). Despite these quotas, commercial line and set-net fisheries for *Polyprion* species have been seasonally important for small inshore fishing vessels in many parts of New Zealand. Annual recreational landings were about 500 t in 1991–94 (Annala and Sullivan, 1997).

This paper addresses age and growth in New Zealand *P. oxy-*

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[1] Manooch, C. S., and J. Potts. 1997. National Marine Fisheries Service, 101 Pivers Island Rd, Beaufort, NC 28516. Personal commun.

Figure 1
Hapuku, *Polyprion oxygeneios* (63 cm TL).
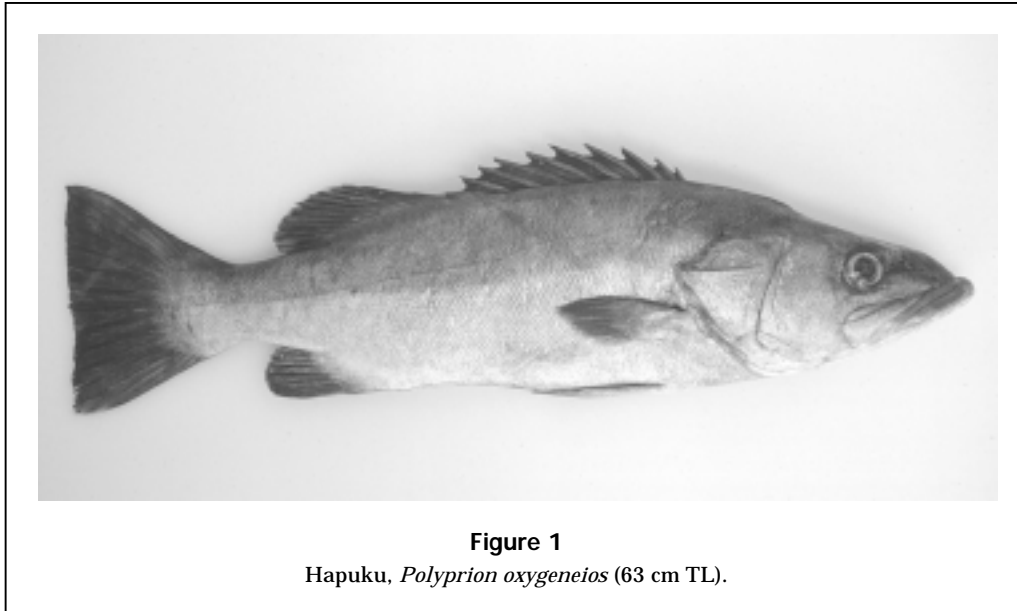
geneios, hereafter called hapuku. However, our results are also relevant to other populations of *P. oxygeneios* and, because both species of *Polyprion* have similar otolith structure, our results should also assist in the interpretation of otoliths of *P. americanus*. We used thin otolith sections to age hapuku and attempted to validate ages using oxytetracycline (as a time marker) and otolith marginal state analysis. We also obtained independent growth rate estimates from length-frequency and tag-recapture data for comparison with growth rate estimates derived from length-at-age data.

Materials and methods

Otolith ageing

Sagittal otoliths were obtained from 1400 hapuku collected from waters off New Zealand, from 1979 to 1995. Many otoliths were collected during studies by Johnston (1983) and Roberts (1986) and made available to us. Since then, additional otoliths have been collected by us during research trawl surveys and sampling trips aboard commercial line vessels, as well as by Ministry of Fisheries scientific observers aboard commercial line and trawl vessels.

Most otoliths were accompanied by information on fish total length (TL, to the centimeter below actual length) and sex. Three subsamples of these otoliths were selected for analysis. The first comprised 44 otoliths collected from five sites between Three Kings Islands and Great Barrier Island (Fig. 2) (hereafter called the "northern" sample). The second consisted of 178 otoliths collected from Cook Strait and Kaikoura (Fig. 2; "central" sample) and the third consisted of 28 otoliths from large hapuku collected from other sites throughout New Zealand ("miscellaneous" sample), selected to boost the number of old fish in the data set.

One otolith from each pair was viewed under transmitted polarized light, and the straightest dorsonuclear ridge was marked with a pen to guide the saw for sectioning. Each otolith was then embedded in a block of clear epoxy resin and sectioned transversely through the core at a thickness of 650 μm by using a dual-blade high-speed diamond saw. One face of the section was polished with carborundum paper and glued on to a microscope slide with thermoplastic cement. The opposite face was then ground and polished to a final thickness of 200–350 μm, depending on the clarity of the otolith bands when viewed under both reflected and transmitted light.

Opaque otolith bands were counted under transmitted light in the dorsal part of each section by two readers. Both readers carried out an initial training exercise by making counts on a subsample of the sections, while knowing the collection details of each fish (TL, sex, and site), and then discussed their results. Subsequent counts were carried out "blind"; i.e. the readers did not know the size, sex, or collection site of the hapuku. Reader 1 counted all sections once (R_1) and reader 2 counted all sections twice, the two counts being separated by two months ($R_{2,1}$ and $R_{2,2}$). The readability of sections was scored on a scale from 1 (unreadable) to 5 (exceptionally clear).

Otolith band counts were assessed for ageing bias and precision (between readers, and between read-
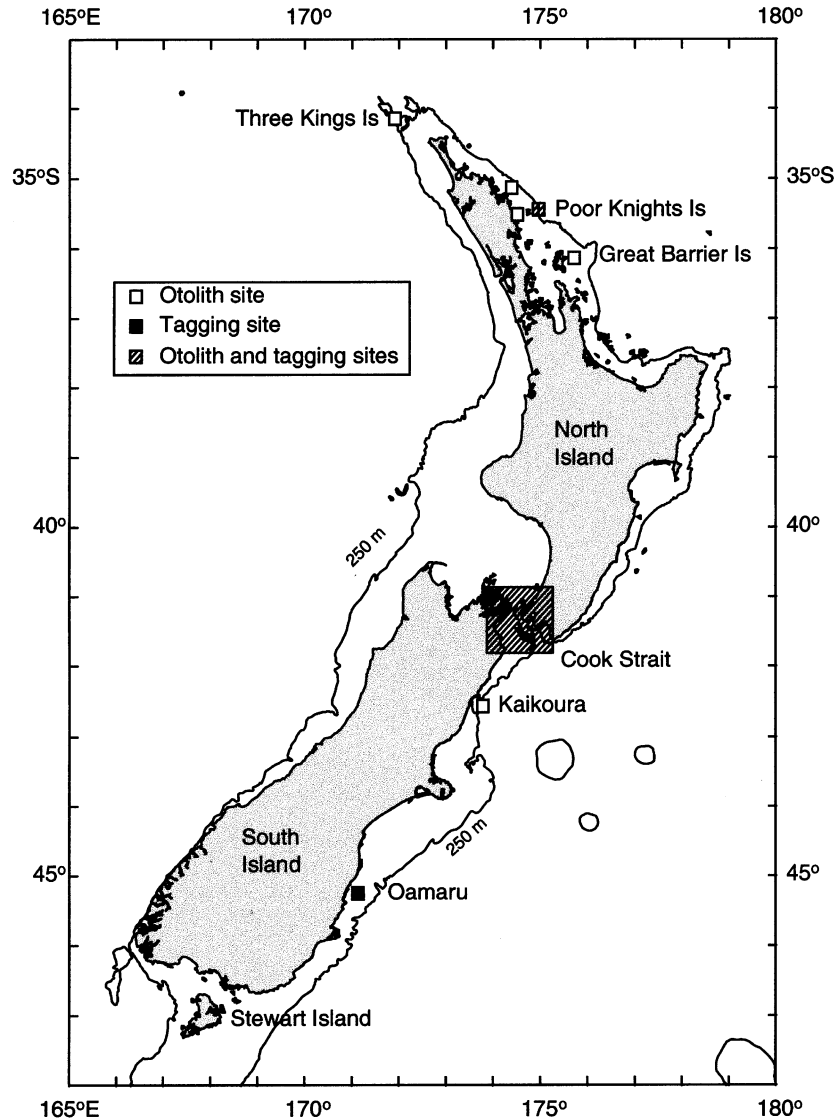
Figure 2
Hapuku otolith collection sites and tag-release sites.

ings by reader 2) by using age-bias plots and plots of the coefficient of variation (CV) against age, as recommended by Campana et al. (1995). These two plots show the means (and their standard errors), and the CVs, respectively, of the band counts made by reader *x* for each "age" as determined by reader *y*. For example, for all the hapuku that were judged by reader *y* to have 10 bands, the mean, standard error, and CV were calculated from the band counts made by reader *x* for the same fish, and plotted at age 10 on the x-axis. Age estimates made by reader 2 on the second reading ($R_{2,2}$) were selected as a baseline against which to compare other estimates because it was anticipated that the experience gained during the first reading would produce more reliable age estimates during the second reading.

Validation of the annual formation of otolith bands was attempted by marginal increment analysis and oxytetracycline injection. The marginal composition of 76 otoliths from northern and central hapuku, aged 3–8 years, was graded as opaque, narrow hyaline, or wide hyaline. The classification of hyaline zones as narrow or wide was based on a comparison of the marginal zone width with the width of the preceding hyaline zone. A qualitative classification was used because the presence of split opaque bands made it difficult to measure the marginal increment. The data were grouped into two-month intervals because not all months were sampled and because sample sizes were small.

Thirty-nine hapuku were tagged (see "Tag-recapture" section), injected intramuscularly with oxytet-

racycline hydrochloride (OTC), and released at the Poor Knights Islands (Fig. 2). Two OTC brands and dosage rates were used: 27 fish were injected with terramycin at a dosage rate of 80 mg/kg; and 12 were injected with engemycin at 35 mg/kg. Five OTC-injected fish were recaptured and their otoliths removed. One otolith from each pair was sectioned as described above and viewed under transmitted white light and reflected UV light. The composition of the otolith (number of opaque or hyaline bands) outside the OTC mark was determined, and the amount of new otolith material laid down along the dorso-nuclear axis was measured.

Growth curves were fitted to the length-at-age data bu using the von Bertalanffy growth model:

$$L_t = L_\infty \left(1 - e^{-K[t-t_0]}\right),$$

where L_t = the expected length at age t years;
L_∞ = the asymptotic maximum length;
K = the von Bertalanffy growth constant; and
t_0 = the theoretical age at zero length.

Length-frequency distributions

Hapuku length-frequency distributions were obtained from a series of four bottom trawl surveys conducted from the research vessel *Tangaroa* (towing a 60-mm mesh codend) off Southland (the southern coast of South Island and the Stewart Island shelf between latitudes 46–49ºS). The surveys were carried out annually in February and March, 1993–96, and covered a depth range of 30–600 m. Further details of the surveys are provided in the studies of Hurst and Bagley (1994) and Bagley and Hurst (1995, 1996a, 1996b).

Von Bertalanffy growth curves were fitted to the four length-frequency distributions by using the MULTIFAN model (Fournier et al., 1990). This model analyses multiple length-frequency distributions simultaneously and uses a maximum likelihood method to estimate the number of age classes represented by the data, the proportions of fish in each age class, and the von Bertalanffy growth parameters L_∞ and K. The main assumptions of the MULTIFAN model are the following: 1) the lengths of the fish in each age class are normally distributed around their mean length; 2) the mean lengths-at-age lie on or near a von Bertalanffy growth curve; and 3) the standard deviations of the actual lengths about the mean length-at-age are a simple function of the mean length-at-age (Fournier et al., 1990).

The growth parameters were estimated by conducting a systematic search across a parameter space of plausible K values (0.005–0.30) and age classes (6–

15). It is possible to constrain the MULTIFAN search further by specifying initial estimates for the mean length-at-age, and the range of the mean length, for one or more age classes (Fournier et al., 1990). However, this is not necessary when the length distributions contain adequate modal structure; therefore such constraints were not used in this study.

For each of the identified age classes, MULTIFAN also estimates the ratio of the last to first length standard deviations (S_R) and the geometric mean of the first and last standard deviations (S_A). The MULTIFAN model was fitted for two different growth hypotheses: 1) constant length standard deviation for all age classes (fitted by setting $S_R=1$ and estimating S_A); and 2) variable length standard deviation across age classes (fitted by estimating both S_A and S_R). Because all four trawl surveys were conducted at the same time of year, the data contain no information on seasonal variability of growth, and no seasonal parameters were fitted.

Each combination of K and the number of age classes constituted a model fit. The constant standard deviation hypothesis was fitted to the data first, followed by the addition of the parameter for variable standard deviation. For each combination of K, number of age classes, and growth hypothesis, the maximum log-likelihood (λ) was calculated. Likelihood ratio tests were used to test for significant improvement in model fit. Twice the increase in λ is distributed as a χ^2 distribution with degrees of freedom equal to the number of additional parameters. Following Fournier et al. (1990), a significance level of 0.10 was used for testing whether there was any gain in introducing an additional age class in the length-frequency analyses. The test for improvement resulting from the addition of the parameter for variable standard deviation was carried out with a significance level of 0.05.

The von Bertalanffy growth parameter t_0 was estimated from the equation

$$t_0 = t_1 - a_1,$$

where a_1 = the age estimated by MULTIFAN (in years since zero length) of the youngest age class at the time it first appeared in the length-frequency samples; and
t_1 = the time elapsed in years between the theoretical birthday and the first appearance of the youngest year class in the samples.

The theoretical birthday was defined as 1 September based on observations of prespawning fish in June–August and postspawning fish in October–December (Johnston, 1983; Roberts, 1986).

Tag recapture

1623 hapuku were tagged at three main sites: Poor Knights Islands (July 1987–August 1989, n=106), Cook Strait (August 1979–June 1984, n=599) and Oamaru (March 1988–April 1990, n=918) (Fig. 2). Fish were caught by longline or drop (dahn) line in depths less than 160 m. Only lively fish without everted stomachs or bulging eyes were tagged. Distended swimbladders were vented by means of a hollow needle inserted through the wall of the body cavity. Hapuku were measured (TL), tagged with a loop, dart, or spaghetti tag, and released. Oamaru hapuku were double tagged with both a loop and a dart tag. Loop and spaghetti tags were inserted through the muscle just anterior to the dorsal fin and clipped or tied together, and dart tags were inserted into the muscle directly below the first dorsal-fin ray. Each tag was printed with a serial number, a return address and notice of a reward. Recapture data and most measurements of recaptured hapuku were provided to the Ministry of Agriculture and Fisheries by the fishermen who caught them, but occasionally whole fish were returned for measurement.

Von Bertalanffy growth estimates were obtained from the tagging data by using the maximum likelihood method and the computer program GROTAG (Francis, 1988). GROTAG also estimates g_α and g_β, the mean annual growth of fish of lengths α and β respectively. The reference lengths α and β were chosen to lie within the range of lengths of tagged hapuku. Francis (1988) showed that these parameters describe the growth information in tagging data better than the more conventional von Bertalanffy growth parameters L_∞ and K do. The expected length increment, ΔL, for a fish of initial length L_1 at liberty for time ΔT is given by

$$\Delta L = \left[\frac{\beta g_\alpha - \alpha g_\beta}{g_\alpha - g_\beta} - L_1 \right] \left[1 - \left(1 + \frac{g_\alpha - g_\beta}{\alpha - \beta} \right)^{\Delta T} \right].$$

Also estimated were m and s (the mean and standard deviation of the measurement error), v (the coefficient of variation of growth variability), and p (the proportion of outliers) (Francis, 1988). Preliminary GROTAG fits suggested that the von Bertalanffy growth model was not appropriate for tagged hapuku; therefore a linear GROTAG function with only one growth parameter (g_α) was fitted to the data. A seasonally varying growth function was also tested. Differences in growth rate between the two sexes in Cook Strait (the sex of recaptured fish was not determined for the other two areas) and among the three tagging areas were also investigated.

The approach used was to fit a simple GROTAG model with few parameters to the data. The complexity of the model was then gradually increased by introducing additional parameters (for example, parameters to allow for seasonal variation in growth). At each stage, new parameter estimates were made and likelihood ratio tests for significant improvement in model fit were carried out as described above for MULTIFAN models. A significance level of 0.05 was used for testing whether there was any gain from introducing additional parameters.

Results

Otolith ageing

Otolith structure   The otoliths of the hapuku we examined had an opaque core (dark in transmitted light) and an opaque line that radiated along the dorsoventral axis (Fig. 3). The line was usually split by 1–3 hyaline bands (light in transmitted light). The sulcus was also mostly opaque. The remainder of the otolith consisted of alternating opaque and hyaline bands. In young fish, the hyaline bands were wider than the opaque bands, but difference in width declined in older fish. Opaque bands usually consisted of multiple, fine, wavy opaque and hyaline zones (Figs. 3 and 4A). The demarcation between each compound opaque band and the adjacent hyaline bands was often indistinct, making the bands difficult to count. The banding pattern was usually clearest in the dorsal half of transverse otolith sections. We used counts of the compound opaque bands as age estimates.

Five otolith sections were considered unreadable, and a further four otoliths were lost or damaged during preparation. Of the remaining 241 otoliths, 78% were scored as poor or moderate (readability 2 or 3); only 22% were good or exceptionally clear (readability 4 or 5).

Validation   Otolith marginal state was difficult to assess because of the presence of split opaque rings. There was no apparent seasonal cycle in marginal composition, and sample sizes in most two-month periods were inadequate to provide good estimates of the percentage of the population with opaque margins (Jan–Feb percent opaque=50.0, n=14; Mar–Apr 37.5, 8; May–Jun 36.4, 33; Jul–Aug 42.9, 7; Sep–Oct 50.0, 10; Nov–Dec 25.0, 4). The same conclusion was reached for the central data alone (n=50).

Five OTC-injected hapuku were recaptured after 0.20–2.66 years at liberty (Table 1). All had distinct, bright OTC bands when viewed under UV light (Fig. 4B). There was no apparent relation between OTC

Figure 3

Photomicrographs (transmitted white light) of the dorsal halves of transverse sections of hapuku otoliths from (**A**) an 85-cm female, northern, readability 3, estimated age (mean of R_1, $R_{2,1}$ and $R_{2,2}$) 11.7 years; C = core, S = sulcus, arrows indicate a compound opaque band, circles indicate opaque bands; (**B**) an 87-cm female, Cook Strait, readability 4, age 14.7 years; (**C**) a 106-cm male, Cook Strait, readability 4, age 19.0 years; (**D**) an 121-cm male, Kaikoura, readability 5, age 45.7 years. Scale bars = 1 mm.
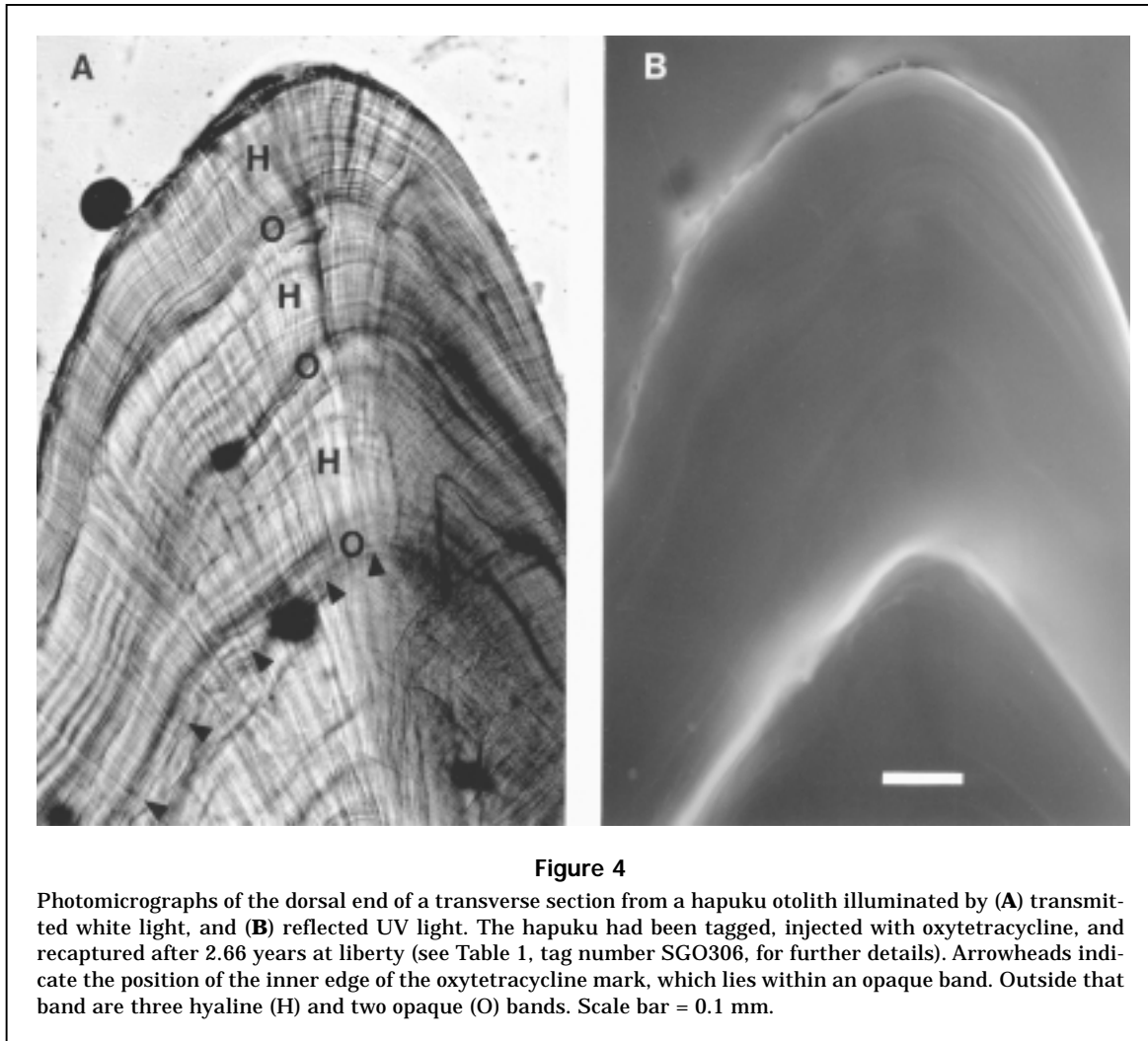
Table 1

Details of recaptured hapuku that were tagged and injected with oxytetracycline (OTC). M = male, T = terramycin, E = engemycin, — = not determined. Increment width is the amount of postinjection otolith material deposited along the dorsonuclear otolith axis. Increment pattern is the type of material (O=opaque, H=hyaline) laid down between the OTC mark (m) and the otolith margin. An "I" subscript indicates an incomplete band, and a question mark indicates uncertainty in determining the composition of the otolith margin.

Tag number	Length at tagging (cm)	Length at recapture (cm)	Sex	OTC brand	Date tagged	Date recaptured	Years at liberty	Increment width (mm)	Increment pattern
SGO306	89	104	M	T	20 Oct 87	19 June 90	2.66	0.61	mO_IHOHOH
SGO322	85	87	M	T	8 Jul 88	21 Dec 88	0.45	0.08	mO_IH_I
SGO328	55	55	—	E	27 Oct 88	10 Mar 89	0.37	0.16	mO_IH_I
SGO329	73	77	—	E	2 Dec 88	12 May 89	0.44	0.05	$mHO_I?$
SGO340	68	65	—	E	2 Jul 89	14 Sep 89	0.20	0.01	$mO_IH_I?$

brand (terramycin or engemycin) or dosage and the width or intensity of the OTC mark. Four hapuku injected with OTC in July–October showed an OTC mark that fell within an opaque band, indicating that opaque bands are formed in the austral winter–spring. The remaining fish was injected in Decem-

ber and had an OTC mark at the distal edge of an opaque band, indicating that hyaline band formation begins in spring–summer.

The OTC results from all five hapuku are consistent with the deposition of one hyaline-opaque band pair on the otolith each year. The hapuku that had

Figure 4

Photomicrographs of the dorsal end of a transverse section from a hapuku otolith illuminated by (**A**) transmitted white light, and (**B**) reflected UV light. The hapuku had been tagged, injected with oxytetracycline, and recaptured after 2.66 years at liberty (see Table 1, tag number SGO306, for further details). Arrowheads indicate the position of the inner edge of the oxytetracycline mark, which lies within an opaque band. Outside that band are three hyaline (H) and two opaque (O) bands. Scale bar = 0.1 mm.

been at liberty for the shortest time (SGO340, 0.20 years) had the OTC mark near the margin (postinjection increment width along the dorsal axis=0.01 mm) (Table 1). Three hapuku with intermediate periods at liberty (0.37–0.45 years) had moderate postinjection otolith increments of 0.05–0.16 mm. SGO328, which was the smallest of the three hapuku at tagging, had the largest increment. SGO322 and SGO328 each had an incomplete opaque band and an incomplete hyaline band outside the OTC mark. SGO329 had a complete hyaline band and possibly an opaque band beginning to form at the margin near the dorsal tip of the otolith. A hapuku that had been at liberty for 2.66 years (SGO306) had a wide postinjection increment (0.61 mm) consisting of a partial opaque band followed by three hyaline and two opaque bands (Fig. 4; Table 1).

Age estimates and growth rates $R_{2,1}$ and $R_{2,2}$ were strongly positively correlated (coefficient of multiple

determination $[R^2]$=94.6), although they differed markedly for some individuals (Fig. 5A). Some of the larger differences were for otoliths that were judged difficult to count (readability 2), but large differences were also found for clearer otoliths (readability 3–5). $R_{2,1}$ tended to be higher than $R_{2,2}$ for fish aged 3–18 years in $R_{2,2}$ (mean difference=1.0 years) (Fig. 6A). Sample sizes were small for hapuku older than 18, but it appears that the same bias occurred for them.

Age estimates made by both readers (R_1 and $R_{2,2}$) were also highly correlated (R^2=92.4) but there were some substantial differences (Fig. 5B). There was no apparent bias between the two sets of estimates for hapuku aged 3–12 in $R_{2,2}$, but there was a slight tendency for $R_{2,2}$ to exceed R_1 over the range 13–18 years (Fig. 6B).

Ageing precision was low and variable, both within and between readers, for hapuku aged 3–18 years (Fig. 7). The CV of the age estimates was slightly lower between the two readings of reader 2 ($R_{2,1}$ ver-
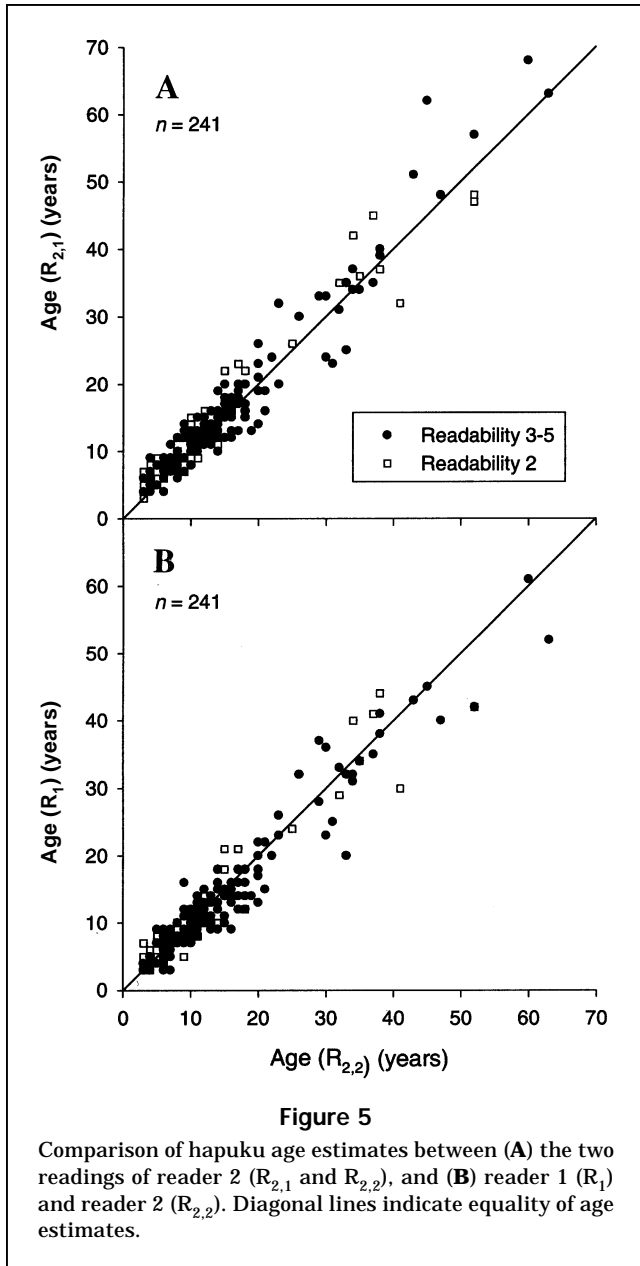
Figure 5

Comparison of hapuku age estimates between (**A**) the two readings of reader 2 ($R_{2,1}$ and $R_{2,2}$), and (**B**) reader 1 (R_1) and reader 2 ($R_{2,2}$). Diagonal lines indicate equality of age estimates.
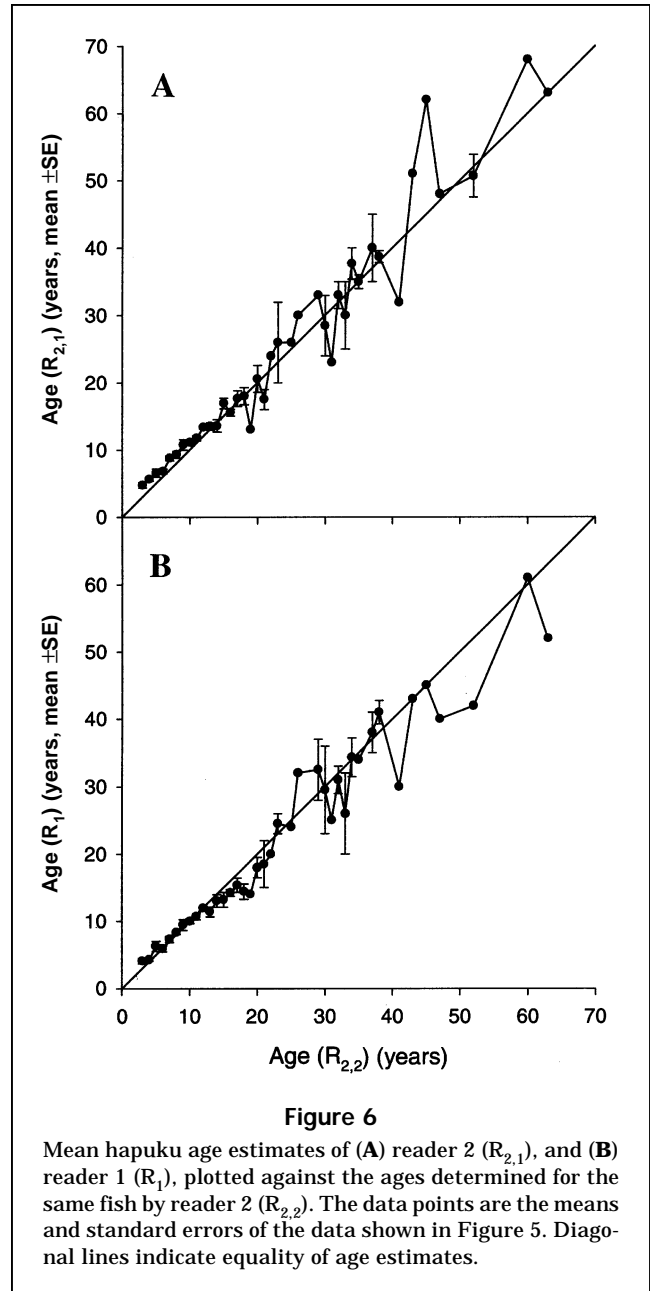
Figure 6

Mean hapuku age estimates of (**A**) reader 2 ($R_{2,1}$), and (**B**) reader 1 (R_1), plotted against the ages determined for the same fish by reader 2 ($R_{2,2}$). The data points are the means and standard errors of the data shown in Figure 5. Diagonal lines indicate equality of age estimates.

sus $R_{2,2}$) (mean=18.0%, range=10.1–26.1%) than between readers (R_1 versus $R_{2,2}$) (mean=21.3%, range=12.6–31.4%). The CV declined slightly with increasing age for both the within- and between-reader comparisons.

The main differences between counts arose from 1) different band counts near the otolith core (potential age difference=1–3 years), 2) different band counts in an unclear central zone around bands 4–8 (several years), and 3) classification of the composition of the otolith margin as opaque or hyaline (one year).

The greatest estimated ages (mean of R_1, $R_{2,1}$ and $R_{2,2}$) were 50.3, 50.7, 59.3, and 63.0 years, but few

fish were found to be more than 20 years old (Fig. 5). The youngest hapuku were 3 years old. The von Bertalanffy growth curve fitted to R_1 data differed little from that fitted to $R_{2,2}$ data (Fig. 8A; Table 2). Females grew faster than males, but the difference was slight, and the overlap of data points was substantial (Fig. 8B; Table 2). The largest male was 134 cm, the largest female 147 cm (with three females longer than 140 cm).

Growth curves fitted separately to the northern and central data were very similar (Table 2). Inspection of the residuals from the central curve again

Table 2

Von Bertalanffy growth curve parameters based on hapuku length-at-age and length-frequency data. Standard error estimates for the MULTIFAN parameters are considered unreliable and are not shown. SE = standard error, R_1 = reader 1, $R_{2,2}$ = reading 2 of reader 2, M = male, F = female.

Sample	Otolith reading	Sex	Sample size	$L_\infty \pm$ SE (cm)	$K \pm$ SE	$t_0 \pm$ SE (years)
Length-at-age data (otoliths)						
All	$R_{2,2}$	M + F	241	131.7 ± 3.2	0.0666 ± 0.0059	−4.63 ± 0.72
All	R_1	M + F	241	131.0 ± 2.3	0.0785 ± 0.0052	−2.96 ± 0.48
All	$R_{2,2}$	M	105	129.2 ± 5.4	0.0618 ± 0.0095	−5.75 ± 1.32
All	$R_{2,2}$	F	110	133.2 ± 4.2	0.0698 ± 0.0084	−4.30 ± 1.01
Northern	$R_{2,2}$	M + F	44	124.0 ± 9.8	0.0699 ± 0.0193	−4.51 ± 1.96
Central	$R_{2,2}$	M + F	172	122.6 ± 5.3	0.0794 ± 0.0117	−4.06 ± 0.89
Length-frequency data (MULTIFAN)						
Southern	—	M + F	1,471	549.2	0.0090	−8.02

suggested that females grew slightly faster than males, although there was strong overlap in the ranges (males: mean residual=−1.8 cm, SD=8.6, n=90; females: mean=1.6, SD=7.8, n=82). All growth curves had strongly negative values for t_0 (Table 2).

Length-frequency distributions

Hapuku from the four southern trawl surveys generally were less than 85 cm long (Fig. 9), and because 50% maturity occurs at about 85 cm and 88 cm for males and females, respectively (Johnston, 1983), these would have been immature. The smallest hapuku was 41 cm long, but few fish were less than 50 cm. This reflects the pattern seen in the entire New Zealand research trawl database which contains length measurements for 5841 hapuku: the smallest hapuku was 40 cm, and only 55 were less than 50 cm long.

The best-fit MULTIFAN model consisted of constant length standard deviation with 11 age classes (see Table 2 for growth parameters). The estimated time elapsed between the theoretical birthday and the first appearance of juvenile hapuku in the length-frequency samples (t_1) (based on an estimated minimum age at first capture from otolith ageing of 3 years, plus 0.5 years elapsed between the theoretical birthday [1 September] and the sampling date midpoint [1 March]) was 3.5 years. The age in years since zero length of the youngest age class at the time it first appeared in the length-frequency samples (a_1) was estimated by MULTIFAN to be 11.52 years, producing a t_0 estimate of −8.02 years. The standard error estimates provided by MULTIFAN for the growth parameters are not presented in Table 2 because they tended to be unrealistically small (Francis and Francis, 1992).
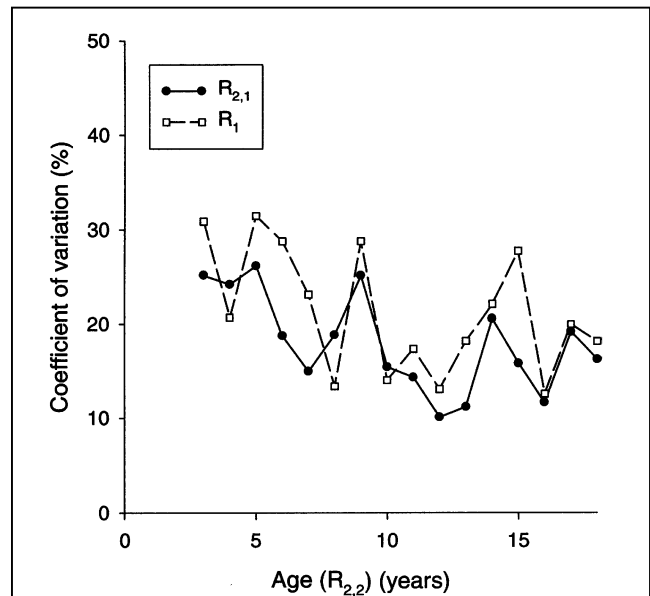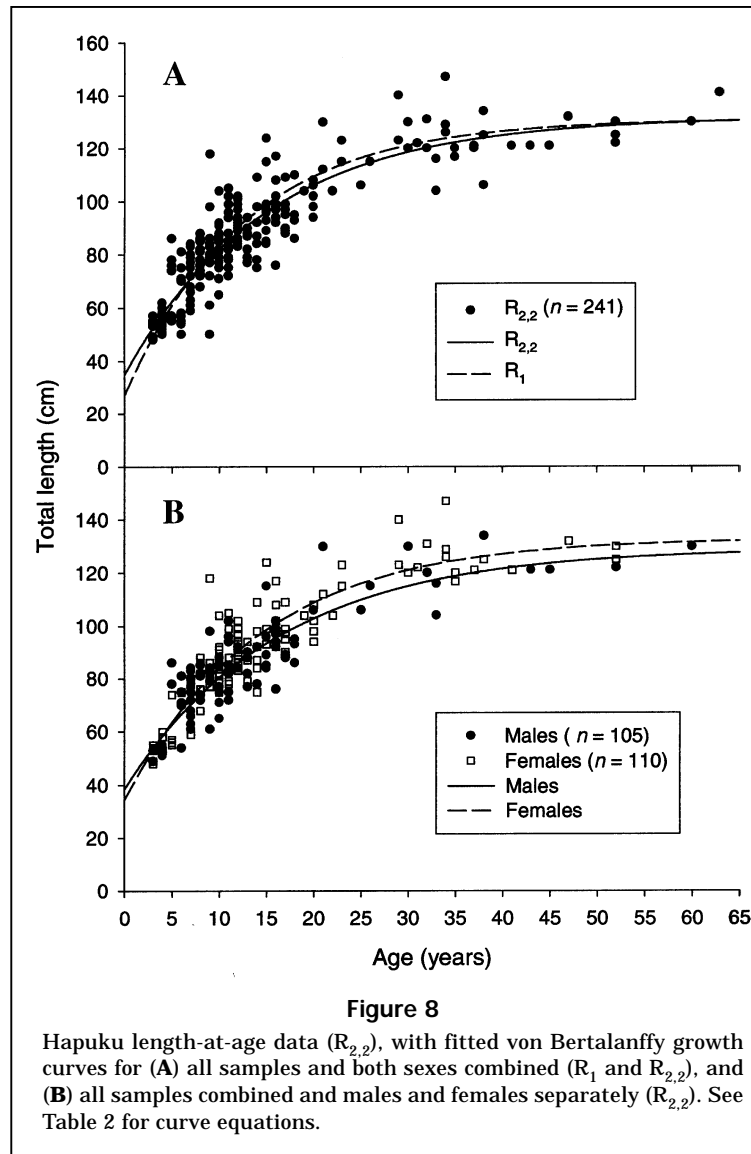

Figure 7

Precision of hapuku age estimates of reader 2 ($R_{2,1}$) and reader 1 (R_1) plotted against the ages determined for the same fish by reader 2 ($R_{2,2}$). The data points are the coefficients of variation of the data shown in Figure 4.

The growth curve resulting from the best MULTIFAN fit to the length-frequency data was nearly linear over the range of the data (Fig. 10). The curve was truncated at 14.5 years, which is the maximum age covered by the data (calculated as the sum of the number of age classes detected by MULTIFAN [11] and the estimated age at first recruitment to the samples [3.5 years]). The MULTIFAN curve should not be extrapolated beyond this point because the

Figure 8

Hapuku length-at-age data ($R_{2,2}$), with fitted von Bertalanffy growth curves for (**A**) all samples and both sexes combined (R_1 and $R_{2,2}$), and (**B**) all samples combined and males and females separately ($R_{2,2}$). See Table 2 for curve equations.
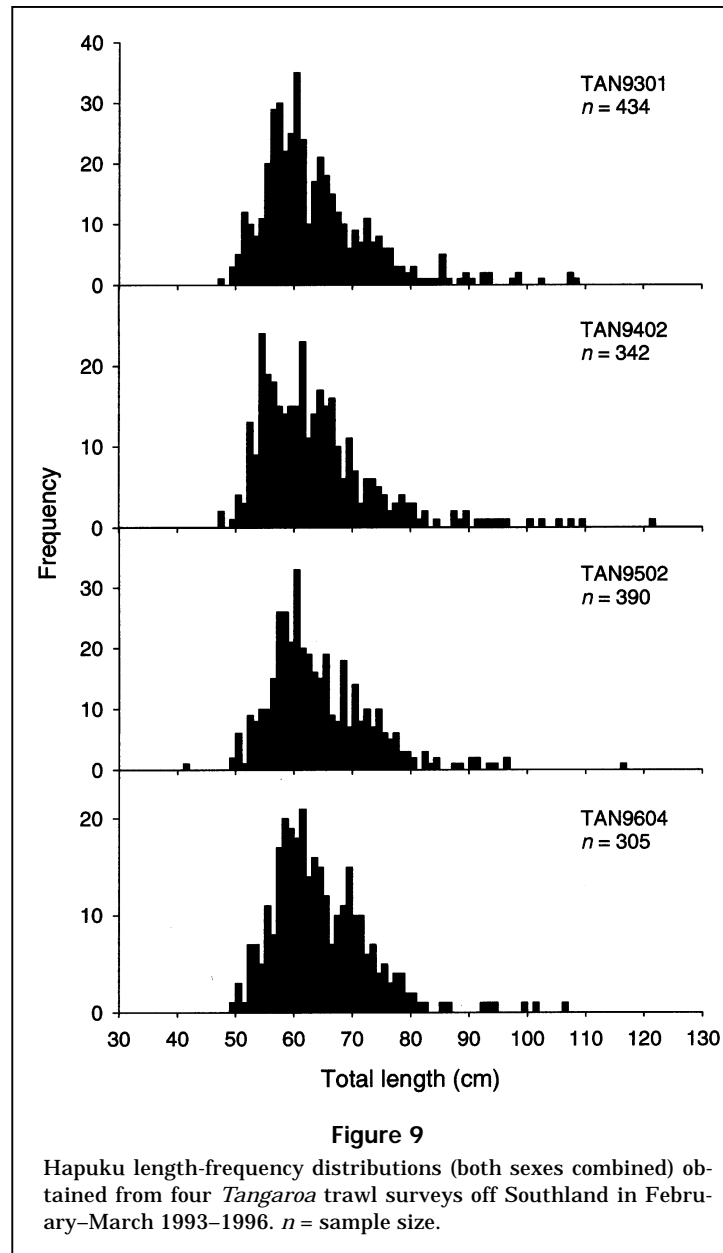
length-frequency data represent only small, immature hapuku. Over the age range 0–12 years, the MULTIFAN growth curve was very similar to growth curves based on otolith ages (Fig. 10).

Tag recapture

One tagged hapuku was recaptured, released with a new tag, and recaptured a second time (Johnston, 1992). It grew from 73 cm to 83 cm during its first 800 days at liberty and from 83 cm to 96 cm during its second 829 days at liberty. This fish was entered into the growth data set three times: once for each of the two periods at liberty and once for the combined period at liberty. All other hapuku used in the growth analysis were recaptured only once.

One hundred and forty four recaptured hapuku had sufficient information (lengths at tagging and recapture, days at liberty) to be used in the growth analysis. Most of these hapuku were between 50 and 90 cm long at tagging (Fig. 11) and would have been immature. The GROTAG reference lengths α and β were set at 55 cm and 85 cm respectively. Periods at liberty ranged from 9 to 3708 days (0–10.2 years), but most fish were at liberty for less than four years (Fig. 12).

Initial GROTAG model fits identified six fish as outliers (fish having absolute standardized residuals greater than 3.0). Five of these fish had negative growth increments of 3–27 cm, and one had a positive increment of 24 cm after 347 days at liberty. These outliers probably resulted from measurement

Figure 9

Hapuku length-frequency distributions (both sexes combined) obtained from four *Tangaroa* trawl surveys off Southland in February–March 1993–1996. *n* = sample size.
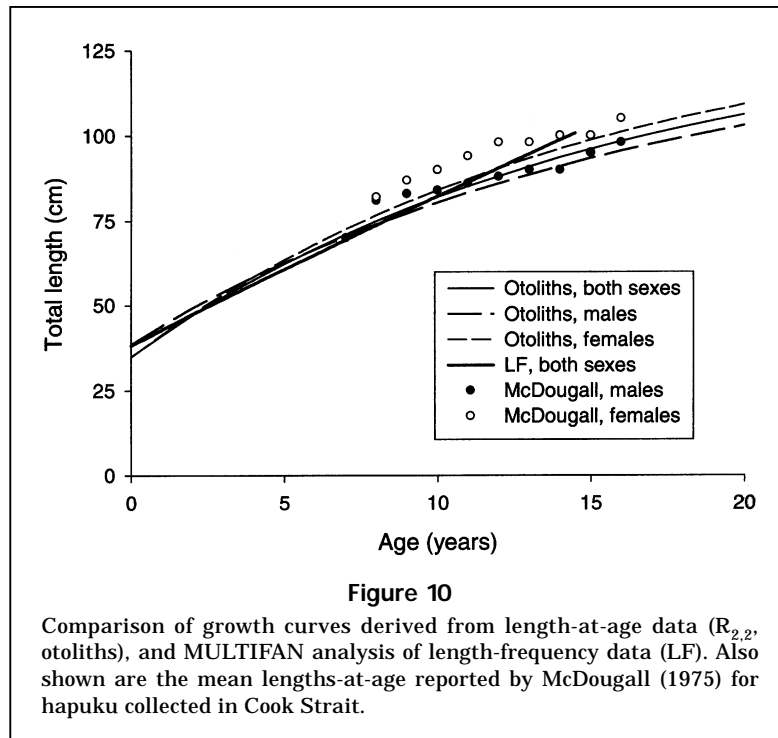
errors and were deleted from the data set, leaving 138 fish.

A simple linear model, with a single growth-rate parameter, produced an estimated growth rate of 4.26 cm/yr (Table 3, model 1). A model with two growth-rate parameters produced no improvement in fit (Table 3, model 2). The addition of parameters for outlier contamination, measurement bias, and seasonal growth did not significantly improve the log-likelihood (Table 3, models 3–5), nor did subdivision of the data into three geographical areas (Table 3, model 6). For the Cook Strait data subset, inclusion of separate growth parameters for male and female

hapuku did not significantly improve the model fit (Table 4). However, sample sizes were small, statistical power was low, and only large differences could have been detected.

Therefore the best GROTAG model (Table 3; model 1) consisted of simple linear growth over the length range 55–85 cm. It had no apparent pattern or trend in the residuals. GROTAG was then run in simulation mode (Francis, 1988) by using parameter estimates from model 1 to determine the accuracy and precision of the growth-rate estimate. The mean annual growth rate was estimated to be 4.25 cm/yr with a standard error of 0.017 cm/yr.

Figure 10

Comparison of growth curves derived from length-at-age data ($R_{2,2}$, otoliths), and MULTIFAN analysis of length-frequency data (LF). Also shown are the mean lengths-at-age reported by McDougall (1975) for hapuku collected in Cook Strait.

Table 3

Parameter estimates from GROTAG growth models for hapuku from all tagging sites (n=138). Seasonal phase is given in years since 1 January. SD = standard deviation; — = parameter not estimated. Models 1–5 are for Poor Knights Islands, Cook Strait, and Oamaru, data combined; model 6 estimated g_{55} separately for the three areas.
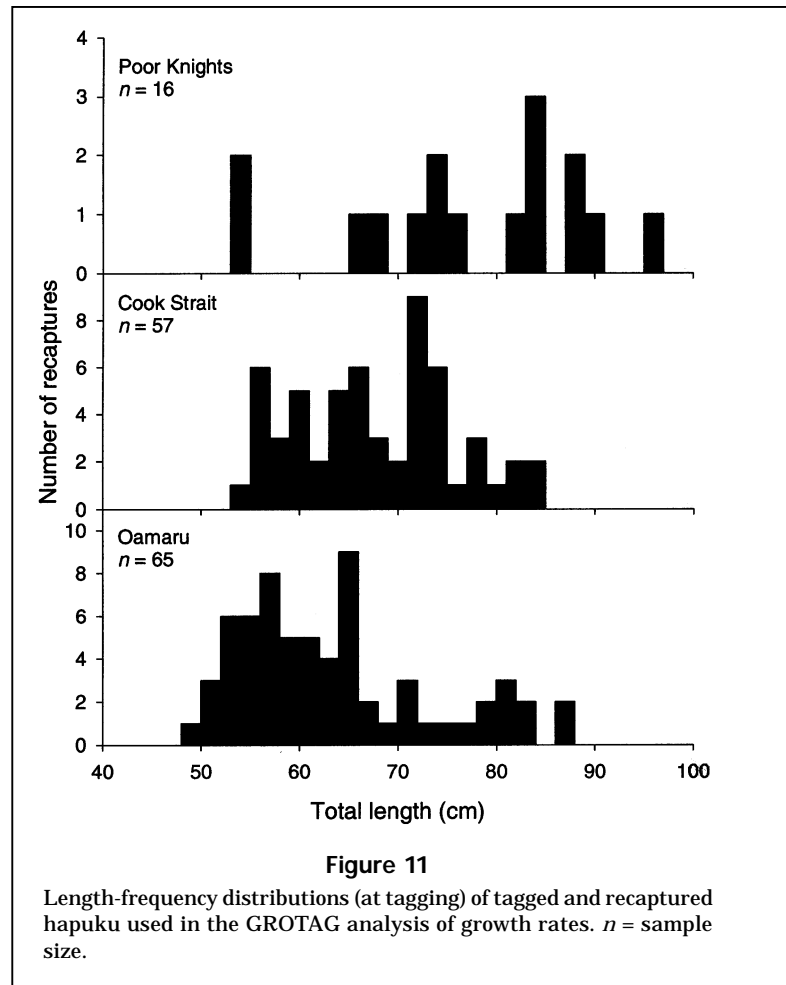
Parameter		All areas combined					Areas separate
		1	2	3	4	5	6
Log likelihood	2λ	697.80	697.42	697.80	697.80	694.30	695.85
Mean growth rates	g_{55} (cm/yr)	4.26	4.01	4.24	4.25	4.25	4.1–5.0
	g_{85} (cm/yr)	—	4.38	—	—	—	—
Growth variability	v	0.38	0.39	0.39	0.39	0.39	0.39
SD measurement error	s (cm)	1.55	1.54	1.55	1.55	1.51	1.51
Measurement bias	m (cm)	—	—	—	0.05	—	—
Outlier contamination	p	—	—	0.00	—	—	—
Amplitude	u	—	—	—	—	0.53	—
Phase	w (yr)	—	—	—	—	0.15	—

Discussion

Hapuku otoliths frequently had split opaque bands and were difficult to age. This led to reduced counting precision and, for some age groups, to a small between- and within-reader ageing bias. Our use of marginal increment analysis to validate hapuku otolith ageing was inconclusive. We attribute this to the compound nature of the opaque bands and to the resulting difficulty in determining whether the material being deposited at the margin was opaque or hyaline.

The results of the OTC injection experiment were consistent with the deposition of one opaque and one hyaline band per year. This does not constitute full validation of the otolith ageing technique because the

Figure 11

Length-frequency distributions (at tagging) of tagged and recaptured hapuku used in the GROTAG analysis of growth rates. n = sample size.

experiment included only five hapuku, only one of which was at liberty for more than one year. Furthermore, all five fish would have been immature or just maturing at the time of injection. Further validation is required, especially for older, mature hapuku.

An independently derived von Bertalanffy growth curve (based on MULTIFAN analysis of length-frequency data) agreed well with the otolith-based length-at-age curves over the age range 0–12 years but indicated faster growth rates for hapuku aged 12–14.5 years (Fig. 10; Table 5). Our previous experience has shown that MULTIFAN growth curves are generally reliable for younger age classes, which often exhibit discernible length modes, but are not reliable for older age classes, which usually lack any modal length structure. This is because MULTIFAN underestimates the number of older age classes present in the data and consequently overestimates the length-at-age of the older age classes (Francis and Francis, 1992; Francis, 1997). Therefore, the discrepancy between the MULTIFAN and length-at-age curves for the older age classes in Fig. 10 probably

arises from bias in the former. This interpretation is supported by the near-linearity of the MULTIFAN growth curve and the implausible MULTIFAN growth parameters, especially L_∞ (Table 2).

Table 4

Parameter estimates from GROTAG growth models for hapuku from Cook Strait (n=43). SD = standard deviation;— = parameter not estimated.

Parameter		Both sexes	Sexes separate	
			M	F
Log likelihood	2λ	240.44	240.26	
Mean growth rates	g_{55} (cm/yr)	4.53	4.44	4.64
	g_{85} (cm/yr)	—	—	
Growth variability	v	0.27	0.27	
SD measurement error	s (cm)	1.94	1.99	

Figure 12

Relationship between growth increment and period at liberty for tagged hapuku. n = sample size.
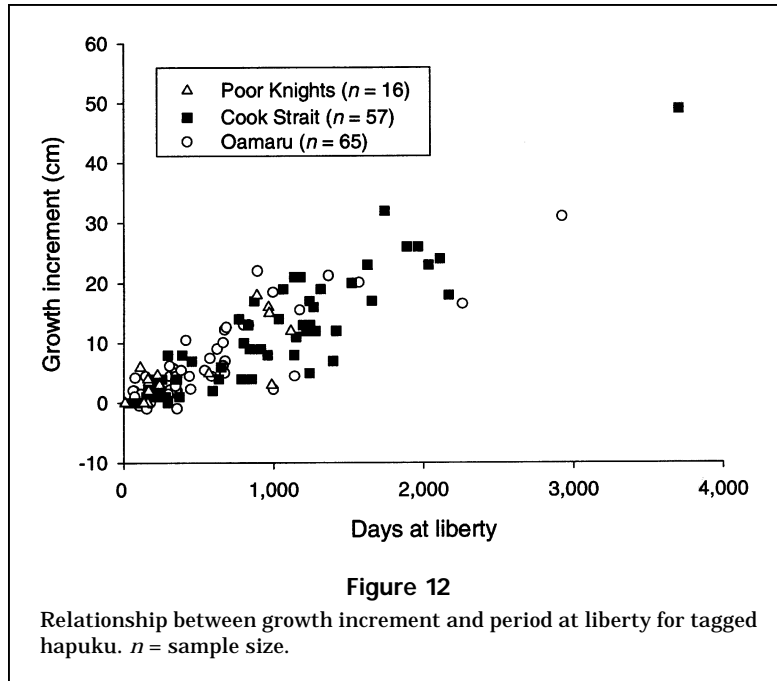
Table 5

Comparison of hapuku annual growth increments at two reference lengths (55 cm and 85 cm) based on length-at-age ($R_{2,2}$), length-frequency, and tag-recapture data.

Total length (cm)	Annual growth increment (cm)		
	Length-at-age	Length-frequency	Tag-recapture
55	4.94	4.40	4.25
85	3.00	4.15	4.25

The best GROTAG model fit estimated the mean annual growth rate to be 4.25 cm/yr over the length range 55–85 cm. That estimate falls between the length-at-age estimates of annual growth for 55-cm and 85-cm hapuku (Table 5). A nonlinear growth model was not significantly better than the linear model, probably because of the narrow length range of the tag-recapture data, and the small sample size (n=138).

We conclude that the growth curves and growth rate estimates derived from length-frequency and tag-recapture data are consistent with those from otolith-based, length-at-age data for the length and age ranges over which the data overlap. In conjunction with the results of the OTC injection experiment, this agreement among growth-rate estimates provides strong support for our hypothesis that otolith band pairs are deposited annually in hapuku.

Our length-at-age growth curve for male hapuku is similar to that of McDougall (1975), who made band counts in broken and burnt otoliths from hapuku collected in Cook Strait (Fig. 10). However, McDougall reported a slightly faster growth rate for females (Fig. 10). It is not possible to determine whether the difference in female growth rates is real, or a result of McDougall's small sample size (n=72). McDougall's largest hapuku was 120 cm and his oldest fish was 26 years.

A study of hapuku growth at Juan Fernández Island, based on scale annuli, reported much faster growth rates and a maximum age of only 12 years (Pavez and Oyarzún, 1985). Scale rings are typically crowded to the point of being unresolvable in hapuku older than 8 years (McDougall, 1975); it is likely therefore that the ages of Pavez and Oyarzún's larger fish were underestimated.

Lack of precision and reader bias mean that otolith ageing is unlikely to be useful when accurate hapuku ages are required (e.g. in the estimation of year-class strength from an age-frequency distribution). However, the precision and accuracy problems experienced in this study had little effect on the shape of growth curves fitted to length-at-age data, and we believe that the growth parameters reported here are relatively robust.

The large negative t_0 values for all growth curves indicate a lack of fit of the von Bertalanffy model to the data for small hapuku. This may result from one or more of the following: 1) lack of fish less than three

years old in our data; 2) underestimation of the ages of hapuku because of failure to recognize and count all the annual bands near the core; or 3) different growth rates of pelagic juveniles, and demersal juveniles and adults. Interestingly, Pavez and Oyarzún's (1985) scaled-based growth curves had t_0 values close to zero, and estimated ages at the length of settlement similar to ours (i.e. 38 cm at age 3 and 49 cm at age 4). Scale bands may therefore help to resolve problems experienced in interpreting otolith cores when ageing small hapuku.

Small juvenile hapuku pass through a pelagic stage in surface waters, usually associated with flotsam, and are rarely caught (Cormack, 1986; Michael, 1988; Roberts, 1996). At the end of the pelagic stage, they become demersal in depths of 50–600 m. Bottom trawl length-frequency data (Fig. 9; NIWA[2]) and bottom set-net and line records (Johnston, 1983; Roberts, 1989) indicate that most hapuku switch from a pelagic to demersal life style at around 50 cm, although hapuku as small as 40 cm have been caught by bottom trawl. A 35-cm hapuku reported caught in Wellington Harbour by Hector (1888) may have been a pelagic juvenile, but no details were given of habitat or fishing method. A small number of pelagic juveniles up to 67 cm long have been caught on surface longlines over 2000 m or more of water (Roberts, 1996; Scientific Observer Database[3]). These large pelagic juveniles may have become "stranded" in the pelagic environment after being carried over deep water by oceanic currents. Presumably they remain in surface waters until they encounter shallower depths, at which time they settle to the seabed.

Our best estimate of the age at which hapuku settle to a demersal habitat is 3–4 years, but our interpretation of the banding pattern near the otolith core was uncertain and somewhat subjective. Counts of possible daily increments in otolith sections also suggest settlement at about 3 years (Roberts, 1996), and a similar age range has been suggested by other studies (McDougall, 1975; Johnston, 1983). *Polyprion americanus* apparently settles at lengths greater than 45–55 cm and ages greater than 1–7 years (Sedberry et al., 1996).

The age at recruitment of hapuku to commercial trawl catches is likely to be the same as the age at settlement to the seabed. Although our research vessel samples were caught with a small mesh (60-mm) codend, hapuku longer than 50 cm are also retained by the larger mesh sizes used by commercial vessels (typically 100–125 mm) (Hurst and Bagley, 1997).

Previous studies have suggested that female hapuku grow larger and faster than male hapuku (McDougall, 1975; Roberts, 1986; 1989). Our results support those conclusions but also indicate that the differences in both maximum length and growth rate are small and, for most purposes, trivial. However, our ability to detect growth rate differences between the two sexes, and between sample sites, was limited by the low precision of our age estimates and the small sample sizes available for the GROTAG analysis.

Hapuku mature at about 85 and 88 cm, males and females, respectively (Johnston, 1983). Based on the length-at-age growth curves given in Table 2, age at maturity is estimated to be 10–13 years for both sexes.

The largest hapuku in our study was 147 cm TL, but they are known to reach 178 cm TL and 76 kg in weight (Roberts[4]). The longevity of hapuku cannot be precisely determined because of difficulties we experienced in estimating ages from otoliths, and because our samples mostly came from populations of hapuku that had been exploited for many years. Our study does suggest that hapuku live at least 50 years, possibly in excess of 60 years.

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