Fisheries Research Bulletin No. 17

Age, Growth, and Condition of the Common River Galaxias, *Galaxias vulgaris* Stokell, in the Glentui River, Canterbury, New Zealand

by

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New Zealand Ministry of Agriculture and Fisheries

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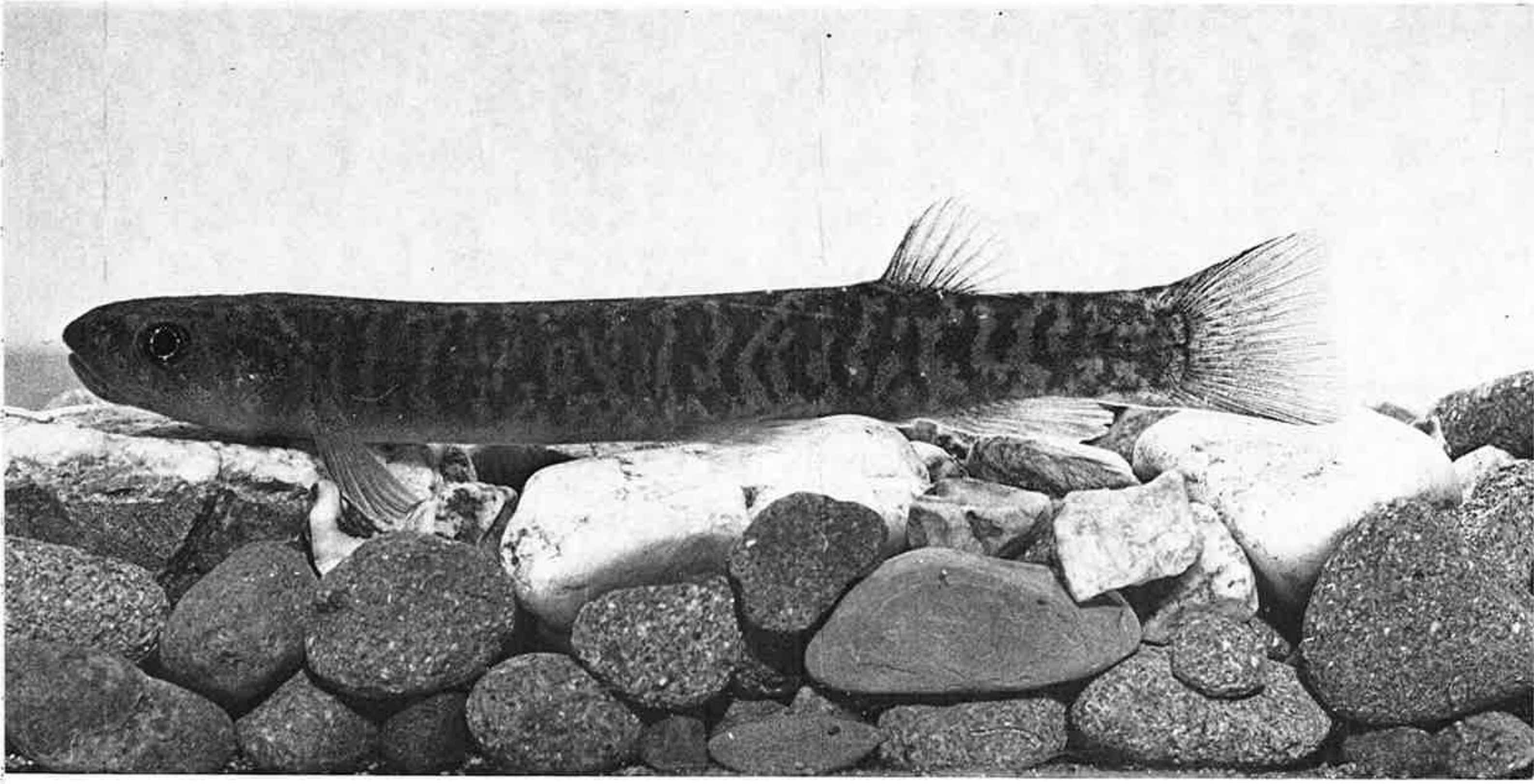

[A. M. R. Burnet photograph

Frontispiece: The common river galaxias, *Galaxias vulgaris,* a fish which occurs in the rivers and streams of the South Island of New Zealand, mainly to the east of the Southern Alps.

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Fisheries Research Division
New Zealand Ministry of Agriculture and Fisheries
1978

Inset 1

Published by the New Zealand Ministry of
Agriculture and Fisheries
Wellington
1978

ISSN 0110-1749

FOREWORD

ONE of the aims of Fisheries Research Division has been to build up a background of information on the indigenous freshwater fishes of New Zealand.

It is therefore a pleasure to acknowledge the work done by Phillip Cadwallader, which represents another worth-while advance in our understanding of one of these little-known species.

G. DUNCAN WAUGH,
Director, Fisheries Research Division.

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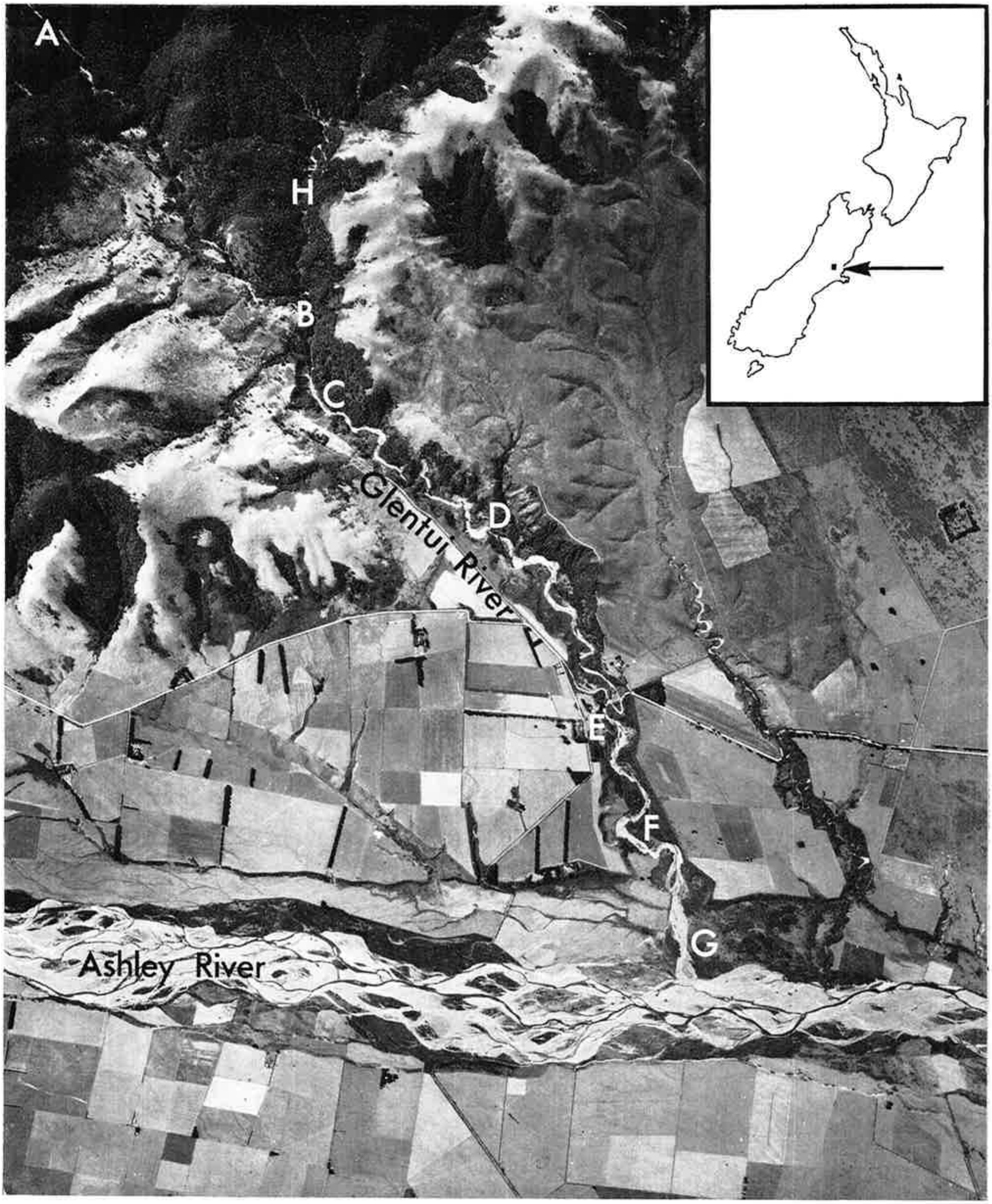
INTRODUCTION

The family Galaxiidae is widespread in the southern temperate region, with species occurring in New Zealand, Australia, South America, and South Africa and also on some islands near these land masses (Stokell 1953, Darlington 1957, McDowall 1970). The taxonomy of the group has been the subject of much confusion. However, the work of Stokell (1938, 1945, 1949, 1959) and McDowall (1967, 1969, 1970, 1972) has greatly clarified the systematics of the New Zealand fauna. Thirteen species are now recognised in New Zealand (McDowall 1970, 1972) and are divided into two genera—*Galaxias* with 10 species and *Neochanna* with 3 species. Apart from *Galaxias maculatus* (Jenyns), which forms the basis of a commercial and sport fishery (Hopkins and McDowall 1970), little attention has been given to the ecology of the New Zealand galaxiids.

This bulletin presents information on some basic population parameters (age, growth, and condition) of the common river galaxias, *Galaxias vulgaris* Stokell, a fish which is restricted to the South Island of New Zealand and which is found in most of the major river basins to the east of the Southern Alps and also in the Upper Buller River System, to the west of the Alps. It occurs beneath and between boulders in fast or broken water of rivers and streams, but it is not usually found in streams entering lakes (Stokell 1949, McDowall 1970).

It was first described by Stokell (1949), who also (Stokell 1959) described *Galaxias anomalus*, which has since been synonymised with *G. vulgaris* by McDowall (1970). Benzie (1968) compared its life history with that of *G. maculatus*, with particular emphasis on embryological development, growth rates, and breeding biology.



[Department of Lands and Survey photograph.

Fig. 1: Aerial view of the study area. A-G: Glentui River. B: Position of the waterfall furthest down stream (height is 2.5 m). C-D: Section of the river, about 1.5 km long, from which samples were taken to obtain data on age, growth, and condition of *G.vulgaris*. E-F: Section of the river from which further samples were taken in March, April, and May 1971. H: Bald Hills Stream, the main tributary of the Glentui River.

THE STUDY AREA

The investigation was carried out in the Glentui River in the provincial district of Canterbury, New Zealand. The Glentui arises at an altitude of about 840 m and flows into the Ashley River at a point (43° 14′ S, 172° 18′ E) 180 m above sea level. It originates in a forest of mountain beech, *Nothofagus solandri* (Hooker), and in its lower reaches flows through cultivated farm land. Its largest tributary is the Bald Hills Stream, which enters the river at an altitude of 300 m. A number of smaller tributaries carry run-off from the surrounding hills (Fig. 1).

LOCAL CLIMATE

The prevailing winds are from the north-west and are fairly warm. Air temperatures in 1970 ranged from a summer maximum of 34.4°c to a winter minimum of −3.9°c, and similarly in 1971 the range was between 33.5° and −4°c. Mean, maximum, and minimum air temperatures from June 1970 to May 1971 are presented (A, Fig. 2).

Mean annual rainfall (1947–70) for the area is 1080 mm and the period of maximum rainfall is usually in spring and early summer, from October to January (data from New Zealand Meteorological Service). Rainfall from June 1970 to May 1971 totalled 880 mm (C, Fig. 2).

THE GLENTUI RIVER

The distance between the origin of the Glentui River and its point of entry into the Ashley River is about 9.5 km. Near its origin there is a series of waterfalls ranging in height from 2.5 to 24 m. Sampling was confined to the stretch of the river below the waterfalls, a section which consisted of riffles interspersed with quiet stretches.

There was great variation in both depth and width of the river within the sampling area. Approximations based on measurements taken throughout the sampling period showed that water depth ranged from 20–30 mm in riffles to 0.7 m in pools formed behind obstacles such as fallen trees, and width varied from 1 to 9 m.

The geological deposits over which the river flows are of two main types. Above an altitude of 305 m they are strongly indurated and consist mostly of graded-bedded greywacke and argillite. Below 305 m the deposits consist mainly of glacial outwash gravels (Gregg 1964).

The river bed is composed of fine gravel, with large boulders up to 0.7 m in diameter in riffles. There is fine mud in quiet backwaters and deep pools. Water velocity (measured with a Gurley No. 625 Pygmy velocity gauge) varied from 0 m/s at the bottom of the deep pools to a mean of 0.4 m/s in riffles. Surface water was in the main channel throughout the investigation, though in the autumn of 1971 there was no surface water in several other local rivers, including parts of the Ashley River. Although the Glentui is more stable than many other similar rivers in Canterbury, severe floods after heavy rainfall often cause the water velocity in the narrowest riffles to exceed 3 m/s. Such flooding precludes the establishment of macrophytes in the main channel and has a pronounced effect on the character of the river bed. Apart from isolated stands of *Myriophyllum* in quieter back-

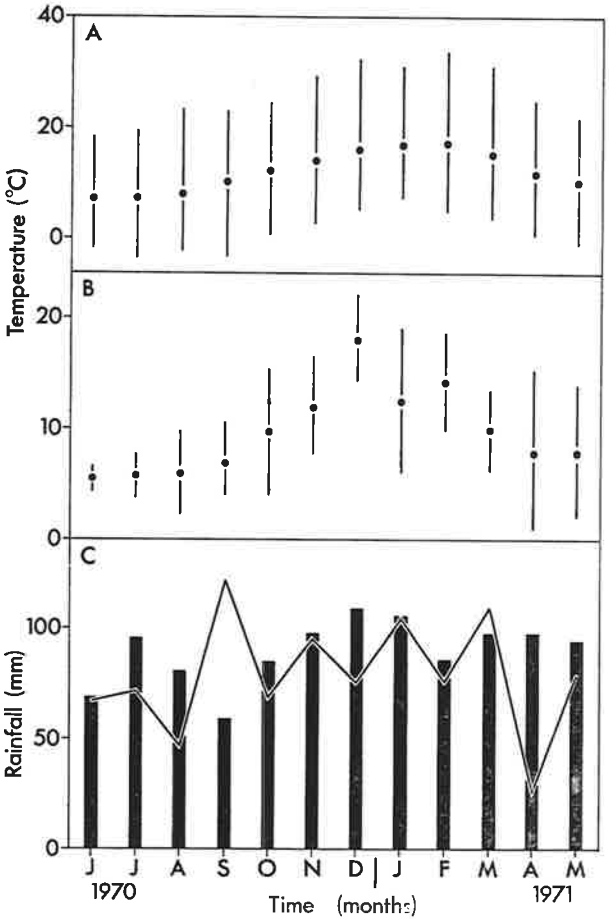


Fig. 2: Temperature and rainfall recorded in the study area from June 1970 to May 1971. A: Mean monthly air temperatures. B: Mean monthly water temperatures. In both A and B the temperature range is indicated by vertical bars. C: Monthly rainfall (graph), compared with mean monthly rainfall for the 25-year period from 1946 to 1970 (histogram).

waters, the only plant cover in the river is that provided by fallen trees and other debris of terrestrial origin carried down by floods.

During the study the pH of water in the regular sampling area varied from 6.8 to 7.3. The water was fairly soft, alkalinity ranging from 41.9 to 62.0 mg of $CaCO_3$/l. Conductivity at 25°c varied from 128 to 150 μS/cm, a moderate value for the Canterbury region.

Water temperatures were taken with a maximum-minimum thermometer at monthly intervals from June 1970 to May 1971 (B, Fig. 2). All readings were made in the same riffle after the thermometer had been in position on the river bed for 24 hours. Ice formed on standing water at the sides of the river for short periods in the winters of 1970 and 1971, but did not occur in the main channel.

BIOLOGICAL CHARACTERISTICS

Diatoms, notably *Gomphonema*, were on most of the boulders on the river bed. *Myriophyllum* was the only macrophyte found in the study area.

The invertebrate fauna was dominated by larval insects, which included species of Ephemeroptera, Trichoptera, Diptera, Plecoptera, Megaloptera, Coleoptera, and Hemiptera (Cadwallader 1975a, 1975c). Other invertebrates were *Gordius* (Nematomorpha) and the gastropod *Potamopyrgus antipodarum* (Gray). Terrestrial arthropods and plant debris were frequently found in the drift, and terrestrial lumbricids (Oligochaeta) were sometimes found in shallow, quiet water at the river margins.

Apart from *Galaxias vulgaris*, other fish in the sampling area were the upland bully (*Gobiomorphus breviceps* (Stokell)), long-finned eel (*Anguilla dieffenbachii* Gray), short-finned eel (*Anguilla australis schmidtii* Phillipps), and brown trout (*Salmo trutta* Linnaeus).

Black shags, *Phalacrocorax carbo* (Linnaeus), were occasionally seen near the river. These birds take galaxiids, eleotrids, salmonids, and anguillids in New Zealand inland waters (Falla and Stokell 1945, Dickinson 1951, Boud and Eldon 1960, Duncan 1968), but they were not considered to be important predators of fish in the Glentui River.

GENERAL METHODS

SAMPLING PROGRAMME

The sampling programme was part of a more extensive plan aimed at studying not only age, growth, and condition of *G. vulgaris*, but also breeding biology, home range and movement, food and feeding habits, and interrelations with other fish in the river. Only that part of the programme concerned with the elucidation of basic population parameters is outlined here.

Regular samples of *G. vulgaris* were taken from a 1.5-km stretch of the river (C-D in Fig. 1) every 28 days from June 1970 to May 1971. All fish in these samples were measured to provide monthly information on growth in length. A stratified subsample of at least two fish of each sex in each 5-mm length class was then taken and preserved in 10% formalin, the remainder being returned to the river. The subsampled fish were later weighed and aged and their fat deposits estimated.

Table 1 shows the number of fish in each sample and subsample taken in the study; it includes only those fish caught in the normal adult habitat, that is, riffles, and does not include age 0+ fish less than 30 mm long which occurred in quieter parts of the river. Information on growth of recently hatched fish was obtained from further samples taken during and after the breeding season in 1970–71.

ELECTRIC FISHING

Most samples were obtained with portable electric fishing equipment. Power was supplied by a Honda E300 generator via a 12-V battery. Positive pulses were passed to the water through an electrode held by the operator. An earth return system consisting mainly of a long, flexible metal cord completed the circuit. The current loading could be altered to four settings with maxima of 0.22, 0.4, and 0.5 A and a setting which could not be overloaded. The output was a positive square wave pulse at about 100 c/s with peak voltages of 300, 150, 100, or 50 V as required. A second pulse with an 80% on duty cycle at about 3 c/s was imposed on this (Woods 1967).

TABLE 1: Regular samples (and subsamples) of *G. vulgaris* taken from the Glentui River

Sample		No. of fish	
1970			
1	27, 28 June	89	(30)
2	25, 26 July	139	(139)
3	22 August	55	(55)
4	19, 20 September	100	(39)
5*	17 October	24	(24)
6	14, 15 November	171	(51)
7	12, 13 December	175	(31)
1971			
8	16, 17 January	146	(24)
9	6, 7 February	128	(50)
10	6, 7 March	176	(27)
11	3, 4 April	262	(111)
12	1, 2 May	180	(29)
13	29, 30 May	163	(25)

*Unfavourable fishing conditions after heavy rainfall.

The use of electric fishing equipment, briefly reviewed by Hynes (1970), is one of the least selective of fishing methods (Lagler 1968, Johnson, Rinne, and Minckley 1970). However, several workers, for example, Saunders and Smith (1954) and Woods (1964), have shown that there is usually some bias towards the larger length classes.

The equipment was highly effective in the Glentui River, where the water was generally shallow and of moderate conductivity and the substrate of gravel and boulders was of high resistance. Its effectiveness decreased in deep pools. The radius of the effective field with the positive electrode at its centre was about 300 mm for fish 100 mm long. Under these conditions all length classes of fish were sampled adequately except recently hatched *G. vulgaris*, which inhabited the still, deep parts of the river. However, these fish were taken easily with dip nets.

Mortality caused by electric fishing was negligible. That which did occur was because of overexposure to the electric field as in fish caught between boulders and not immediately seen by the operator. Towards the end of the sampling period some *G. vulgaris* (fewer than 20) showed reddening of the caudal peduncle. This condition was caused by the rupture of blood vessels and is related to the type of pulse produced by the electric fishing equipment. Hauck (1949) reported a similar condition in rainbow trout (*Salmo gairdneri* Richardson) that were shocked with 110 V alternating current. Spencer (1967), working with bluegill (*Lepomis macrochirus* Rafinesque), channel catfish (*Ictalurus punctatus* (Rafinesque)), and large-mouth bass (*Micropterus salmoides* (Lacépède)) exposed to 230 V alternating current, showed that fractures and dislocations of the vertebral column occurred in the caudal region. Large fish are more susceptible to this type of damage than fish of the size of the *G. vulgaris* taken in this study, the largest of which was only 125 mm long.

MEASUREMENT OF LENGTH AND WEIGHT

After capture and before further handling all fish were anaesthetised with benzocaine. Total length (TL), that is, length from tip of snout to the distal end of the central rays of the caudal fin, was read to 0.1 mm with a measuring board fitted with a vernier scale (Woods 1968). Wet weight of both fresh and formalin-preserved fish was measured to the nearest milligram. Correction factors for the effect of formalin on length and weight of *G. vulgaris* were obtained from Cadwallader (1974). Throughout this bulletin length refers to total length unless otherwise indicated.

SEX DETERMINATION

From May to November, during the ripening, spawning, and post-spawning stages of the reproductive cycle, adult *G. vulgaris* were sexed externally with a dissecting microscope at low magnification (× 6.3). During this period the anatomy of the genital region differs in males and females. Males have a papilla, at the tip of which is the genital opening. Females lack a papilla, and the genital region is much more bulbous than in males. The male papilla can be made to protrude by flexing the body.

This method of sex determination was unreliable during the resting and early-ripening stages of the reproductive cycle, from December to April. At this time the female genital region is less bulbous and the male papilla is less distended and cannot always be made to protrude. Sex determination of age 0+ fish by this method was unreliable, because, though mature males were easily identified, immature males could not be distinguished from females. Fish which could not be sexed externally were sexed by examination of the gonads after dissection.

AGE DETERMINATION

Methods for the determination of age in fish are numerous, and the extensive literature has been reviewed by Chugunova (1959) and Tesch (1968). Benzie (1961) described the otoliths of *Galaxias maculatus*. McDowall (1968) found that otoliths and length-frequency analysis could not be used to age *G. maculatus* because of its prolonged breeding season from September until June. Pollard (1971), working with a landlocked population of *G. maculatus*, used length-frequency analysis with some success, but found otoliths of little use as an aid to ageing the fish. Hopkins (1971) used both length-frequency analysis and otoliths to age *Galaxias divergens* Stokell, but did not validate the use of otoliths for this species. In this study sagittal otoliths and length-frequency analysis were used in combination to age *G. vulgaris*.

OTOLITHS

The use of otoliths to age fish depends on changes in the rate of growth or metabolism, which are reflected in the otoliths as alternating bands of visibly different material. The sagittal otoliths of *G. vulgaris* are plano-convex and basically discoidal, with a forward projection at the antero-ventral corner. This projection is not well developed in small otoliths, but becomes more prominent when the otoliths increase in size.

Both sagittal otoliths were removed from fish subsampled from regular monthly samples and from recently hatched fish sampled after the breeding season from September 1970 to January 1971 and these were stored dry in tube vials.

Interpretation of Otoliths

Otoliths were read under a microscope at × 80 magnification; they were immersed in xylol and viewed with reflected light against a black background. With this method a number of opaque (light) and translucent (dark) zones were visible in the otoliths (Fig. 3). The outer border of each translucent zone forms a distinct ring where it abuts the next outer opaque zone. Since the edges of the otolith are thinner than the central nucleus, they often appear translucent and this must be borne in mind in the interpretation of otolith zones.

It is important to distinguish between rings laid down on a regular temporal basis, that is, primary rings or annuli (A. C. Jensen 1965), and those which result from non-periodic variation in growth, that is, secondary rings. Rings were considered to be annuli on the criteria that they were more distinct, were uniformly spaced, and extended right around the otolith (Staples 1971). The consistency of recognition of annuli was tested in the July 1970 sample of 139 fish. In this sample the number of annuli in each otolith was counted twice, the second reading being 6 months after the first. Out of 139 otoliths, all but 3 were read the same on both occasions—a consistency of 97.8%. The criteria for distinguishing annuli were therefore considered to be adequate. Only annuli were used to determine age, and the number in each otolith was counted.

In some otoliths two translucent zones occurred close together. On the criterion of spacing they were considered as representing one annulus. Secondary rings were more readily seen in the thin otoliths of young fish. Typically, there were two of these narrow translucent rings. One, surrounding the central nucleus, was formed at total lengths ranging from 12 to 17 mm and coincided with the end of larval life. The other ring formed at total lengths of from 30 to 50 mm and coincided with the transition from the juvenile to the adult way of life. These rings were considered not to be annuli on the first criterion mentioned above. Similarly, Gambell and Messtorff (1964), working with whiting, *Merlangius merlangus* Linnaeus, considered the nuclear edge to reflect a change from pelagic to benthic habits rather than to be an indicator of age.

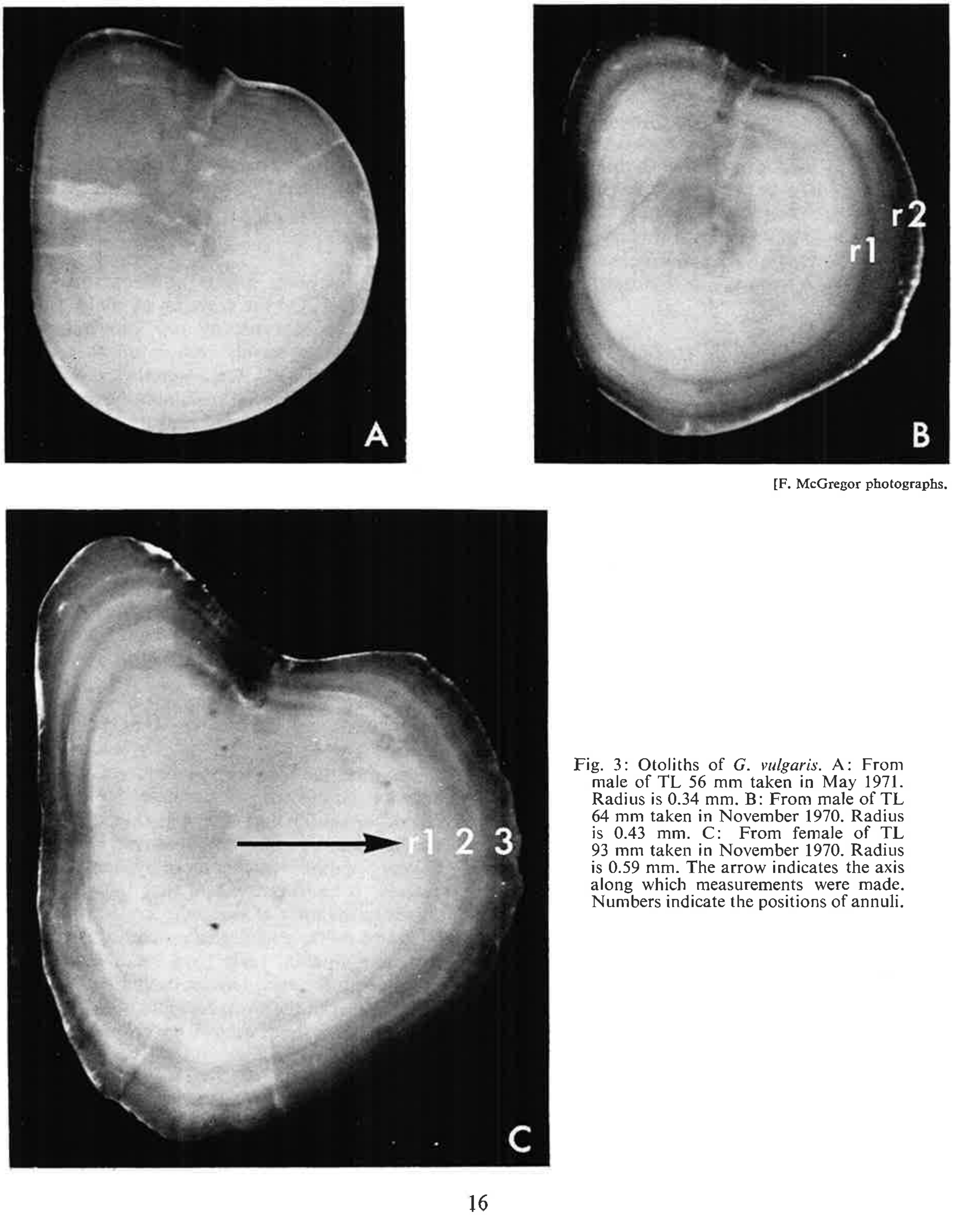
The sagittal otolith of one side of the head was the mirror image of that on the other side in all fish examined, except two, in both of which one otolith was normal and the other was underdeveloped. In one instance the nucleus was normally developed, but the rest of the otolith was extremely thin and transparent. In the other instance the abnormal otolith, though showing annuli, was of a more hyaline nature than is normal. It has been shown that inorganic material, chiefly in the form of aragonite, is laid down throughout the otolith, and organic material is restricted to the more opaque parts (Irie 1955, Dannevig 1956, Mina 1968, Degens, Deuser, and Haedrich 1969). It appears that in the two abnormal otoliths there was a breakdown in the processes governing the deposition of organic material.

Although both otoliths were generally similar, to standardise procedure all measurements were made on the flat side of the left otolith.

Validation of the Otolith Method

For annuli to be used to age *G. vulgaris* it had to be shown that they were formed at regular time intervals.

The pattern of annulus formation was examined by considering the relationship between the radius of each annulus and the total length of the fish over a period of a year, as described by Matsuura (1961), Mio (1961), and Yunokawa (1961). The otolith radius (R) and the radius of each annulus (r_n) were measured from the centre of the nucleus along the dorso-ventral axis (see Fig. 3) with a micrometer eyepiece. Each r_n was measured to the point where the annulus abutted the opaque zone. The r_n measurements were then stan-



[F. McGregor photographs.

Fig. 3: Otoliths of *G. vulgaris*. A: From male of TL 56 mm taken in May 1971. Radius is 0.34 mm. B: From male of TL 64 mm taken in November 1970. Radius is 0.43 mm. C: From female of TL 93 mm taken in November 1970. Radius is 0.59 mm. The arrow indicates the axis along which measurements were made. Numbers indicate the positions of annuli.

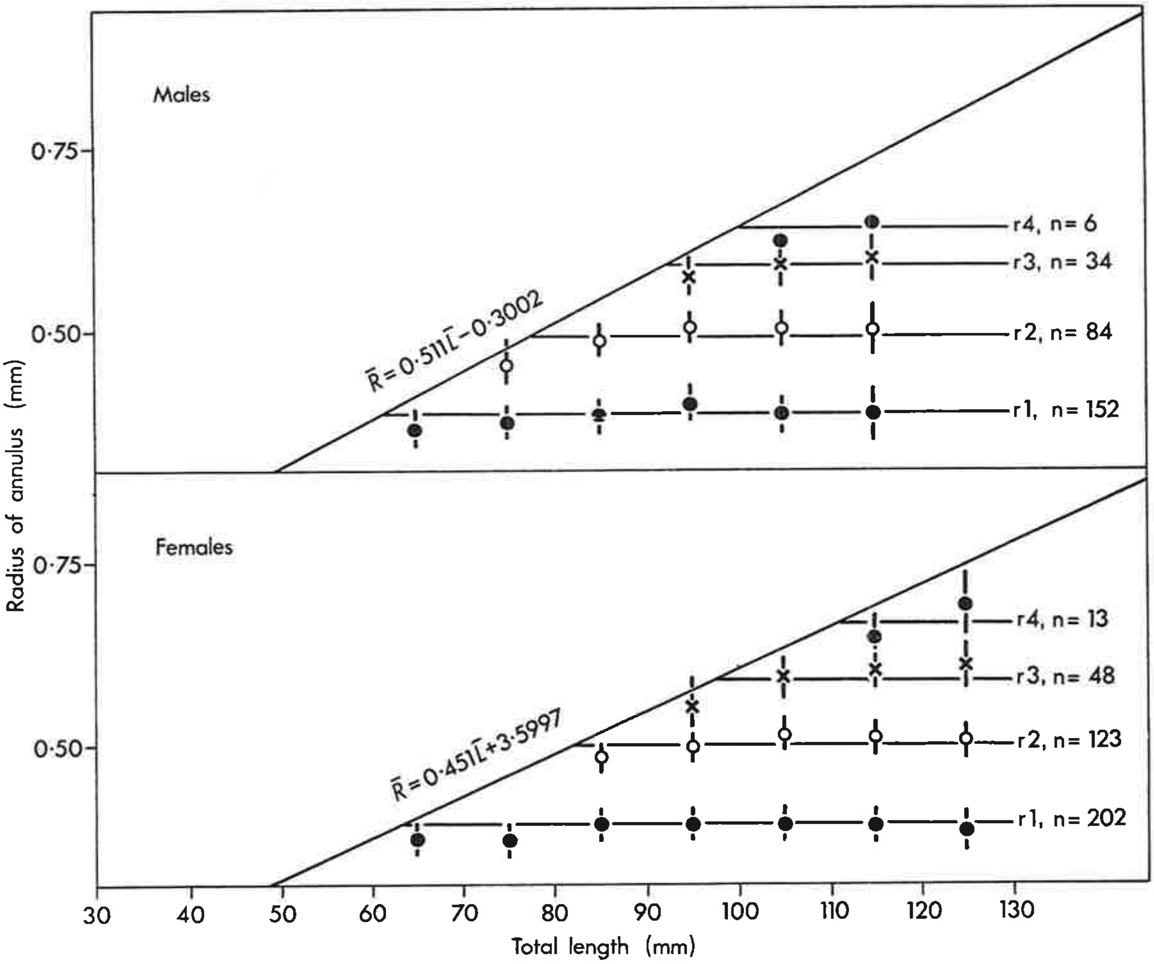


Fig. 4: The regression of otolith radius on total length, and correspondence of annuli (r1–r4) in male and female *G. vulgaris*. Vertical bars denote the 95% confidence intervals of the mean values of each annulus radius in each 10-mm TL group. (The confidence limits for the fourth annulus in males are 47.98 and 52.18 (100- to 110-mm group) and 40.65 and 64.54 (110- to 120-mm group).)

dardised to adjust for individual variation in growth by multiplying by the factor $\bar{R}/R$, where $\bar{R}$ was the mean otolith radius for any observed total length. $\bar{R}$ was determined separately for males (252 fish) and females (293 fish) from the relationship between total length and otolith radius. This relationship is indicated by the diagonal regression lines in Fig. 4.

(The regressions of otolith radius on total length for males and females were compared by analysis of covariance (Snedecor and Cochran 1967) after Bartlett's test of homogeneity of variances (Sokal and Rohlf 1969) indicated that the test was valid ($\chi^2 = 0.4769$, d.f. = 1). Analysis of covariance indicated that though there was no significant difference ($P > 0.01$) between intercepts ($F = 1.1603$, d.f. = 1 and 542), there was a significant difference ($P < 0.01$) between slopes ($F = 16.4223$, d.f. = 1 and 541). This indicated that the rate of deposition of otolith material was different for males and females. Therefore all subsequent analyses were carried out separately for the two sexes.)

The mean values of standardised annulus radii ($\bar{r}_n$) were then determined for a subsample of fish in each 10-mm length class and are given with 95% confidence intervals (Fig. 4). In Fig. 4 straight lines can be drawn parallel to the total length axis through each annulus radius, which shows that equivalent annuli occur in the same position in the otolith irrespective of both the total length of the fish and the number of annuli in the otolith. For example, the position of annulus 1 in a 2-annulus otolith from the 80- to 90-mm length class is similar to that of annulus 1 in a 4-annulus otolith from the 110- to 120-mm length class. Such correspondence of annuli indicates the regular temporal pattern in which they were formed.

Although it has been assumed by some workers that annuli are formed once a year, this is not always so (for example, see Yunokawa (1961)). The time of annulus formation in *G. vulgaris* was estimated from monthly changes in the marginal growth index of the otolith. The growth index, as given by Matsuura (1961), is represented by:

$$G_I = \frac{R - r_n}{R - r_{n-1}}$$

where G_I is the marginal growth index, R is the total otolith radius, and r_n and r_{n-1} are the radii of the ultimate and penultimate annuli respectively. All measurements were made to the outer edge of each annulus where it abutted the next outer opaque zone. The mean marginal growth index was determined monthly for fish of each sex. The indices from June 1970 to May 1971 are presented (Fig. 5) with their 95% confidence intervals. As shown by the decrease in the growth index, the annulus formed in the otolith from August to October. Within this period the exact time of formation varied between fish, and 1 October was chosen arbitrarily as the date of annulus formation. It is apparent that one annulus was formed during the year, in winter and early spring, and one opaque zone was laid down in late spring, summer, and autumn.

Fish in their first year of life with no annulus formed were designated by international convention (Tesch 1968) as age 0+. The first annulus was formed by the following October, about 1 year after hatching (which extended from late September to November in the Glentui River (Cadwallader 1976a)). After formation of the first annulus fish entered their second growing season and were designated age 1+, and so on.

Factors Affecting the Formation of Annuli

Several workers have indicated a correlation between the time of annulus formation and certain external parameters, for example, temperature (K. W. Jensen 1957, Ouchi 1969) and food (Bhatia 1931a, 1931b, 1932). Hartley (1947) considered annuli to be spawning marks, but Brown (1946a), van Someren (1950), and Holden (1955) thought that condition or some internal cycle played a major role. Even though experiments such as those of Bhatia and Ouchi indicate that certain external factors play an important role in some species, it is difficult to isolate the particular factor or factors directly responsible for annulus formation (De Bont 1967). Recently Pannella (1971) demonstrated the occurrence of daily growth in the sagittae of all the species he studied. He suggested that there is a relation between the rate of calcification and reproduction.

Annulus formation in *G. vulgaris* occurred during late winter and early spring, when day length and water temperature were increasing and when growth rate was at a minimum. This coincided with the breeding season. However, annuli formed at the same time in young-of-the-year fish irrespective of whether or not they spawned. Thus, all young-of-the-year females formed annuli, though none of them shed eggs or were even ripe, and all young-of-the-year males formed annuli, though only some of them spawned (Cadwallader 1976a). Therefore, spawning as such did not effect annulus formation, at least in young-of-the-year fish.

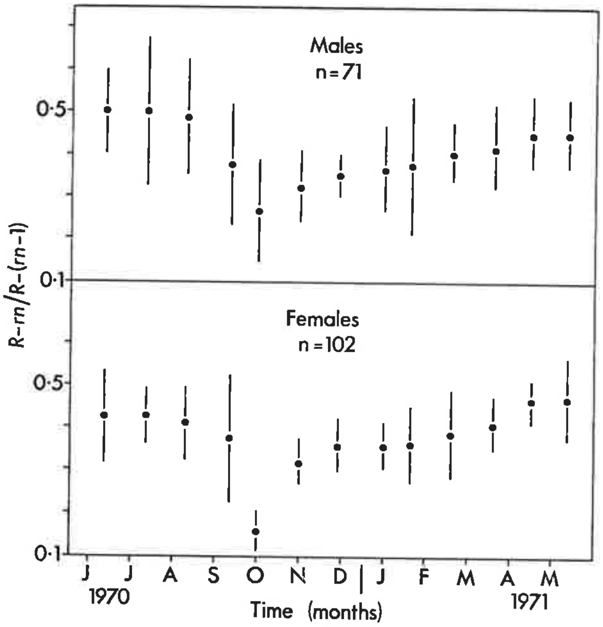


Fig. 5: Time of annulus formation in the otoliths of *G. vulgaris* as indicated by changes in the marginal growth index. The mean value for each index is given with its 95% confidence intervals (vertical bars).

At the same time of the year there was a reduction in the condition of fish. This occurred not only because of the decrease in gonad weight in those fish which spawned, but also because of the depletion of fat reserves which were at a minimum in August and September. During the same period there was a reversal of the diel activity pattern (Cadwallader 1975b) and a change in the normal sedentary habits of the fish (Cadwallader 1976b). It was therefore a time of physiological readjustment.

As Nikolsky (1963) pointed out, it would be incorrect to assume that annulus formation occurred merely as a response to changes in growth or metabolism brought about by altered external conditions. He concluded that annulus formation depended on a number of simultaneous processes. Similarly, in *G. vulgaris* annulus formation appears to depend on a physiological mechanism affected by factors both internal and external.

LENGTH-FREQUENCY ANALYSIS

Length-frequency distribution analysis may be used to age fish which have a fairly limited spawning season. At any one time a population of such fish consists of a series of discrete age groups. The size range of each age group tends to be distinct from that of adjacent groups and may be indicated by a mode in a length-frequency distribution. This method of ageing is applicable to *G. vulgaris*, which has one well-defined spawning season in late winter-early spring.

The number of fish in each 2-mm length class was recorded for each regular monthly sample and for samples of recently hatched fish. The resulting polymodal length-frequency distributions from June 1970 to May 1971 are presented in Fig. 6 (1970 August and October samples are omitted because of small sample sizes). In most months two, and in some months three, distinct length groups are indicated, but for most of the year only the first two groups can be separated by this method. Since the whole population was represented in the samples referred to above, the first group represents fish in their first year of life, designated age 0+, the next group represents fish in their second year of life, designated age 1+, and so on.

For a comparison of the otolith and length-frequency distribution methods the age of each fish in the July 1970 sample was determined from otoliths. The length-frequency distribution of fish in each age group was then plotted and is given (Fig. 7) with the total length-frequency distribution for that month. Fish designated 0+ and 1+ by both methods coincide. This further validates the use of otoliths for ageing *G. vulgaris*.

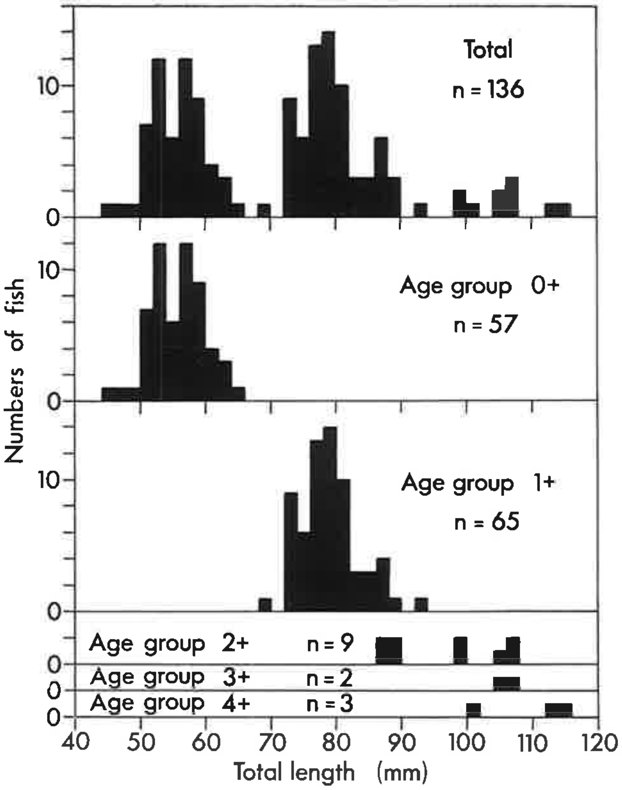


Fig. 7: Length-frequency distribution of *G. vulgaris* in the Glentui River in July 1970, with the length-frequency distributions of the component age groups as determined from otoliths.

The method of length-frequency distribution analysis is inadequate for ageing older fish, mainly because of the small numbers of fish surviving for more than 3 years. There is also an increasing overlap in the length-frequency distributions of older fish produced by individual variation and reduced growth rate. The situation is further complicated by different rates of growth in males and females after the first year of life (page 21). This is indicated by the bimodal nature of the second (age 1+) and third (age 2+) length classes in most months and is shown particularly well in the December 1970 and the January and February 1971 length-frequency distributions (Fig. 6).

In practice smaller fish were aged by length-frequency distribution analysis, and larger fish were aged by reading of otoliths.

Most *G. vulgaris* taken in the present study belonged to the age groups 0+, 1+, and 2+; a few were in the 3+ and 4+ age groups, none were in the 5+ age group, and one was in the 6+ age group.

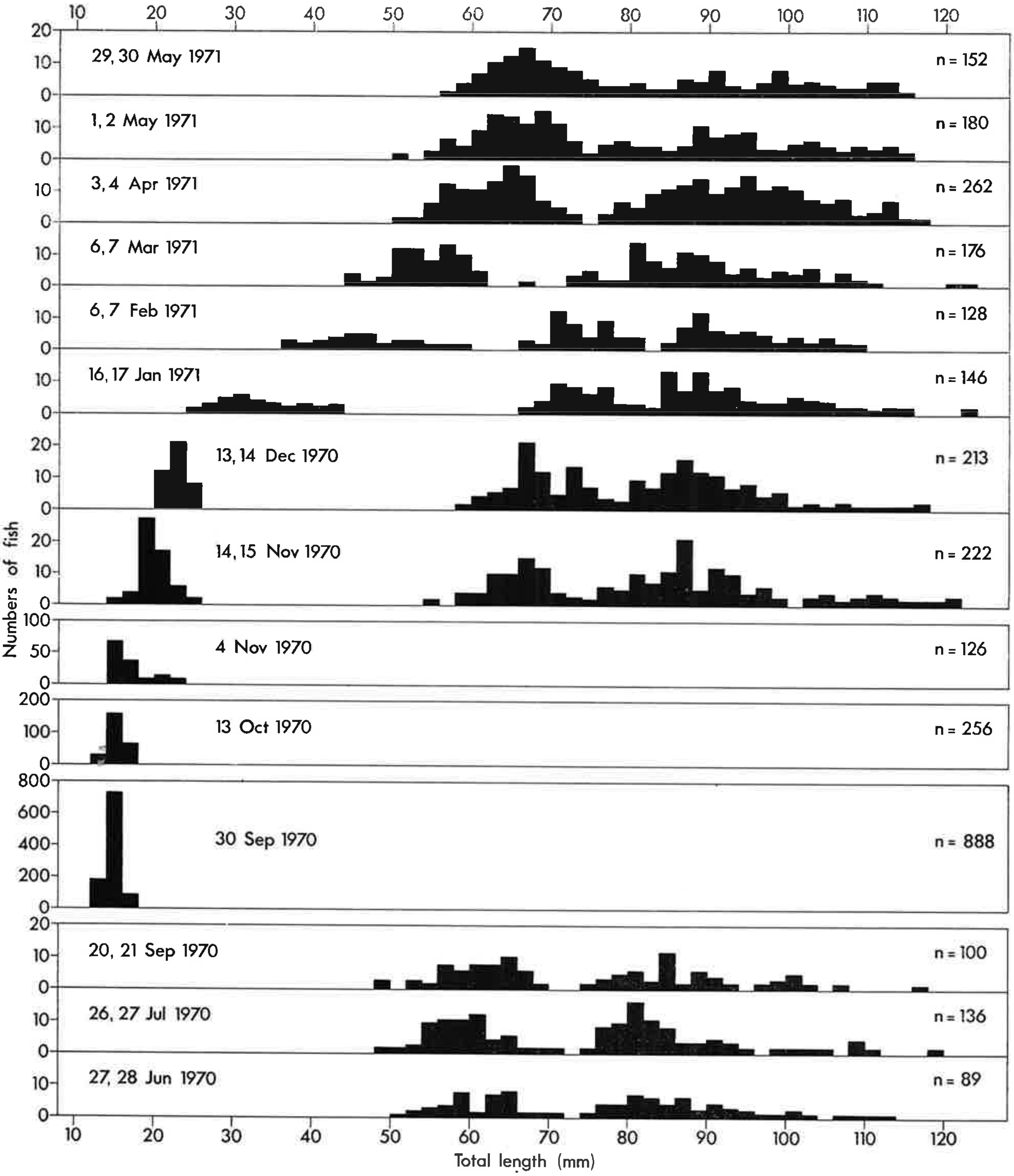


Fig. 6: Length-frequency distributions of *G. vulgaris* from June 1970 to May 1971. From September to December samples of recently hatched fish were obtained from quiet stretches of the Glentui River immediately below the riffles in which the adults were found. From January onwards all fish were sampled in riffles.

GROWTH

ANNUAL GROWTH IN LENGTH

Data on annual growth in length of *G. vulgaris* were derived by back calculation from otoliths with the formula given by Nikolsky (1963):

$$L_n = \frac{R_n}{R}\ (L - c) + c$$

where L_n is the length of the fish at age n (that is, when the nth ring was formed), L is the length of the fish and R is the otolith radius when the sample was taken, R_n is the radius of ring n, and c is the hypothetical length of the fish at the moment the otolith began to form. The value of c is derived by extrapolation from the regression of otolith radius on total length (Fig. 4) and is the intercept on the total length axis; for males $c = 0.56$ and for females $c = -8.08$.

TABLE 2: Mean, annual, back-calculated lengths (TL) of *G. vulgaris* derived from otoliths, with their 95% confidence limits (CL)

Age (years)	Mean TL (mm)	95% CL	No. of fish
Males			
1	61.33	±0.7156	157
2	79.06	±1.2872	85
3	91.12	±1.9425	32
4	97.81	±4.3493	8
Females			
1	61.66	±0.7307	208
2	81.52	±1.0791	122
3	97.45	±1.8622	45
4	110.07	±3.8940	14

For fish aged from 1 to 4 years mean back-calculated lengths with their 95% confidence limits are presented (Table 2).

Length reached at the end of the first year of life was not significantly different ($P > 0.05$) between males and females ($t = 0.6351$, d.f. $= 363$). However, after the first year, growth in length of males lagged behind that of females. Student's t tests, used to compare the mean lengths achieved at the end of the second, third, and fourth years of life, showed significant differences ($P < 0.01$) between males and females ($t = 2.9068$, d.f. $= 205$; $t = 4.7828$, d.f. $= 75$; $t = 4.7572$, d.f. $= 20$ for comparison of lengths achieved at the end of the second, third, and fourth years of life respectively).

The von Bertalanffy equation (von Bertalanffy 1938) adequately described annual growth in length of *G. vulgaris*. The equation is represented by:

$$l_t = L_\infty(1 - e^{-K(t - t_0)})$$

where l_t is the length at age t, L_∞ is the average "maximum" or asymptotic length, K is a constant determining the rate of change in the length increment, t is age in years, and t_0 is the hypothetical age when length is zero. The equation parameters were computed by the Allen (1966) method from data from individual fish up to age 4+. For males (n = 157):

$$l_t = 112.6\ (1 - e^{-0{\cdot}4271\ (t\ +\ 0{\cdot}8405)})$$

and for females (n = 208):

$$l_t = 158.9\ (1 - e^{-0{\cdot}2295\ (t\ +\ 1{\cdot}1397)}).$$

TABLE 3: Mean lengths (in millimetres, with 95% confidence limits (±) in parentheses) of *G. vulgaris* in the Glentui River from June 1970 to May 1971. (Age 0+ fish have been included as males; August and October samples are omitted because of small sample sizes.)

	1970					1971					
Age group	Jun 27–28	Jul 26–27	Sep 20–21	Nov 14–15	Dec 13–14	Jan 16–17	Feb 6–7	Mar 6–7	Apr 3–4	May 1–2	May 29–30
Males and females 0+			11.3* (0.1) 12.1† (0.1)	13.3‡ (0.4) 16.3§ (0.5)	19.2 (0.8)	29.9 (1.9)	43.2 (2.0)	51.4 (0.9)	59.7 (1.0)	61.6 (1.1)	63.5 (1.1)
Males 0+/1+	57.8 (1.5)	56.3 (1.1)	58.3 (1.3)	61.4 (0.8)	62.8 (1.4)	67.7 (0.9)	67.5 (0.6)	70.6 (1.0)	75.4 (0.5)	76.0 (1.2)	76.8 (1.2)
Females 0+/1+					68.6 (1.6)	73.4 (0.9)	73.8 (0.8)	77.9 (0.6)	82.6 (1.0)	85.4 (0.9)	85.3 (1.7)
Males 1+/2+	76.6 (1.1)	77.6 (1.1)	75.6 (1.5)	76.3 (1.5)	77.4 (0.3)	81.0 (0.8)	84.7 (0.8)	84.7 (0.5)	90.3 (0.8)	90.7 (0.6)	94.6 (1.5)
Females 1+/2+	82.8 (0.8)	81.6 (1.6)	83.1 (0.9)	82.2 (0.5)	84.0 (1.4)	85.4 (0.4)	91.1 (0.9)	90.9 (0.8)	95.8 (0.7)	98.2 (1.6)	100.5 (1.2)

* Sample taken on 30 September.
† Sample taken on 13 October.
‡ Sample taken on 4 November.
§ Sample taken on 20 November.

SEASONAL GROWTH IN LENGTH

Seasonal growth in length was estimated from monthly changes in the mean length of each age group. Mean lengths were calculated directly from groups of recently hatched fish where there was no overlap in length distribution with older age groups. For other groups in the regular monthly samples mean lengths were estimated from length-frequency distributions by the probability paper method (Cassie 1950). This method was used to measure seasonal growth in fish up to age 2+; the small numbers in the population did not permit the use of this method to follow seasonal growth in older fish. Mean lengths of *G. vulgaris* from June 1970 to May 1971 are presented (Table 3).

The period of increase in length for both males and females extended from November to the following May, with maximum growth occurring from December to April. Growth ceased from June to October, in winter and early spring. Benzie (1968) found a similar pattern of growth in length in age 0+ *G. vulgaris* in another Canterbury river (the Cass River), where fish reached a mean length of 58.6 mm in their first year of life, with no significant growth occurring between June and September*.

Differences in growth in length between year classes were apparent; for example, in the May (29–30) 1971 sample, age 0+ fish had reached a length of 63.5 mm, whereas in the June 1970 sample age 0+ fish had attained a length of only 57.8 mm.

Seasonal growth in length also varied in different parts of the Glentui River. This was indicated by comparing the length-frequency distributions of fish caught at the same time in different parts of the river. Figure 8 shows the length-frequency distributions of the regular samples taken in March, April, and May 1971 with those of samples taken during the same periods from further down stream. The greatest

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*Benzie's data were converted from standard lengths to total lengths with a conversion factor of 1.149 (derived from the ratio between these two measurements in *G. vulgaris* given by McDowall (1970)).

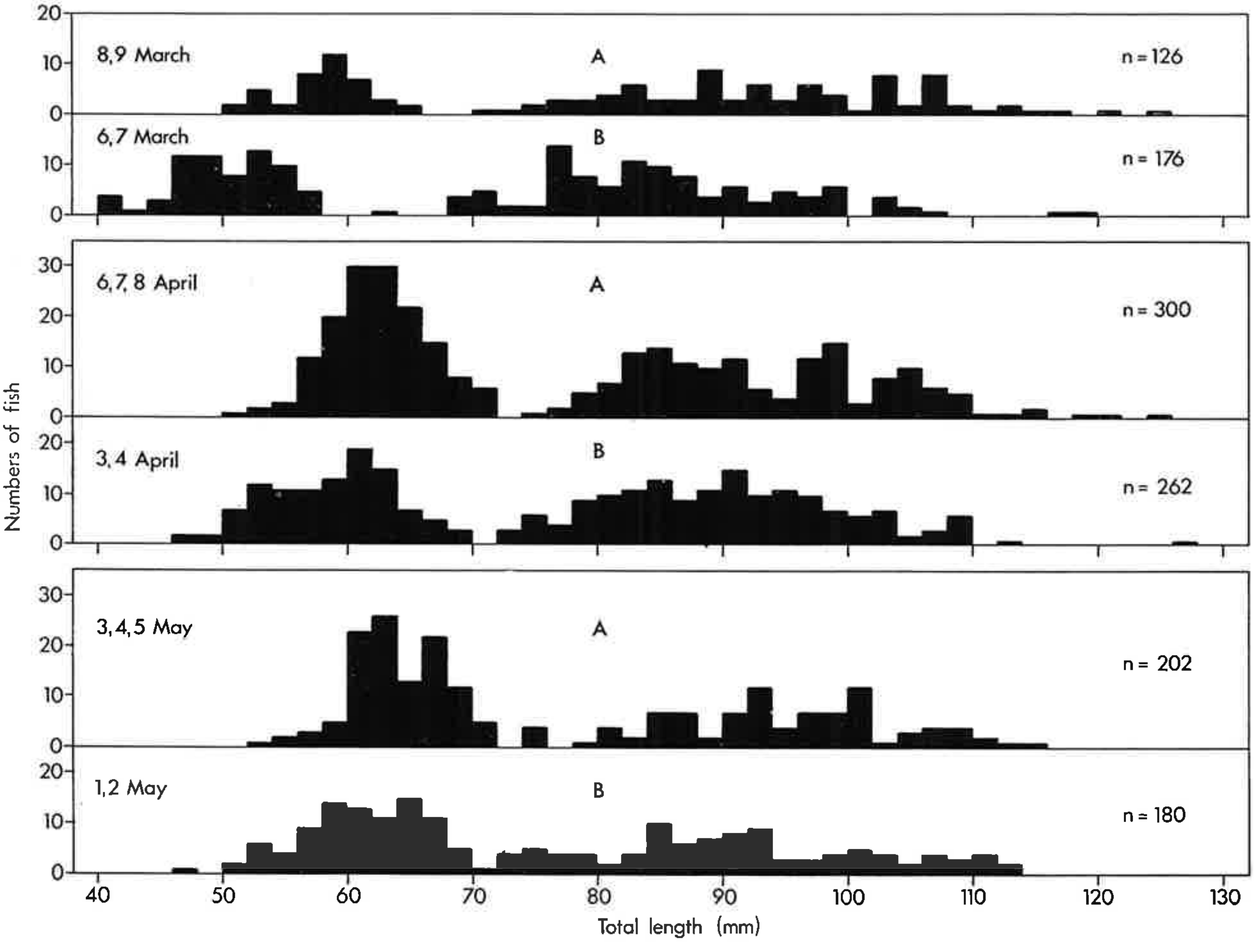


Fig. 8: Length-frequency distributions of samples of *G. vulgaris* taken in different parts of the Glentui River in 1971. A: Samples taken from section E-F (see Fig. 1). B: Samples taken from section C-D (see Fig. 1) during the regular sampling programme.

TABLE 4: **Mean lengths and 95% confidence limits (±) of age 0+ *G. vulgaris* caught during the same periods in different parts of the Glentui River. (The difference between paired means is significant at the 0.001 probability level.)**

Regular samples (C-D, Fig. 1)			Other samples (E-F, Fig. 1)					
Date	Mean length (mm)	95% CL	Date	Mean length (mm)	95% CL	Difference between means (mm)	*t*	d.f.
6, 7 March	51.4	0.9	8, 9 March	59.2	1.1	7.8	10.579	107
3, 4 April	59.7	1.0	6, 7, 8 April	63.5	0.6	3.8	6.433	254
1, 2 May	61.6	1.1	3, 4, 5 May	65.4	0.8	3.8	5.797	206

differences were those between age 0+ fish; mean lengths of this age group with the differences between samples are presented (Table 4). Different rates of growth in fish of the same species in different parts of a river have been reported also by Went and Frost (1942) and Purkett (1958).

SEASONAL GROWTH IN WEIGHT

Wet weights were obtained from fish subsampled from regular monthly samples. Data on growth in weight for fish in the younger age groups are shown (Fig. 9); older fish were too few to provide adequate data on growth in weight.

Fish in the 0+ and 1+ age groups of each sex generally gained weight throughout the year, though most weight was added during summer and autumn. Similarly, growth data for age 2+ and 3+ fish of each sex approximate parabolas with the low point at September-November (the post-breeding period), which indicates that most weight was gained in summer and autumn, from January to May. Growth in length ceased during the spawning period, but growth in weight was most affected because of shedding of the sexual products.

The largest *G. vulgaris* taken in the present study was an age 4+ female which weighed 20.9 g and was 125 mm long; the largest male was also age 4+, weighed 13.5 g, and was 107 mm long.

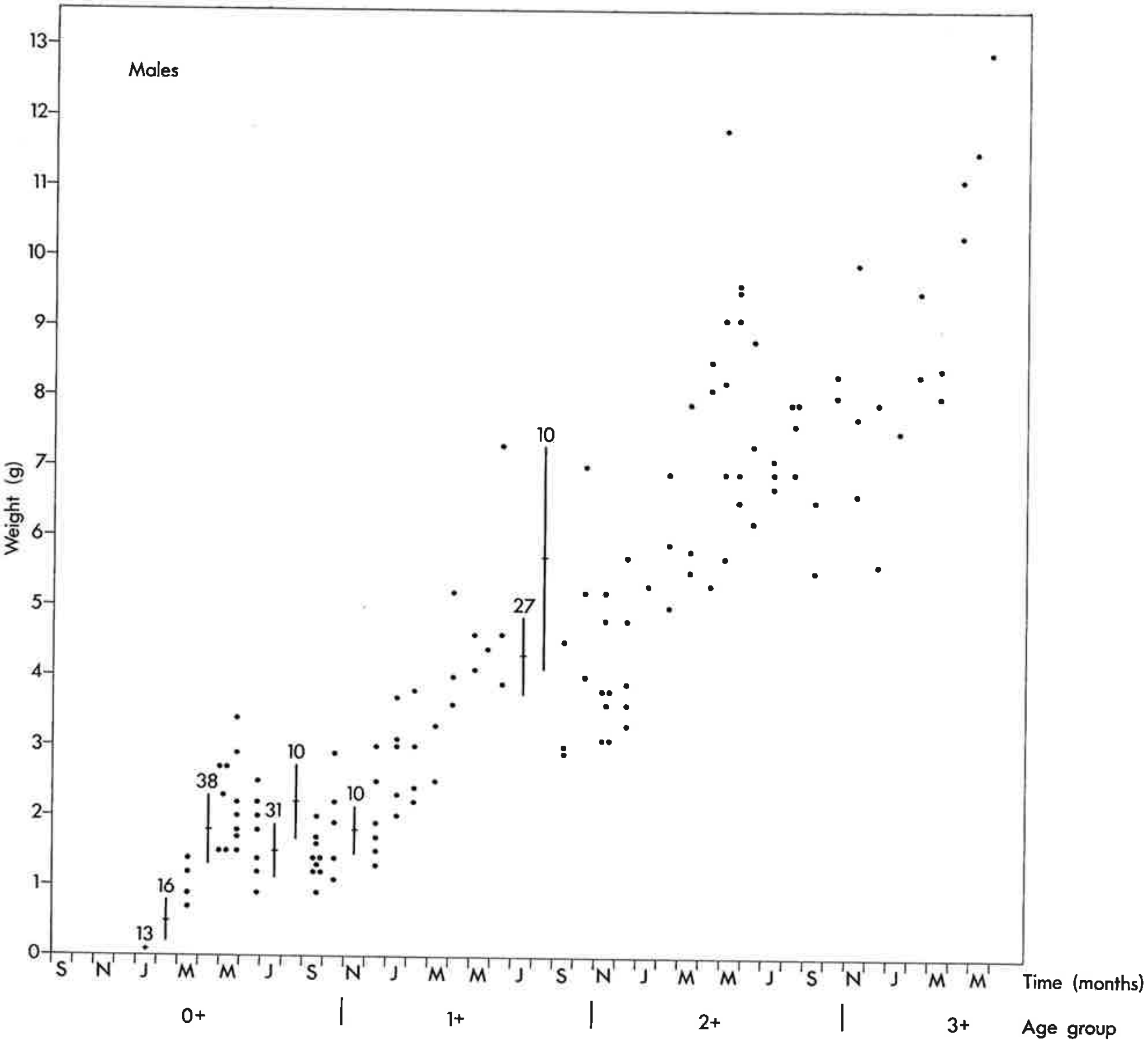
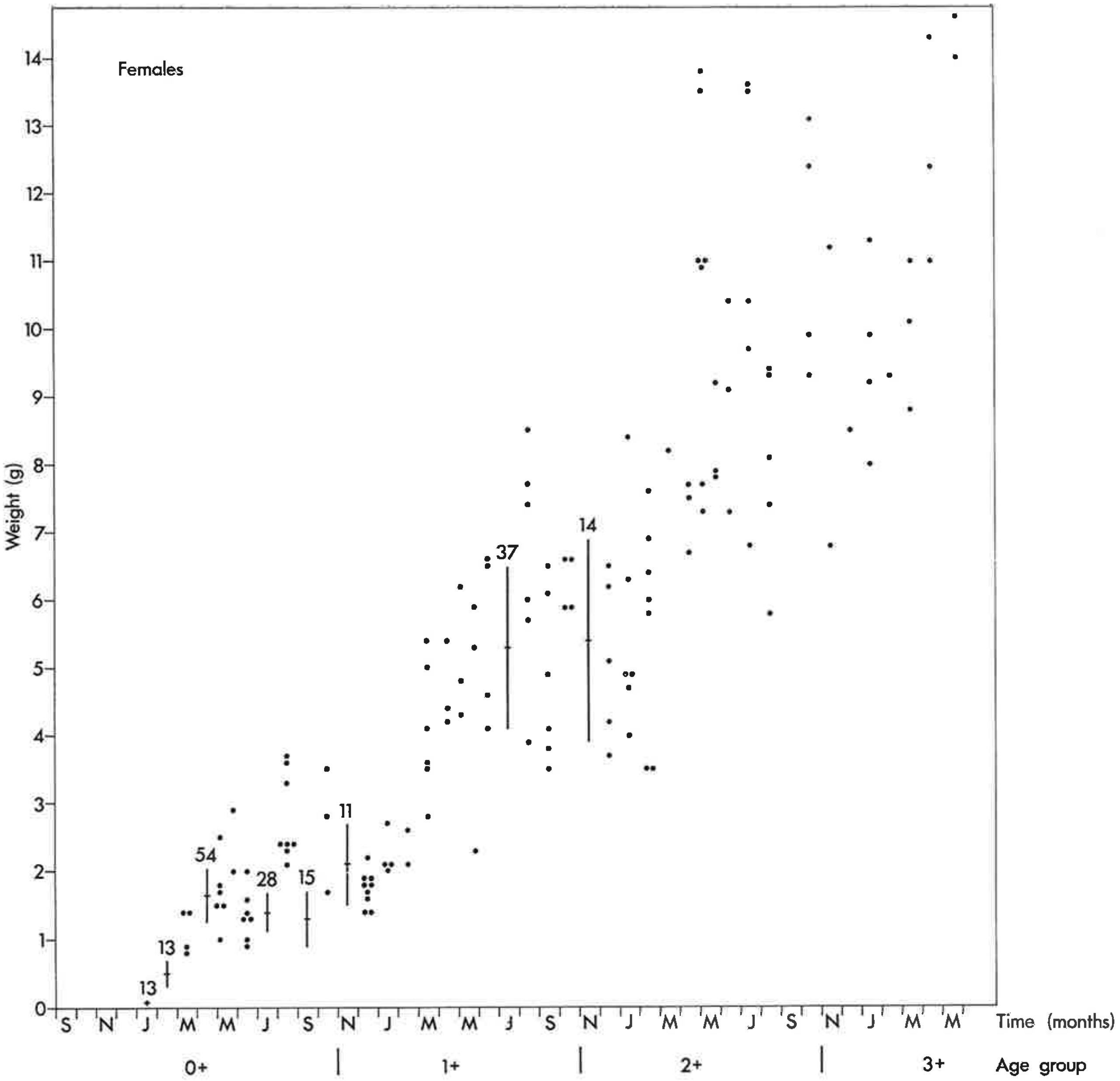


Fig. 9 (above and right): Seasonal growth in weight of male and female *G. vulgaris* from June 1970 to May 1971. Individual data points are given if there were fewer than 10 fish in the sample. If there were 10 or more fish in the sample, the mean weight of the fish is given with the standard deviation (indicated by the vertical bar). The number of fish on which the mean is based is given above each mean.


Females
Weight (g)
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
13
13
54
28
15
11
37
14
S N J M M J S N J M M J S N J M M J S N J M M
Time (months)
0+
1+
2+
3+
Age group

LENGTH-WEIGHT RELATIONSHIP AND CONDITION

Data on length and weight for each 2-monthly period were combined for analysis of the length-weight relationship in *G. vulgaris*. Males and females were treated separately and, for each sex, fish older than 0+ were lumped together in one group and treated separately from age 0+ fish. Regression lines for the two age groups of each sex were used to describe the length-weight relationship for each 2-monthly period; regression coefficients (with their 95% confidence limits) for these relationships are presented (Table 5).

A b coefficient of 3.0 indicates isometric growth and characterises a fish having an unchanging body form and unchanging specific gravity (Ricker 1958). Values of b normally range from 2.5 to 3.5 (Carlander 1969), but there may be regression slopes outside this range at certain stages of growth (Macphee 1960).

Values of b which differed significantly from 3.0 were detected by use of the formula given by Snedecor and Cochran (1967):

$$t = \frac{b - \beta}{S_b}$$

where t is a critical value of the t distribution and has $n-2$ degrees of freedom, b is the observed gradient, β is the expected gradient (in this case $\beta = 3.0$), and S_b is the standard error of b.

For *G. vulgaris* immediately after hatching, in October and November, the b coefficient was not significantly different from 3.0. However, during the juvenile phase, from December to March, extremely high b coefficients were recorded for both males and females, which indicated a rapid increase in weight for a small increase in length. From the end of the juvenile phase to the end of the first year of life the b coefficients were again not significantly different from 3.0. Similarly, Macphee (1960), working with the large-scale sucker, *Catostomus macrocheilus* Girard, reported b coefficients of 4.9125 and 3.3496 for fish below and above 20 mm in length respectively. He concluded that the point of intersection of the two regression lines indicated the upper limit of the post-larval stage of development. The b coefficient of female *G. vulgaris* older than age 0+ was significantly greater than 3.0 in 8 out of 12 months; with males b tended to be lower than for females and was significantly greater than 3.0 in only 4 months. For both sexes b was significantly greater than 3.0 just before the breeding season and was reduced during spawning from August to September.

Unless the b coefficient is the same for all groups of fish whose condition is being compared, coefficient a cannot be used as a measure of their relative condition (Le Cren 1951). This applies particularly when changes in the two coefficients are correlated, which is usual

TABLE 5: Length-weight relationships of *G. vulgaris* from June 1970 to May 1971. Relationships are of the form: log $w = a + b \log l$. (Length is in millimetres, weight in grams; CL is confidence limits (±) and RH is recently hatched fish.)

	Males					Females				
	No. in sample	Coeff. *a*	95% CL	Coeff. *b*	95% CL	No. in sample	Coeff. *a*	95% CL	Coeff. *b*	95% CL
Age 0+										
Jun, Jul	38	−5.695	0.015	3.303	0.542	33	−5.063	0.013	2.944	0.511
Aug, Sep	24	−4.928	0.019	2.880	0.454	26	−6.013	0.031	3.508	0.675
Oct, Nov (RH)	7	−5.776	0 060	3.051	1.210	..	..	..	..	..
Dec, Jan	13	−7.452	0.028	4.415**	0.843	..	..	..	..	..
Feb, Mar	20	−6.642	0.024	3.895**	0.372	18	−6.177	0.030	3.602*	0.628
Apr, May	50	−5.263	0.012	3.109	0.346	62	−4.695	0.011	2.765	0.359
Age >0+										
Jun, Jul	41	−5.731	0.011	3.333**	0.295	53	−5.798	0.009	3.376**	0.226
Aug, Sep	22	−5 637	0.020	3.274	0.508	20	−5.267	0.027	3.084	0.580
Oct, Nov	27	−5.771	0.020	3.343**	0.238	39	−5.551	0.017	3.238*	0.205
Dec, Jan	22	−5.481	0.022	3.189	0.306	33	−5.637	0.014	3.276**	0.158
Feb, Mar	16	−5.507	0.018	3.213	0.301	23	−5.515	0.013	3.230*	0.183
Apr, May	25	−5.135	0.011	3.054	0.218	28	−5.475	0 015	3.236	0.253

*Significant deviation from 3.0 at the 5% probability level.

**Significant deviation from 3.0 at the 1% probability level.

In the age 0+ fish, numbers for October and November males and females are combined; the regression line is based on the weights of 7 samples each of known mean length (total number of fish is 471). Numbers for December and January males and females are also combined; the regression line is based on the weights of 13 samples each of known mean length (total number of fish is 130).

(Hile 1936). Thus, the regression line is affected by differential changes in weight in fish of different lengths. Coefficient b differed significantly between 2-monthly samples for each group of *G. vulgaris*, and for both age groups of each sex b was negatively correlated with a throughout the sampling period ($r = -0.972$ (males, age 0+); $r = -0.995$ (males, age >0+); $r = -0.974$ (females, age 0+); $r = -0.984$ (females, age >0+)). Therefore, for each group changes in coefficient a could not be used to compare condition at various times of the year, and so changes in condition were considered in terms of predicted weight values for hypothetical fish of 30, 80, and 100 mm TL (from the regression coefficients given in Table 5) and are presented (Fig. 10).

The condition of age 0+ fish increased throughout the growing season. In older fish both males and females showed similar trends, with an increase in condition in late spring and autumn and a reduction in condition in early spring and summer. Females were generally in better condition than males.

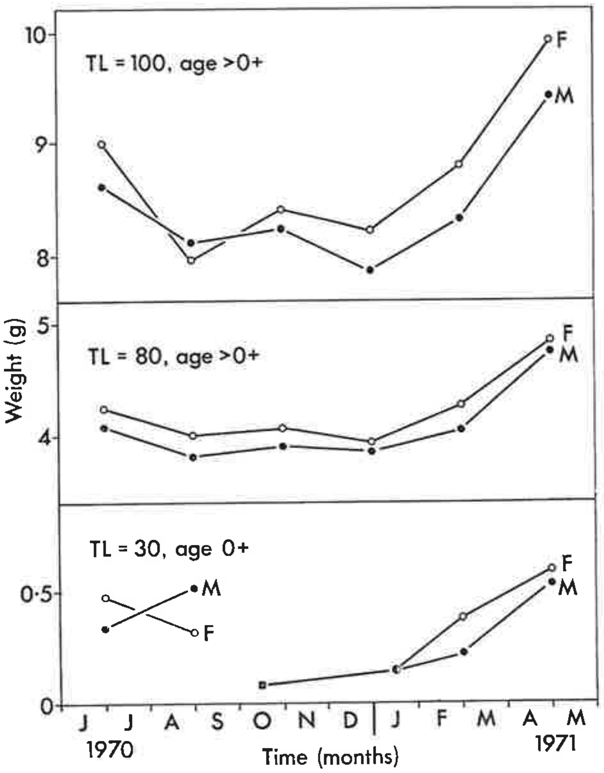


Fig. 10: Two-monthly variation in the length-weight relationship of *G. vulgaris*. Points are predicted weight values calculated from 2-monthly length-weight regressions (Table 5) for males (M) and females (F) of three hypothetical TL's—100, 80, and 30 mm. The solid square indicates that data for males and females are combined.

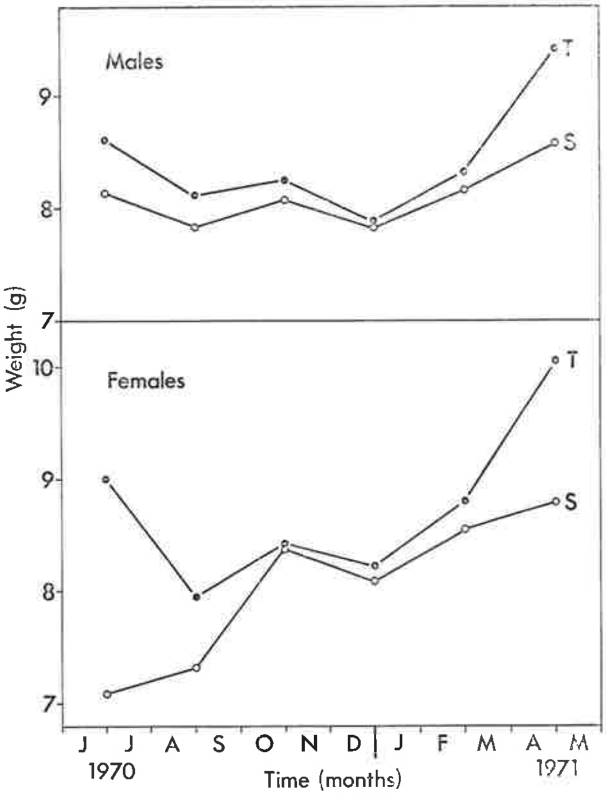


Fig. 11: Two-monthly variation in the length-weight (that is, total weight) relationship (T) and the length-somatic weight relationship (S) for hypothetical male and female *G. vulgaris* of 100 mm TL.

To eliminate the effects of changes in gonad weight, regression lines were fitted to length-somatic weight (that is, total weight of fish with gonad weight subtracted) data, and modified condition factors were calculated. The modified condition factors followed the same trends as the condition factors based on total weights, which indicates that somatic tissue undergoes seasonal changes irrespective of gonad development. The 2-monthly variation in the length-weight (that is, total weight) relationship and the 2-monthly variation in the length-somatic weight relationship for hypothetical fish of 100 mm TL are shown (Fig. 11). Though both relationships follow the same trend in each sex, the development of gonads has a greater effect on condition in females than in males.

The trends in condition referred to above were reflected in the fat deposits overlying the stomach and posterior part of the alimentary tract. A scheme based on that of Prozorovskaia (cited by Nikolsky 1963, page 211) was used to estimate fat deposits in fish subsampled from regular monthly catches. These deposits were at a minimum in spring after the breeding season, but they increased in summer, reaching a peak in February and March, and were gradually reduced throughout autumn and winter.

FACTORS AFFECTING THE GROWTH OF *G. VULGARIS*

Growth results from the consumption of food, its assimilation, and its transformation into body constituents. As indicated by Coche (1967), it may be regarded as the energy surplus transformed to tissue after the metabolic requirements for maintenance have been met. Thus, any factor which affects either directly or indirectly the consumption and assimilation of food and its transformation into tissue may be regarded as having an effect on growth.

The importance of both the quantity and quality of food in affecting the growth of fish has been demonstrated in a number of experimental situations, for example, Pentelow (1939), Brown (1957), Paloheimo and Dickie (1965, 1966a, 1966b), and Warren and Davis (1967). However, it is difficult to demonstrate the importance of food availability as a factor influencing growth under natural conditions unless detailed information is available on the feeding behaviour of the fish and on the relative abundance and accessibility of the prey. At no time during the present investigation did the abundance of prey species appear to be a limiting factor. Since *G. vulgaris* is basically an open-water feeder (Cadwallader 1975a, 1975d), the availability of much of its prey will depend on invertebrate activity patterns and on those factors causing invertebrate drift.

In *G. vulgaris* the proportion of empty stomachs was highest in samples taken during autumn and winter, and lowest in samples taken during spring and summer, when most growth occurred. Metabolic requirements are reduced at low temperatures, so that in temperate regions food consumption may be expected to be less in winter than in summer (the food supply being assumed to be constant). However, within the normal temperature range of a species, the rate of gastric digestion is higher at high temperatures than at low temperatures (Sokolov and Chvaliova 1936, Reimers 1957, Molnár and Tölg 1962a, 1962b, Tyler 1970, Elliott 1972), so that in summer food is generally digested more quickly than in winter. This would tend to increase the number of empty stomachs found in summer if the same amount of food was consumed throughout the year. The rate of gastric emptying and feeding may also be affected by the quantity of food consumed. Windell (1967), Kitchell and Windell (1968), and Tyler (1970) demonstrated that an increased quantity of food in the stomach resulted in an increase in the rate of gastric emptying. Thus, if it is assumed that the feeding chronology of *G. vulgaris* is constant throughout the year (evidence presented by Cadwallader (1975b) suggests that this is so, with the exception of the immediate pre-spawning and spawning periods), the low proportion of empty stomachs in samples taken in spring and summer may be regarded as an indication of an increase in food consumption then.

The effect of temperature on metabolism, food intake, and growth has been demonstrated by a number of workers, for example, Markus (1932), Brown (1946b), Baldwin (1957), Frost and Kipling (1968), Elwood and Waters (1969), and McCormick, Hokanson, and Jones (1972), and under natural conditions changes in growth rate have often been correlated with changes in temperature (Swift 1961, Nikolsky 1963, May, Pinhorn, Wells, and Fleming 1965, Frost and Kipling 1967, Muth 1969, J. E. Johnson 1970).

In *G. vulgaris* most growth occurred when the highest water temperatures were recorded, and growth ceased when water temperatures were low. The importance of the influence of temperature on the length of the growing season was pointed out by Van Oosten (1944). Temperature appeared to affect the length of the growing season of *G. vulgaris*, particularly for age 0+ fish, in that higher temperatures were correlated with earlier spawnings, so that those fish which hatched from early spawnings had a longer growing season than those hatched from late spawnings. The onset of spawning differed by up to 6 weeks in different parts of the Glentui River (Cadwallader 1976a), so that differences in length-frequency distributions in samples from different parts of the river (Fig. 8) were to be expected.

As suggested by the work of L. Johnson (1966), the seasonal growth cycle may be influenced by light acting through changes in day length. Gross, Roelofs, and Fromm (1965), working with green sunfish, *Lepomis cyanellus* Rafinesque, showed that photoperiod had a pronounced effect on food consumption, food conversion efficiency, and growth. *Galaxias vulgaris* is usually active mainly at night and obtains its food when it is active (Cadwallader 1975b). However, maximum growth occurred at a time when nights were shortest and consequently the potential time for food consumption was reduced.

A number of workers, for example, Hile (1936) and Frost and Kipling (1967), have shown an inverse relationship between population density and growth rate. This is normally explained by different degrees of intraspecific competition for food. At high density competition is severe and individual growth rate is reduced. Various interspecific relationships may also affect the rate of growth (Nilsson 1967, Weatherley 1972). Furthermore, Brown (1957), Ivlev (1961), Chen and Prowse (1964), and Chen (1965) described experiments in which it was shown that space factors had an effect on growth; both the total volume of water and the degree of crowding of the individuals (acting independently of competition for food) were thought to be important. Space factors and intraspecific competition for food may be significant for recently hatched *G. vulgaris*, which are gregarious. With adults the situation is different in that direct intraspecific competition for food is reduced by the establishment of feeding territories.

Observations on adult *G. vulgaris* in a laboratory stream tank (Cadwallader 1975e) indicated that though they do not have distinct, patrolled territories, each appears to have a feeding station or a "diffuse station territory" of the type described by Kalleberg (1958). As Kalleberg pointed out, the number of such territories on the stream bed may depend on the topography of the bottom, with more territories potentially available in areas where there are plenty of obstacles (such as boulders) to prevent visual contact between fish. However, as indicated by Chapman (1966), since the supply of drift passing a given point is proportional to water velocity, it is conceivable that drift feeders such as *G. vulgaris* require less space to guarantee adequate food when velocities are high. Since large boulders are usually associated with rapid flows, the two factors probably exert complementary effects on the size and therefore the number of territories. Finally, the physico-chemical condition of the water may also affect growth (Hile 1936).

Growth in *G. vulgaris* under natural conditions may depend on any one, or a combination, of the factors discussed above. Experimental analysis may indicate the importance of some of the major factors in controlling the growth rate, but under natural conditions the growth rate must be considered to be the result of a number of factors, both internal and external, some of which may have an effect only at certain stages of the life cycle.

SUMMARY

In this study of the age, growth, and condition of *Galaxias vulgaris* in the Glentui River, Canterbury, New Zealand, fish were aged by sagittal otoliths and length-frequency distribution analysis. Most *G. vulgaris* belonged to the age groups 0+, 1+, and 2+, a few to the 3+ and 4+ age groups, none to the 5+ age group, and one to the 6+ age group, in its seventh year.

Annual growth in length was estimated by back calculation from otoliths. Length reached at the end of the first year of life was not significantly different between males and females. However, after the first year, growth in length of males lagged behind that of females. The von Bertalanffy equation adequately described annual growth in length of both males and females.

Seasonal growth in length was estimated from monthly changes in the mean length of each age group. Increase in length of both males and females occurred from November to May, and growth ceased from June to October, in winter and early spring. Differences in growth in length were apparent between year classes and between fish sampled in different parts of the river.

Wet weights were obtained from fish subsampled from regular monthly samples. Fish in the 0+ and 1+ age groups of each sex generally gained weight throughout the year, though most weight was added during summer and autumn, at the time when fish in the 2+ and 3+ age groups also gained most weight.

The length-weight relationship was calculated separately for males and females and for age 0+ and older fish of each sex. Since the values of the *b* coefficient for the various groups differed significantly between 2-monthly samples, changes in coefficient *a* could not be used to compare condition at various times of the year. Changes in condition were therefore considered in terms of predicted weight values derived from the 2-monthly regression coefficients calculated for each group. The condition of age 0+ fish increased throughout the growing season. In older fish, both males and females, there was an increase in condition in late spring and autumn and a reduction in condition in early spring and summer. Females were generally in better condition than males. Somatic tissue underwent seasonal changes irrespective of gonad development. The seasonal changes were reflected in the fat deposits overlying the alimentary tract.

Possible factors affecting the growth of *G. vulgaris* are discussed.

ACKNOWLEDGMENTS

This work was done at the Department of Zoology, University of Canterbury, during the tenure of a research fellowship from the New Zealand Ministry of Agriculture and Fisheries. I am grateful to the following, all of whom are members or former members of the staff of the Department of Zoology, University of Canterbury: Professor G. A. Knox for the provision of suitable facilities, Dr D. J. Staples for initial advice on the project, Dr V. L. Benzie for helpful discussion, and Dr V. M. Stout for water analyses. I thank Professor P. A. Larkin, of the University of British Columbia, for the use of a computer programme for fitting the von Bertalanffy equation.

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E. C. KEATING, GOVERNMENT PRINTER, WELLINGTON, NEW ZEALAND—1978

92774H—78G

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