BULLETIN OF MARINE SCIENCE, 54(2): 385–402, 1994

AGE AT MIGRATION FROM THE SEA OF JUVENILE *GALAXIAS* IN NEW ZEALAND (PISCES: GALAXIIDAE)

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ABSTRACT

Daily growth rings begin to form in the otoliths of juvenile galaxiids several days before they hatch. These rings show that life at sea lasts for 103–202 days in *Galaxias maculatus* (N = 99), 93–128 days in *G. fasciatus* (N = 44), 110–155 days in *G. brevipinnis* (N = 70), 113–137 days in *G. argenteus* (N = 10), and 120–136 days in *G. postvectis* (N = 5). Return to fresh water takes place in the spring following spawning the previous autumn–winter. The peak spawning period for *G. maculatus*, *G. fasciatus*, and *G. brevipinnis* appears to be during April to mid May, and perhaps to mid-June in *G. postvectis* and *G. argenteus* (though data for the last two species are meager). The tendency for fish to be smaller at migration towards the end of the migration period is associated with their return to fresh water at a younger age (rather than being caused by slower growth). The semelparous, largely annual life cycle of *G. maculatus*, with its high relative fecundity, small eggs and larvae, is compared with the iteroparous, perennial life cycle of the other species, with lower relative fecundity, and larger eggs and larvae.

At least seven species of *Galaxias* (Pisces: Galaxiidae) are diadromous (McDowall, 1990, 1992), spending part of their lives at sea. There are four such species in Australia, viz. *Galaxias maculatus* (Jenyns), *G. truttaceus* Valenciennes (in Cuvier and Valenciennes), *G. brevipinnis* Günther, and *G. cleaveri* Johnston. Two of these, *G. maculatus* and *G. brevipinnis,* occur also in New Zealand, where three additional species are diadromous, viz. *G. fasciatus* Gray, *G. argenteus* (Gmelin), and *G. postvectis* Clarke. In Patagonian South America, *G. maculatus* is the only species for which diadromy is confirmed (Fulton, 1986; McDowall, 1988, 1990).

Little is known about the reproduction of most diadromous galaxiids, but spawning is probably during autumn and winter; however, it is well known that *G. maculatus* spawns in river estuaries, mostly during autumn, and that the larvae move to sea soon after hatching (McDowall, 1990). Other species are known or thought to spawn in fresh water (Humphries, 1986—*G. truttaceus*; Mitchell and Penlington, 1982—*G. fasciatus*; Koehn and O'Connor, 1992—*G. brevipinnis*). Knowledge of when other *Galaxias* species spawn is limited. There are only two confirmed observations of spawning in other New Zealand diadromous galaxiids (*G. fasciatus*—Mitchell and Penlington, 1982; Mitchell, 1991); other information on spawning is largely anecdotal. Koehn and O'Connor (1992) reported autumn–winter spawning by *G. brevipinnis* in Australia.

The larvae of these species appear also to go to sea soon after hatching (Ots and Eldon, 1975—*G. fasciatus*). After feeding and growing at sea the juveniles re-enter fresh water during spring usually at length of 40–55 mm; they do this in huge, mixed-species shoals at which time they are harvested in New Zealand in the traditional "whitebait" fisheries (McDowall, 1984). They were formerly also fished in Tasmania (Fulton, 1984), and there is a similar, though small, fishery in Chile (Campos, 1973). Some immigration of juveniles may take place over much of the year, and in particular, some "fresh-run whitebait" of *G. maculatus,* have been recorded in rivers in all months (McDowall, 1968). However, in all species much more concentrated movements take place from about August to November (the southern spring).

The age at which juvenile galaxiids return from the sea has long been debated but it has customarily been thought that the upstream spring migrations of juveniles result from spawning the previous autumn/winter, so that the returning fish are about 5–6 months old (Benzie, 1968a; McDowall, 1984, 1990)—though not all agree (Stokell, 1955). Results of limited sampling of juvenile galaxiids from seas around New Zealand (McDowall et al., 1975) suggest that only one year-class is present at any time, and this is consistent with the fish being at sea only from one autumn/winter to the following spring.

In many species of fish, fine striations in the otoliths represent daily growth increments, commonly called "daily growth rings" (Pannella, 1971; Brothers, 1981; Campana and Neilson, 1985; Jones and Brothers, 1987; Radtke, 1989). These rings allow fish age to be estimated.

Many diadromous fish spend their larval and juvenile life at sea and return to fresh water later in life (McDowall, 1988). They are difficult to study while at sea, but daily growth rings in the otoliths of fish returning to fresh water from the sea make it possible to estimate age, growth rates, and growth patterns (Eckmann and Rey, 1987). For the galaxiid species, for instance, counting daily growth rings enables resolution of the issue of time spent at sea and age at migration back to fresh water, discussed above. Furthermore, if the age of galaxiid juveniles at migration can be determined, it is possible to estimate hatching date by back calculation, and thereby clarify understanding of the spawning season.

Preliminary analysis of galaxiid otoliths showed that rings, comparable with "daily growth rings" described in other fish, do occur. It was therefore concluded that study of galaxiid whitebait juveniles, using daily growth rings as estimators of age, was worthwhile.

Many questions about life histories and ecologies of these fish can be answered using daily growth rings. The primary one is: 1. **At what age do the various species of *Galaxias* migrate from the sea; i.e., is age at migration about 5 to 6 months as has been widely postulated, or is it distinctly different?** Size at migration from the sea varies, with differences between species, as well as differences within species at different times and geographical locations. Thus in addition to the general question (1. above) additional issues can be examined: e.g., 2. The five diadromous New Zealand galaxiids differ in size at migration (McDowall and Eldon, 1980): **How does age at migration equate with the different sizes of the juvenile fish at migration?** 3. Particularly towards late spring, the size of migrating fish declines substantially but it is not known whether these fish are younger or slower growing (McDowall and Eldon, 1980): **How does age at migration equate with seasonal differences in size?**

In addition to these variations, it is known that galaxiid juveniles vary in size both geographically (McDowall, 1965), and between seasons (McDowall and Eldon, 1980) raising the likelihood of geographical and seasonal variation in age at migration.

This leads to the general question, viz: **Do differences in fish size relating to species, time, and location reflect different growth rates or different ages at migration, or perhaps both?**

This paper analyses age and size at migration by examining *inter*specific differences, and *intra*specific chronological differences in size at migration. The questions of interseasonal and geographical variation require careful collection of substantial, long time-series of fish in more than one season and from diverse locations, and are not addressed here.

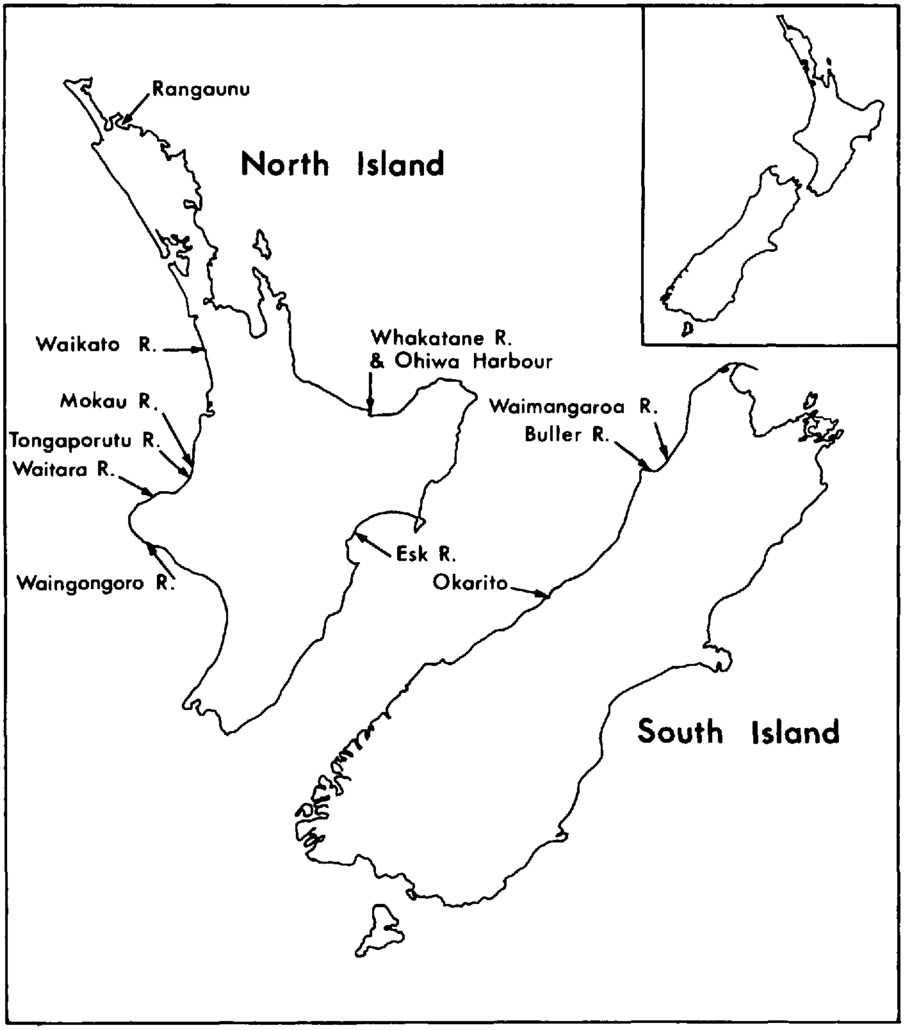

Figure 1. New Zealand locations from which fish were collected for otolith studies.

METHODS

Galaxiids whitebait juveniles were collected from widespread New Zealand locations (Fig. 1) during 1985–1986, and at various times during their migration. Samples were either studied fresh, were frozen, or stored in 70% ethanol. Time series of samples were collected from one locality, to provide material for the study of within-season, chronological variation in age at migration. In particular, whitebait of *G. maculatus* were collected during 1986 at monthly intervals from three small streams flowing into Ohiwa Harbour in northeastern New Zealand (Bay of Plenty). Care was taken to select only still-transparent and obvious fresh-run fish from each sample (after some days in fresh water body pigmentation develops in the young fish, which can be thereby distinguished from fresh-run fish—McDowall and Eldon, 1980). Efforts were made to obtain multi-species samples to provide data on interspecific variation in size at migration (Fig. 1; Table 1).

Two methods were used to count daily growth rings in otoliths. The first (E.B.B.) is described fully elsewhere (Brothers, 1987) and was based on the use of a light microscope fitted with video-viewing systems and polarized light sources. Otolith rings were counted from the video monitor at a maximum magnification of 2,300×. Some material was also examined using scanning electron microscopy (see Jones and Brothers, 1987, for methods).

Table 1. Data on age and size of whitebait of five species of *Galaxias* from diverse New Zealand locations (see Fig. 1)

Location and date		*Galaxias maculatus*			*Galaxias brevipinnis*			*Galaxias fasciatus*		
		SL (mm)	No. of rings	Day of first ring*	SL (mm)	No. of rings	Day of first ring*	SL (mm)	No. of rings	Day of first ring*
Rangunu Harbour tributary	Mean	38.00	106.1	144.9	—	—	—	32.38	95.2	160.8
12–13 Sept. 1985	Range	35.9–41.1	103–110	146–153	—	—	—	30.5–33.7	93–98	157–163
	SD	2.07	2.69	—	—	—	—	0.98	2.09	—
	N		9						10	
Whakatane River	Mean	—	—	—	40.34	115.7	160.2	—	—	—
3 Oct. 1985	Range	—	—	—	37.8–41.8	110–124	152–165	—	—	—
	SD	—	—	—	0.99	4.05	—	—	—	—
	N					20				
Waikato River	Mean	44.01	156.40	99.6	43.46	128.0	128.0	35.67	97.5	158.5
13 Sept. 1985	Range	41.8–47.6	116–195	61–140	41.0–45.5	124–132	124–132	34.7–36.9	92–101	155–163
	SD	1.73	23.58	—	1.68	3.35	—	0.69	2.77	—
	N		10			5			10	
Waikato River	Mean	—	—	—	43.64	125.6	142.4	—	—	—
25 Sept. 1985	Range	—	—	—	42.8–44.7	112–138	130–156	—	—	—
	SD	—	—	—	0.74	8.31	—	—	—	—
	N					5				
Mokau River	Mean	45.24	120.05	110.5	—	—	—	—	—	—
15 Sept. 1985	Range	44.0–47.6	135–173	85–123	—	—	—	—	—	—
	SD	1.43	10.96	—	—	—	—	—	—	—
	N		10							
Tongoporutu River	Mean	45.63	177.0	142.0	—	—	—	—	—	—
15 Nov. 1985	Range	43.6–47.1	138–203	116–181	—	—	—	—	—	—
	SD	1.22	19.32	—	—	—	—	—	—	—
	N		10							
Waitara River	Mean	44.68	179.1	78.9	40.11	122.40	135.60	36.09	115.86	142.1
15 Sept. 1985	Range	41.4–47.8	145–200	58–113	36.5–44.3	115–132	126–142	34.4–37.4	108–123	135–150
	SD	1.79	20.09	—	2.56	4.92	—	0.87	5.69	—
	N		10			10			7	
Waingongoro River	Mean	44.95.	152.70	105.3	44.66	126.20	131.80	36.39	112.43	145.6
15 Sept. 1985	Range	43.0–47.8	129–169	89–129	43.9–47.5	123–129	129–135	35.3–37.3	103–128	130–155
	SD	1.91	12.22	—	1.34	2.14	—	0.78	7.09	—
	N		10			10			7	

Table 1. Continued

Location and date		*Galaxias maculatus*			*Galaxias brevipinnis*			*Galaxias fasciatus*		
		SL (mm)	No. of rings	Day of first ring*	SL (mm)	No. of rings	Day of first ring*	SL (mm)	No. of rings	Day of first ring*
Esk River	Mean	43.21	168.10	100.9	43.71	132.30	136.7	38.30	124.50	144.5
25–26 Sept. 1985	Range	41.1–45.1	146–195	74–123	43.4–44.9	115–142	127–154	38.1–38.5	123–126	143–140
	SD	1.08	13.99	—	0.54	7.95	—	0.20	—	—
	N		10			10			2	
Esk River	Mean	43.20	155.50	154.5	41.82	141.50	168.5	36.11	118.88	191.1
5–6 Nov. 1985	Range	41.1–45.4	141–173	137–166	39.0–44.6	135–155	155–177	34.7–37.5	110–138	172–200
	SD	1.35	9.12	—	1.40	5.90	—	0.72	9.20	—
	N		10			10			8	
Waimangaroa River	Mean	45.72	150.50	117.5	—	—	—	—	—	—
23 Sept. 1985	Range	44.5–47.4	140–169	99–128	—	—	—	—	—	—
	SD	0.95	7.77	—	—	—	—	—	—	—
	N		10							
Buller River	Mean	39.81	156.70	147.7	—	—	—	—	—	—
26 Nov. 1985	Range	37.8–42.5	129–180	130–170	—	—	—	—	—	—
	SD	1.66	17.32	—	—	—	—	—	—	—
	N		10							
		Galaxias postvectis			*Galaxias argenteus*					
		SL (mm)	No. of rings	Day of first ring*	SL (mm)	No. of rings	Day of first ring*			
Cemetery Creek Okarito	Mean	33.54	131.25	—	38.44	120.0	211.0			
27 Nov. 1985	Range	30.0–34.5	20–136	—	36.0–39.6	113–137	194–218			
	SD	1.77	6.53	—	1.03	8.06	—			
	N		5			10				

* Back-calculated from number of rings counted and capture date.

The second (C.P.M.) used monochrome photography of otoliths through an oil-immersion light microscope. Photographic negatives were projected onto a field of white paper and the rings marked onto the paper as a permanent record. Where the focus of the rings differed in depth, a series of photographs was taken. These were correlated by use of distinctive markings, such as flaws in the otoliths, to provide counts of rings. Two photographs normally provided a complete series of rings for whitebait juveniles. Some otolith preparations had gaps in the rings, normally towards the margins, and occupying 5–15% of the otolith radius. Gaps were bridged by assuming that mean ring width for the remainder of the otolith applied to the gap. Preparations with even larger gaps were discarded; and if possible the other otolith from that fish was used for age estimation.

Both observers (E.B.B. and C.P.M.) employed various techniques for mounting and grinding otoliths to improve ring visibility (Brothers, 1987).

Growth of otoliths results in greater elongation along the anterior axis. Growth rings were easiest to resolve and count in that direction because they were more widely and evenly spaced (Fig. 2B). Counts were therefore made along the longest axis, between the otolith margin and an intense band around the nucleus which is referred to here as the "hatch check," so-called because the diameter of the circle known as the "hatch check" corresponds to the diameter of otoliths of freshly hatched larvae (Fig. 2A, B).

VERIFICATION OF DAILY GROWTH INCREMENTS AND THE ONSET OF RING FORMATION

Known-age larvae were obtained from hatching eggs in captivity and the fish reared (Mitchell, 1989). Otoliths from captive-reared fish were more difficult to read than those of wild fish as they had finer and less regular increments especially at the innermost regions (Fig. 2B). There was also uncertainty about hatch date for some fish for which a range of up to 7 days is possible.

Studies of larval galaxiids showed that otolith growth begins before hatching (as was also shown for the salmoniform *Plecoglossus altivelis* from Japan—Tsukamoto et al., 1987). Benzie (1968a) illustrated developing embryos of *G. maculatus* and the otolith is clearly visible. If the supposed "hatch ring" is truly related to hatching, then up to 12 rings observed inside this ring can be attributed to pre-hatch growth (C.P.M.). These pre-hatch rings tended to be very fine and difficult to count reliably (see Fig. 3A). High magnifications possible with SEM revealed fine rings at the centre of otoliths that are unlikely to be counted using light microscopy (E.B.B.), suggesting that counts probably underestimate age (Fig. 3B). Uncertainty of counts, plus some ring formation before hatching contributed to errors in ages determined from ring counts. Counts of rings from different samples of known-age larvae were carried out by E.B.B. and C.P.M.

Data derived by E.B.B. (Fig. 4) show increments plotted against estimated days from hatching in the larvae of seven *G. maculatus.* The plot contains three incremental figures: 1. cross—the minimum count estimate; 2. square—the maximum count; and 3. triangle—the maximum count plus seven increments (added because of uncertainty of hatch date up to seven days, noted above). Regardless of which of these sets of counts is accepted, but especially for the maximum count and the maximum plus seven count, there is a good similarity to a linear, 1:1 relationship between expected increments (based on hatch date) and observed increments—most data points lying slightly below the 1:1 plot.

Data obtained by C.P.M. on 137 fish of certain hatching dates are shown in Figure 5. These also show a linear relationship between age and number of rings. The number of rings counted is again lower than the age-since-hatch in days, and this can be attributed to the difficulties in identifying all growth rings. In captive-reared fish the disparity between observed number and the 1:1 relationship between known and observed increases with age owing to the same causes. This disparity may reach 20 or more days at a known age of 150 days so that errors in age estimation of this magnitude may occur. However, difficulties in reading

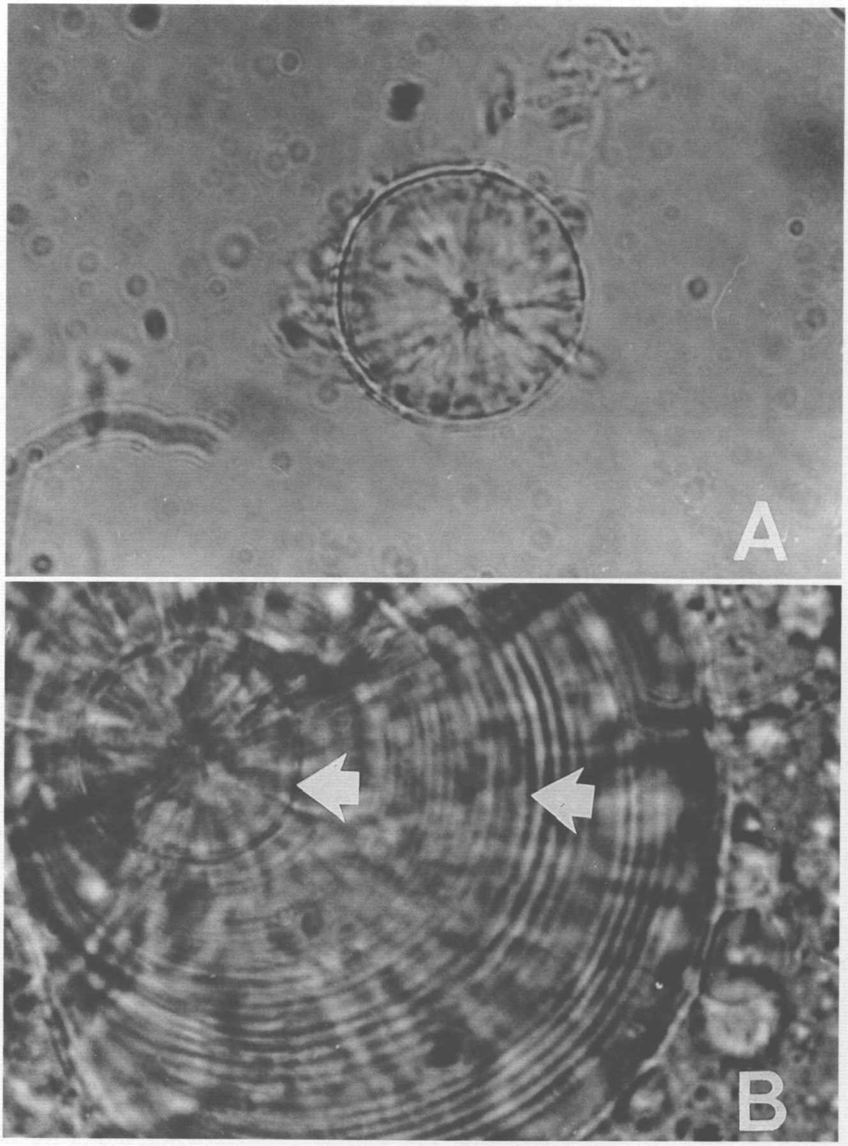

Figure 2. A. Otolith of newly hatched *Galaxias maculatus*; this otolith corresponds to the portion of the otolith indicated by hatch check (left arrow). (×1,250). B. Otolith of a captive reared *Galaxias maculatus*, showing more rapid growth along one dimension providing more widely spaced growth rings; right arrow shows point at which growth was stimulated by extra feeding; left arrow shows margins of "hatch check" (×1,250).

otoliths of captive-reared fish may have contributed to this error. Nevertheless, these results indicate that formation of daily increments is highly likely and give confidence that in studies of juvenile fish, at least of *G. maculatus* (ca. 45–50 mm long), age in days can be estimated from counts of otolith growth increments.

No similar data are available for verifying daily growth rings in other species of *Galaxias*, but for the rest of this account a similar relationship between age and daily growth increments is assumed.

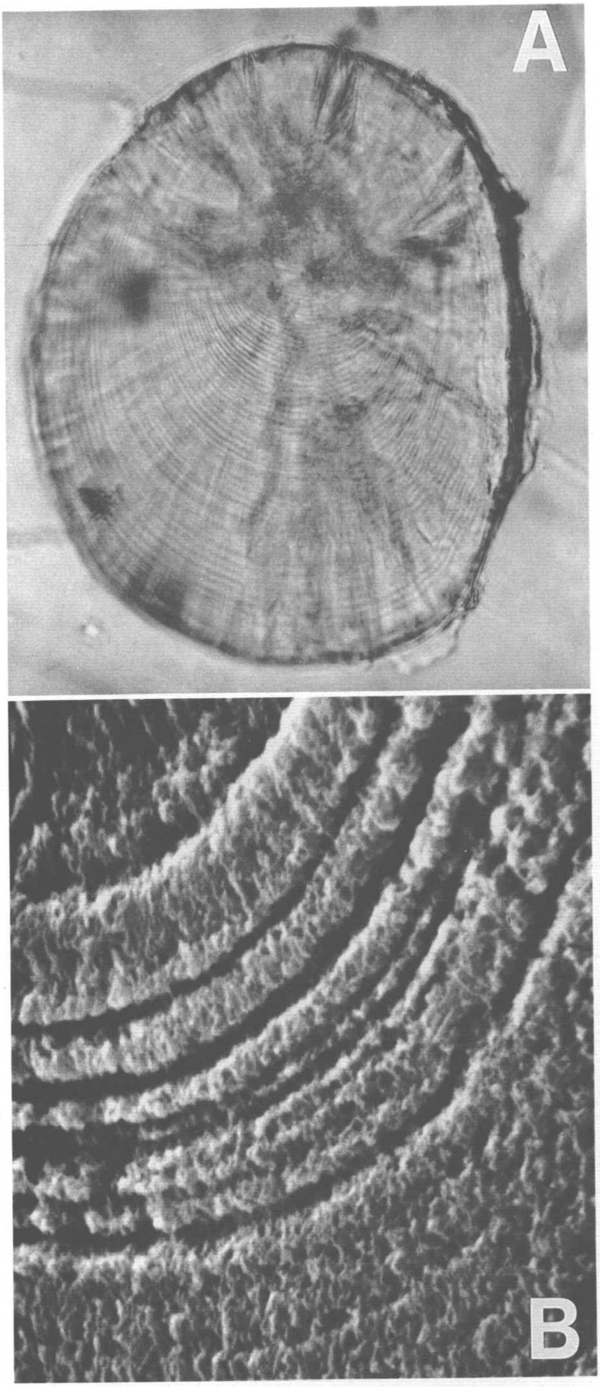

Figure 3. A. Otolith of a 62-day-old laboratory reared *Galaxias maculatus* (×1,000). B. SEM of centre of otolith of *Galaxias maculatus*, showing fine rings unlikely to be revealed by light microscopy (×10,000).

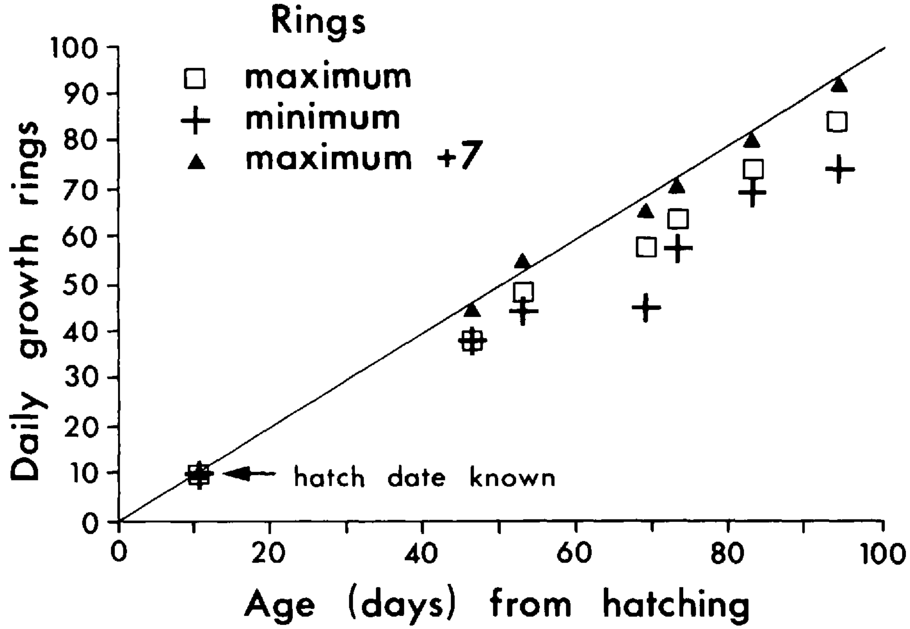

Figure 4. Counts for seven larvae of *Galaxias maculatus* of approximately known age, counted by E.B.B.; square—maximum count; cross—minimum count; triangle—maximum count plus seven rings; line is expected relationship between days and rings, assuming that rings begin formation at hatching.

INTERSPECIFIC VARIATION IN AGE AND SIZE AT MIGRATION

Age estimates at migration from daily growth rings for up to 10 locations per species are shown in Table 1. These data support the conclusion that *Galaxias* juveniles return to fresh water during the first spring after hatching.

Age at migration in *G. maculatus* was found to be highly variable, with sample means ranging from 106.1 to 179.1 days, and overall age varying from 103 to 203 days (range 100 days). This variation probably is due in part to problems in precisely reading otoliths, but also to this species' known very extended spawning period (McDowall, 1968, 1990). It may also be a product of the large number of samples examined, though within-sample variation was also high (mean within-sample range 46.5, range 8–80 days).

Age at migration for *G. fasciatus,* gave sample means of 95.2 to 124.5. Overall age varied from 93 to 138 days (range 45 days). Within-sample range was lower (mean 12.4, varying from 4 to 26 days). For *G. brevipinnis* sample mean age varied from 115.7 to 141.5, with overall age varying from 110 to 155 days (range 46 days). Within-sample range was, again, low (mean 15.8, varying from 2 to 28 days). Based on sparse data, age at return is about 120 days in *G. argenteus* (10 fish) and 131 days in *G. postvectis* (5 fish).

Size at migration differs between species. At any time and location, *G. maculatus* is typically larger than *G. brevipinnis,* which is, in turn, larger than *G. fasciatus* (McDowall and Eldon, 1980). These size differences were consistent with observed differences in age: the species that are larger at migration are older (Table 1; Fig. 6). Differences between species in size at migration are therefore due, at least in part, to the species that have larger juveniles spending longer at sea.

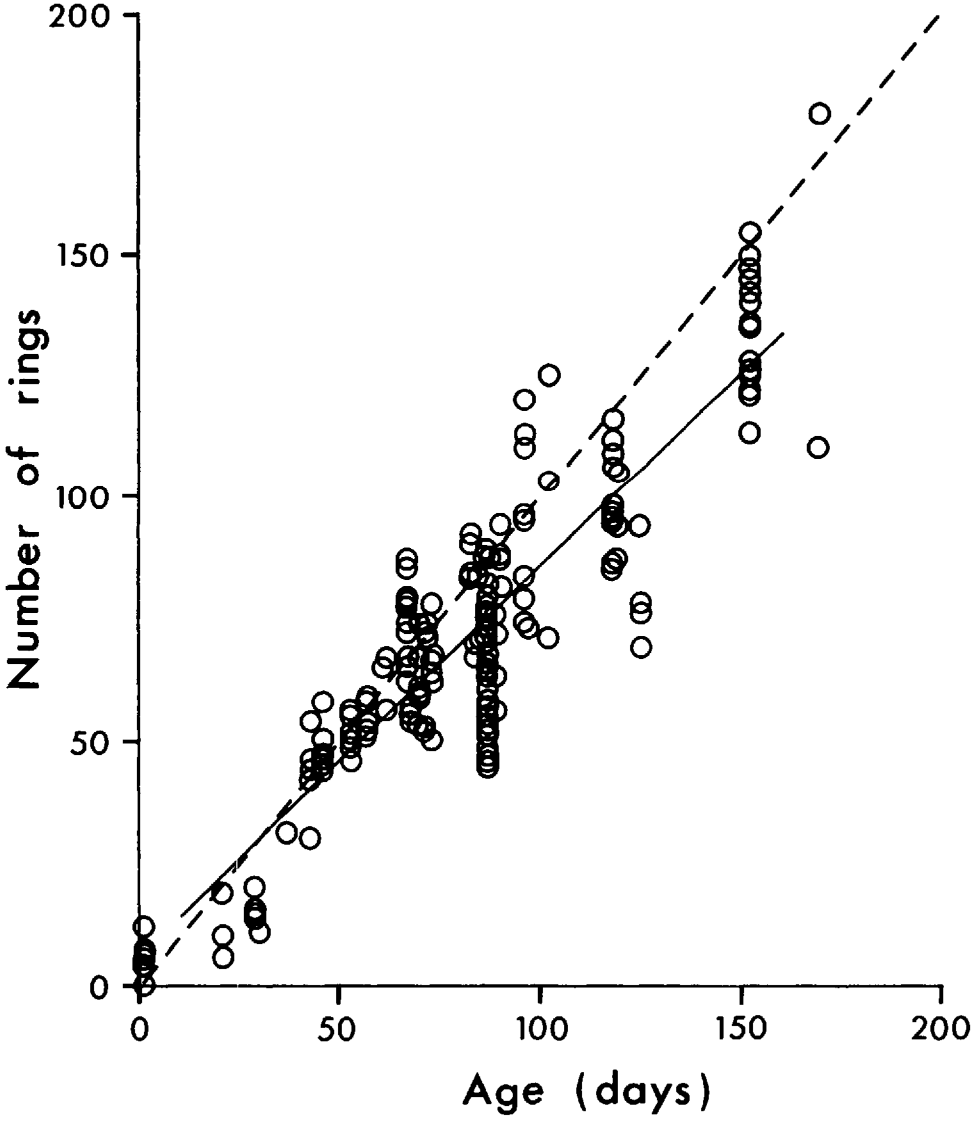

Figure 5. Counts for 137 larvae of *Galaxias maculatus* of known age, counted by C.P.M.; the data show a good linear and close to 1:1 relationship between rings counted and known age in days.

TEMPORAL VARIATION IN SIZE AT MIGRATION

Studies have shown that size of galaxiid juveniles at migration varies seasonally, with fish tending to be smaller at later dates (though there is also quite substantial day-to-day variation in size—McDowall and Eldon, 1980). A temporal series of fish was collected from several small streams flowing into Ohiwa Harbour, in the Bay of Plenty. Figure 7 shows a decline in size during the spring for both fresh-run whitebait and immediate post-migration whitebait (inanga). Age of whitebait in this time series (Fig. 8) shows that mean age falls even more markedly than size, dropping from 150 days in September to 116 days in October and only 94 days in November.

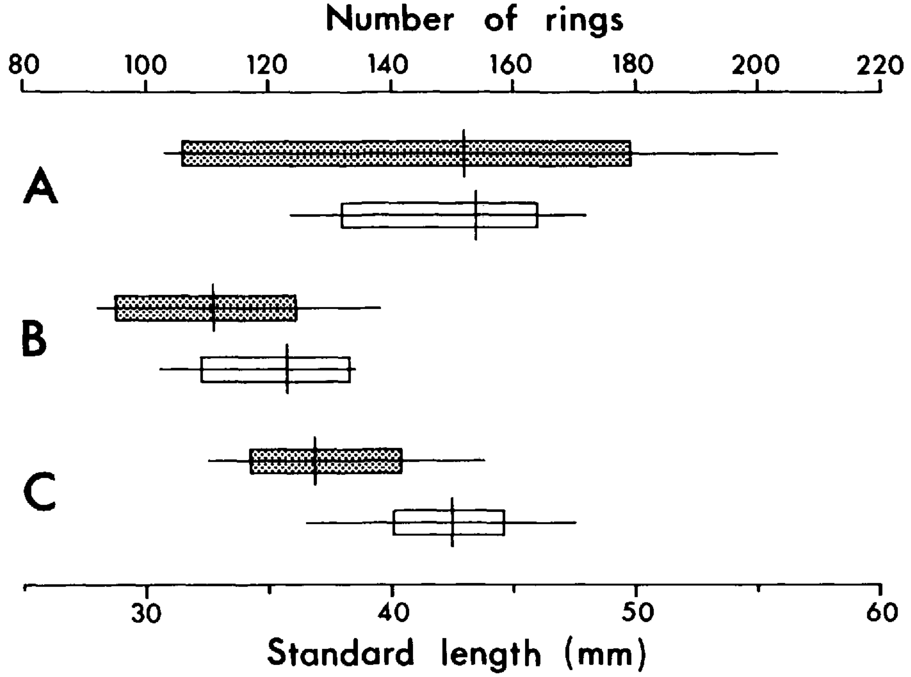

Figure 6. Relationship between age and size at migration for the three principal diadromous whitebait species in New Zealand: A, *Galaxias maculatus*; B. *G. fasciatus*; C. *G. brevipinnis* (shaded = no. of rings, unshaded = fish length; each bar gives range, standard deviation and mean).

Hatching Date

Life cycles in diadromous galaxiids are based around a winter at sea, followed by growth in fresh water for one summer (*G. maculatus*) or several years (remaining species—McDowall, 1990). Although the general timing of spawning and hatching in all species is broadly similar (autumn–winter), details differ between *G. maculatus, G. fasciatus,* and *G. brevipinnis* and hatching dates in the three species did not synchronize (Figs. 9, 11, 12). Tidally controlled spawning and hatching are known in *G. maculatus,* though some hatching may also depend on flooding (presumably when flooding reimmerses fully mature eggs before a spring tide—Benzie, 1968b; McDowall, 1968, 1990). *G. fasciatus* is thought to spawn at sites where terrestrial development occurs, but hatching probably depends on reimmersion of the eggs by stream flooding events (Ots and Eldon, 1975). The same has been shown for *G. brevipinnis* in Australia (Koehn and O'Connor, 1992) and is likely true in New Zealand.

If growth increments in otoliths are laid down on a daily basis, as the data for *G. maculatus* suggest, hatch dates can be estimated. Recognizing that there are potential errors of 5–10 or even more days the data nevertheless provide strong indications of spawning season.

The date for the hatch ring (Fig. 2), given as the number of days in the calendar year after 1 January, is shown for each sample in Table 1. Thus, in *G. maculatus* the estimated sample mean birth dates are on days 79–155 (mid-March to early June); for *G. fasciatus* days 142–196 (mid-May to mid-July); for *G. brevipinnis* days 131–169 (early April to mid-June); for *G. postvectis* day 200 (mid-July);

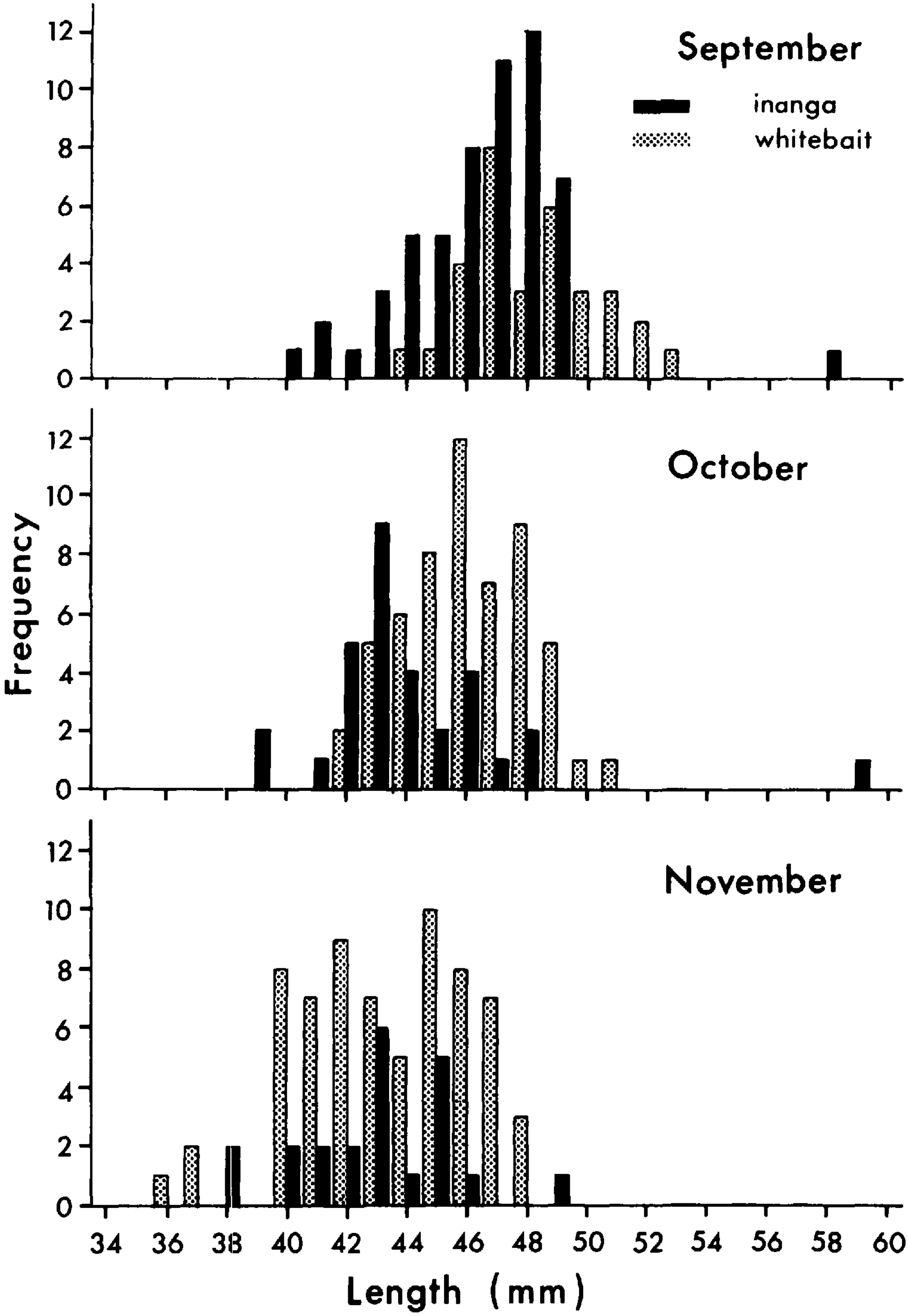

Figure 7. Seasonal change in size of whitebait of *Galaxias maculatus* at migration into Ohiwa Harbour streams, 1986.

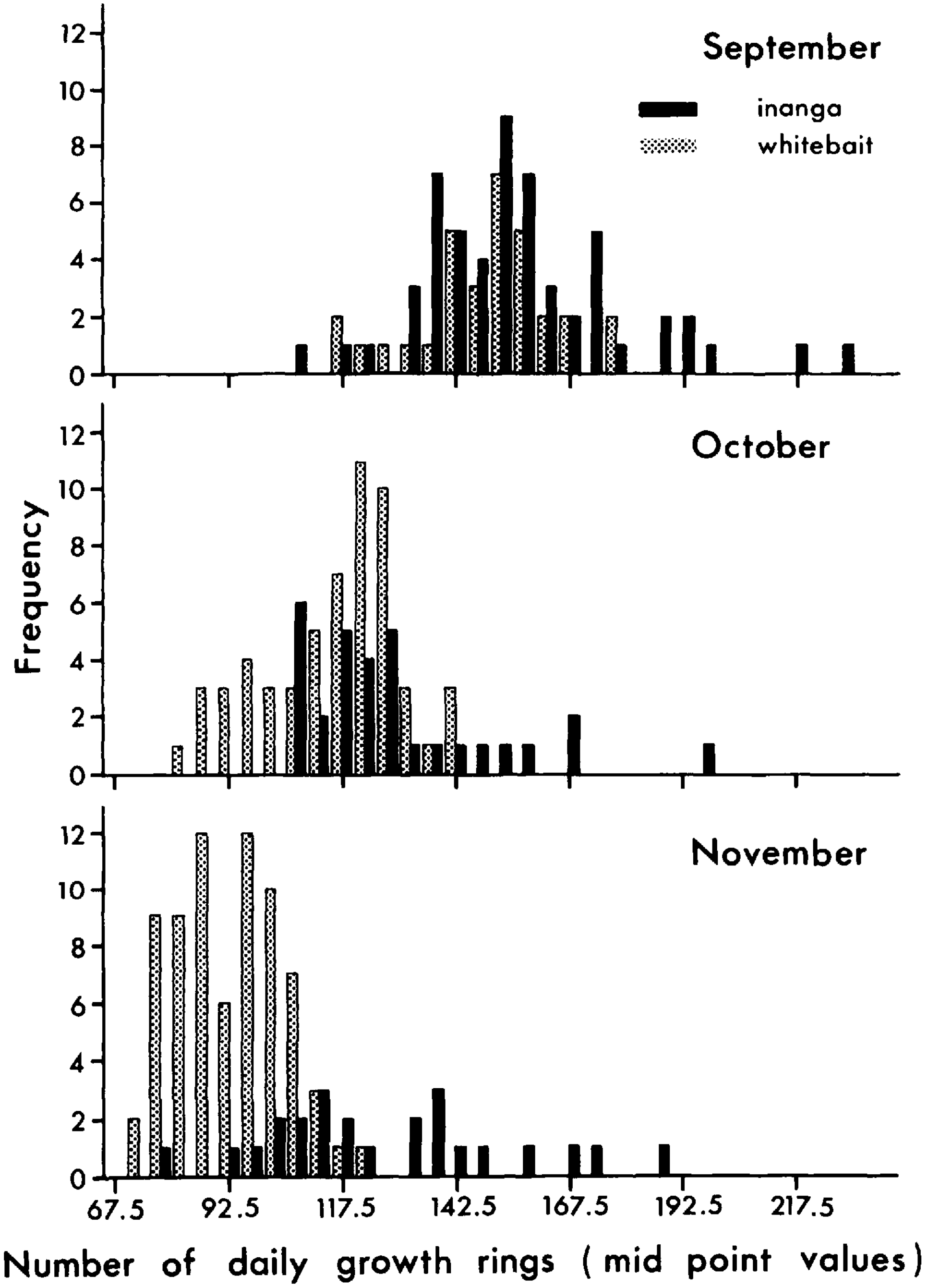

Figure 8. Seasonal change in age of whitebait of *Galaxias maculatus* at migration into Ohiwa Harbour streams, 1986.

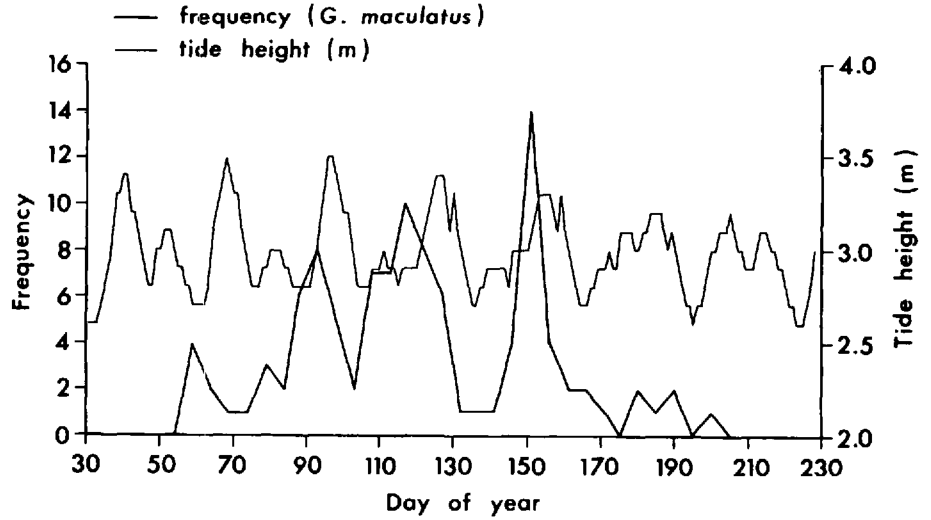

Figure 9. Relationship between hatching date and spring tidal patterns in 109 *Galaxias maculatus* from diverse New Zealand localities (from Table 1).

and for *G. argenteus* days 211–212 (mid-July—the data for these last species, again being very meager and no more than general indicators of hatch date). Judging by developmental rates known for *G. maculatus* (Benzie, 1968a; McDowall, 1968) spawning date would be about 15–40 days earlier than hatch date (depending on temperature).

G. maculatus has a spawning cycle based on lunar and tidal rhythms (Burnet, 1965; Benzie, 1968b). The eggs are laid amongst supratidal, estuarine vegetation and develop largely out of the water amongst the damp herbage there. Combining a New Zealand-wide data set of age data for 109 fish (Table 1), and smoothing with a 5-day age class centered on peak spring tides (N.Z. Nautical Almanac, 1985), gave a cyclical pattern of hatching (Fig. 9). These data suggest that most hatching occurs as tides increase towards spring peaks.

Studies on *G. maculatus* spawning grounds have shown that mature eggs usually hatch when first flooded, when the height of the tides each day is still increasing towards peak spring tide (Mitchell, 1989). An exception in our data was the peak at 117 days (27 April). Over half the Waimangaroa and Mokau samples hatched on this cycle, whereas the importance of this cycle to the other rivers was less. Hatching at Ohiwa shows a peak at about 140 days, and this appears to have been precipitated by a rainfall/flood event prior to a spring tide (Fig. 10).

Data for hatching in *G. fasciatus* appear to be synchronous but almost unimodal, and the same appears true in *G. brevipinnis*—a major peak is followed 35–40 days later by a secondary hatching pulse (Figs. 11, 12). If spawning and hatching events in *G. fasciatus* and *G. brevipinnis* are related to floods then, with additional data, correlations between hatching and flood events should be possible. The peak hatching period in *G. brevipinnis* and *G. fasciatus* should depend on flood events during the late autumn and early winter.

The peak hatching period for *G. maculatus* was over days 110 to 170 (mid-April to mid-June). In *G. brevipinnis* it was early May, whereas in *G. fasciatus* it was early June. Thus, allowing 20 days from spawning to hatching at the beginning of the season, and 30 days at the end (development will take longer as

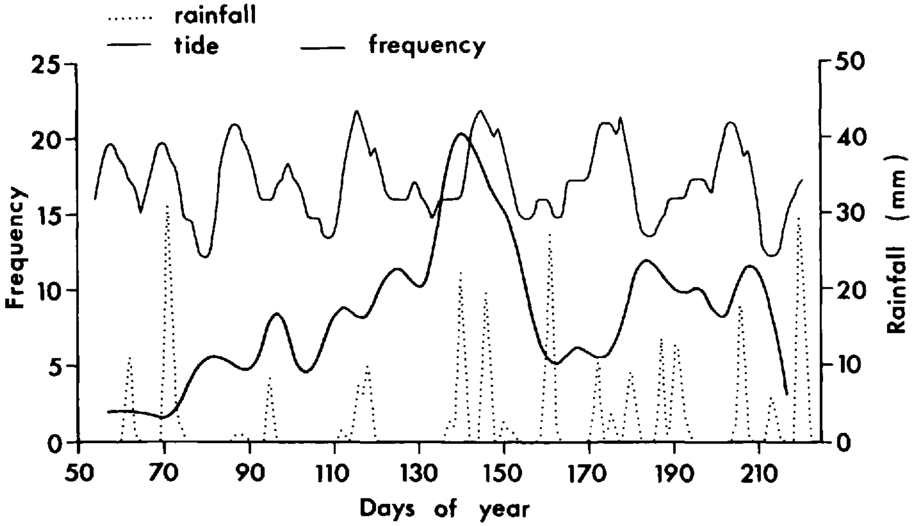

Figure 10. Relationship between number of *Galaxias maculatus* eggs hatching, and date, rainfall and tide, data smoothed by aggregating 5-day age classes, and showing a major hatch pulse centered on day 140, corresponding to a significant rain event.

cooler winter temperatures ensue—see Benzie, 1968b), it can be concluded that April through mid-May is the peak spawning time for these three galaxiids. Spawning in *G. argenteus* and *G. postvectis* may be a little later, perhaps early to mid-June.

Estimated spawning dates are generally consistent with the broad time period over which *G. maculatus* is known to spawn (McDowall, 1968, 1990), and are not inconsistent with what little is known about maturity and spawning in *G. fasciatus* (Hopkins, 1979b; Mitchell and Penlington, 1982; Mitchell, 1991; Ots

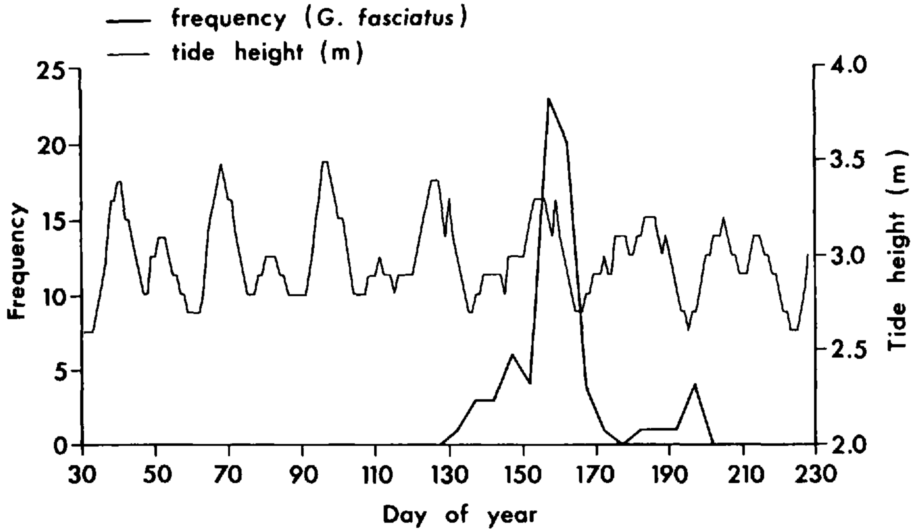

Figure 11. Estimated hatching date for 44 *Galaxias fasciatus* from diverse New Zealand locations (Table 1).

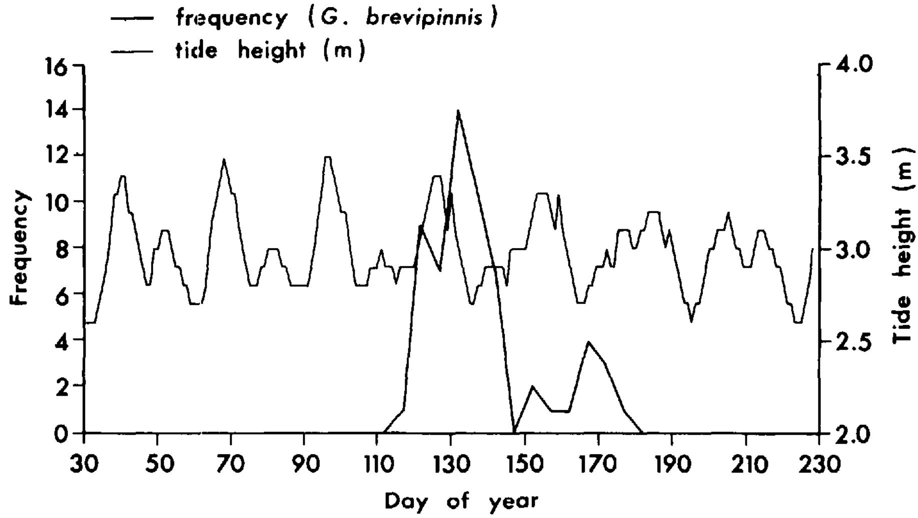

Figure 12. Estimated hatching date for 70 *Galaxias brevipinnis* from diverse New Zealand locations (Table 1).

and Eldon, 1975) and *G. brevipinnis* (McDowall, 1990; Koehn and O'Connor, 1992). Spawning was predicted to occur in autumn or early winter in the other two species on the basis of observations of mature and ripe fish (McDowall, 1990); estimations of hatching times from daily growth rings suggest that spawning date is consistent with these predictions.

LIFE HISTORY AND EVOLUTIONARY ISSUES RELATING TO AGE AT MIGRATION

Intense runs of galaxiid whitebait begin some time during July–August and decline about mid–late November. However in *G. maculatus*, about which there is much more information than for the other species, some whitebait enter fresh water in every month of the year (McDowall, 1968), and this may prove to be true for other species as well.

There is an interesting relationship between egg size, larval size at hatching, whitebait size at migration, and age at migration (Table 2): In *G. maculatus*, small eggs produce small larvae which stay at sea longest and return as the largest whitebait, which mature and spawn soonest (age one) and at smallest size (ca. 65–80 mm); and they are semelparous, dying after spawning; the subadults and adults are shoaling and open-living (McDowall, 1990).

By contrast, *G. fasciatus*, and probably the other diadromous species, have larger eggs which produce larger larvae. Their life at sea is briefer, they return

Table 2. Influence of egg size on size and growth of whitebait

Species	No.	Egg diameter (mm)	Larval length (mm)	Whitebait length (mm)	Mean time at sea (days)	Growth rate (mm·day^{-1})
Galaxias maculatus	42	1.35	7.1	44	159	0.23
Galaxias fasciatus	42	2.00	9.0	35	107	0.24
Galaxias argenteus	15	1.96	9.5	39	119	0.25

to fresh water at a smaller size, and delay maturity and spawning until older and larger (at least age two in males and four in females—Hopkins, 1979a, 1979b); they are repeat (iteroparous) spawners over several to many years and the subadults and adults are more cryptic and solitary in habit. In spite of these differences, growth rates at sea are similar for all three species. The risks for survival at sea are assumed to be similar.

Presumably, *G. maculatus* has adopted a high-risk life style with a tendency for total commitment to a single spawning event. It produces more, smaller eggs per unit body weight, takes longer advantage of the highly productive feeding environment of the oceanic plankton, returns to fresh water at a larger size, matures as rapidly as possible to minimise mortalities in fresh water, and spawns and dies.

The other species also take advantage of the productive marine plankton but spend less time there. They place emphasis on getting back sooner into freshwater habitats. There they settle down for a longer-term existence, growing to a much larger size and having higher absolute fecundity; these are repeat spawners over a longer period, and they invest in relatively fewer, larger eggs and thus larvae.

These indicative conclusions form the basis for additional studies of life history strategies in these species. Detailed life tables are needed to provide further data on such parameters as age, size, relative mortalities relating to age and sex, fecundity, egg and larval size, etc. Data on some of these points are available. Hopkins (1979a), for instance, showed that in *G. fasciatus* there is differential sexual maturity and mortality which leads to later female maturity and a predominance of females amongst the larger, older fish. This is consistent with early maturing males providing more than enough sperm for fertilization—thus, they mature earlier, foregoing larger size and greater age while females adopt a strategy of increased fecundity in later maturing and larger females. Similarly, although *G. maculatus* is an essentially semelparous and annual species, the few fish that do survive until age two or three are invariably females (Burnet, 1965). Given this flexibility, *G. maculatus* is successful in its annual semelparous life cycle and only remnants of the tendency for a longer life and iteroparity persist in this species.

ACKNOWLEDGMENTS

We are grateful to the various whitebaiters who generously provided samples from their catches, and which form the basis for much of this study. The figures were drawn by G. Kelly. Two anonymous referees made particularly helpful comments on the text. Completion of this work was funded by the N.Z. Foundation for Research, Science and Technology.

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DATE ACCEPTED: February 22, 1993.

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