# SOME ECOLOGICAL ASPECTS OF THE SPAWNING BEHAVIOUR AND EARLY DEVELOPMENT OF THE COMMON WHITEBAIT,

## GALAXIAS MACULATUS ATTENUATUS (JENYNS)

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## INTRODUCTION

It may seem unorthodox to begin a paper that purports to describe the ecology of the early stages of the fish, *Galaxias maculatus attenuatus* (Jenyns), (taxonomy revised by Stokell, 1966), with a lengthy description of its breeding habits, but this is necessary; the adults select their breeding sites and so set the conditions for the development of the young.

The spawning habits of *G. m. attenuatus* are not commonly known, yet they were the subject of accounts by Captain Hayes (1930, 1931, 1932) and have also been mentioned by Burnet (1965). Scott (1938) studied the biology of the Tasmanian subspecies of *G. maculatus* and Pollard (1966) described the breeding habits of a land-locked population in Victoria, Australia. At present we cannot be sure if Pollard's population corresponds with either the New Zealand or Tasmanian subspecies as described by Stokell (1966).

Briefly, the life cycle of *G. m. attenuatus* is as follows: Great shoals of ripe adult fish gather in the freshwater streams in which they have become sexually mature during summer. They begin a migration downstream so that they reach areas of tidal influence and eventually spawn communally in estuaries at the peak of spring tides between early January and early May. The present study was undertaken to examine the timing of this process and to attempt to find the factors that could trigger off the migration. I have also tried to link the above behaviour with certain features of embryology and development. The paper falls into three sections: a description of the study area and spawning behaviour, an account of the characteristics of the spawning area, and a discussion of the factors affecting the development of the eggs.

## STUDY AREA AND METHODS FOR OBSERVATION OF SPAWNING HABITS

This study was carried out in only one area, Saltwater Creek, which runs into the Ashley River estuary north of Christchurch, in Canterbury. The particular stream runs into Saltwater Creek beside the Main North Road bridge, and a diagram of the area is given in Figure 1. All areas submerged at normal spring tides are within the dotted contour, the present spawning area is marked in diagonal lines and the past, additional, extensive spawning area (which was destroyed when a new bridge was built) is shown in broken hatching.
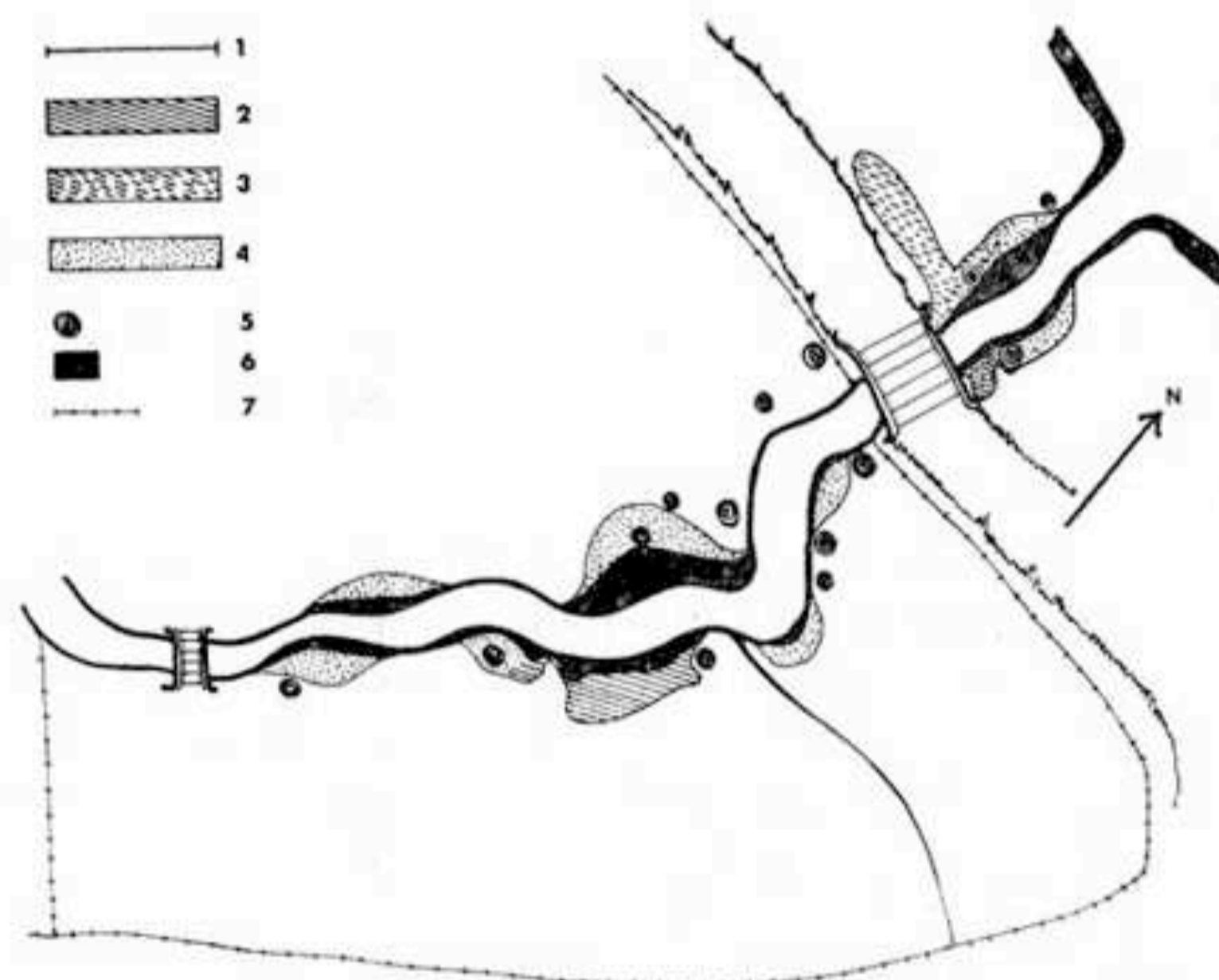


FIGURE 1. *Saltwater Creek spawning area.*
KEY
1. Scale — 3 metres.
2. Present spawning areas.
3. Past spawning areas.
4. Areas apparently suitable for spawning.
5. Tree.
6. Estuarine area of bank.
7. Fence.

The areas within the contour are all alike in that they are lower than those outside and have a gentle upward slope (0 to 10 degrees) until the inner edge of the contour is reached, when the rise is usually about 30 to 60 degrees. A pasture grass and clover mixture covers the ground almost down to the bank of the river. Saltwater influence is clearly indicated by the associated vegetation which

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is usually a small sedge (*Scirpus* sp.) and by the fauna which is entirely composed of saline-tolerant species. A salt-intolerant fauna (earthworms, spiders, collembola and nematodes) was always found in the pasture, even among the eggs.

During 1959–62, shoals of fish moving down to spawn were caught in a seine net spanning a narrow part of the stream. These catches were made as the tide dropped. The sex ratio was calculated for spawning shoals in different months for comparison with the ratio on the feeding grounds inland.

Naturally spawned eggs were collected by cutting out grassy slabs (turfs) and enclosing these in plastic bags. Artificially spawned eggs were used to obtain the earliest developmental stages.
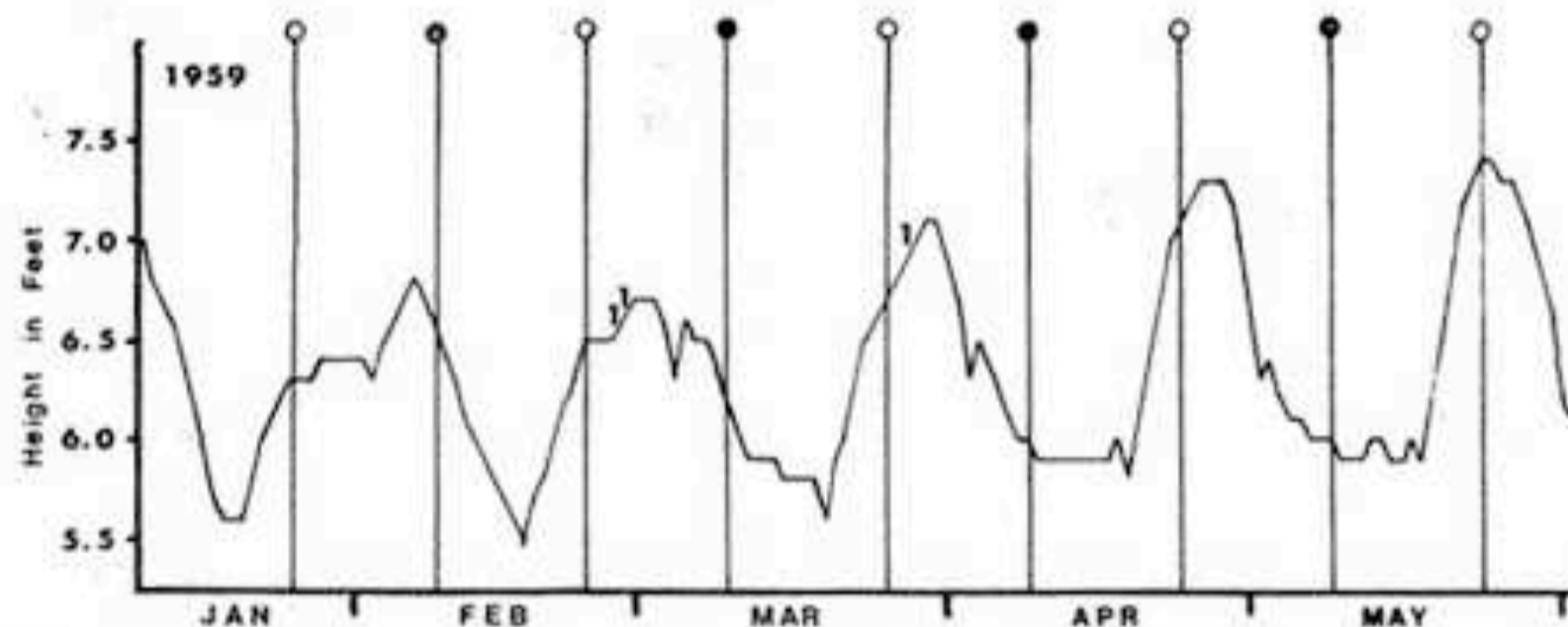


FIGURE 2. *Saltwater Creek. Predicted tides and actual spawning dates, 1959.*

*Results*

The predicted tides, the times of full and new moon and the days on which spawning occurred, in successive years of study, are indicated in Figures 2, 3, 4, 5 and 6. Observed and predicted tidal levels were not always the same but there were only two occasions when there was a gross discrepancy. These were at times of abnormally high tides. Fish aggregated in the spawning area two or three days before spawning.
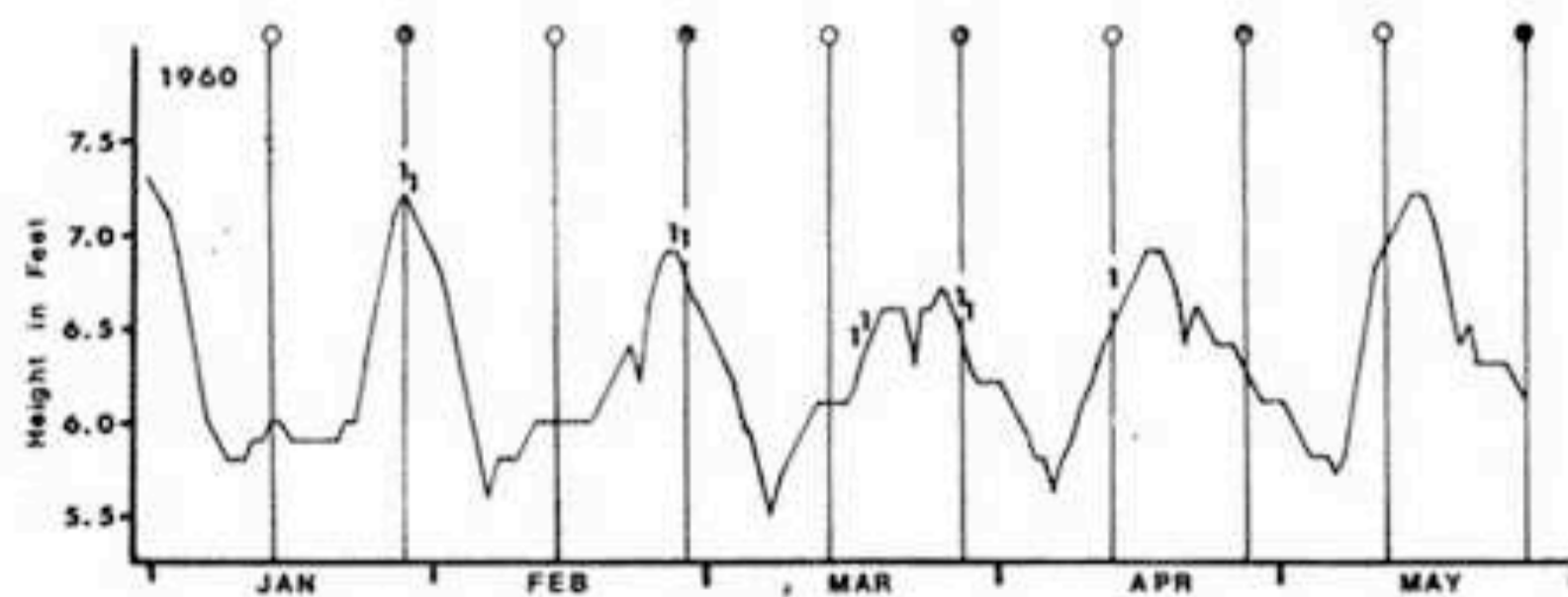


FIGURE 3. *Saltwater Creek. Predicted tides and actual spawning dates, 1960.*

In 1959 only two spawnings were observed, each in a separate month, but other spawnings would have occurred in that year. At that time work was concentrated on the embryology of the fish rather than on its spawning habits. The years 1959, 1961,

1962 and 1967 all show features in common. The spring tides were associated with either the new moon or the full moon in each season and spawning began from one to three days after the appropriate moon phase. Eggs were laid on morning and evening tides for up to three days after spawning began.
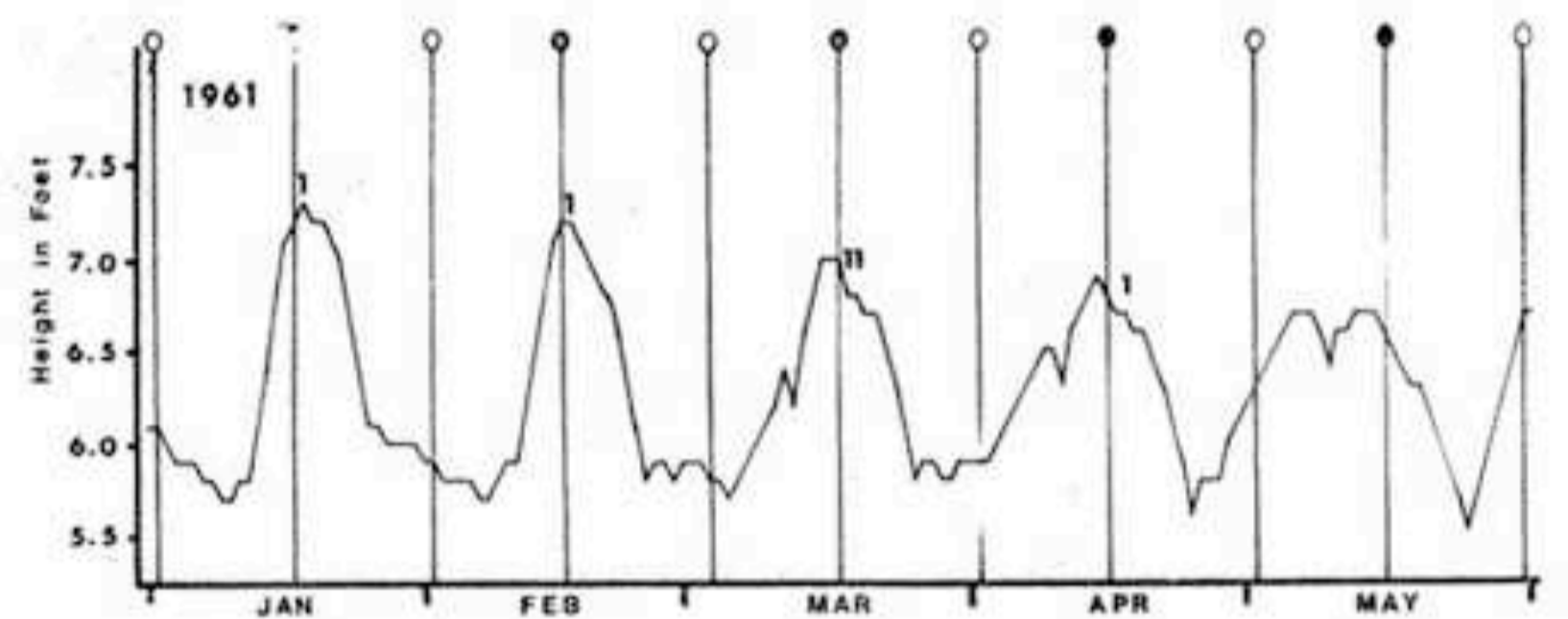


FIGURE 4. *Saltwater Creek. Predicted tides and actual spawning dates, 1961.*

In 1960 (Fig. 3) an especially interesting phenomenon occurred: the spring tides shifted from the new moon to the full moon during the spawning season. Only in this year was any irregularity of spawning seen. The January and February spawnings were apparently normal but the fish spawned again just twenty-five days later on rising tides and again ten days later at the new moon. This spawning shared with the January and February spawnings at the new moon the somewhat unusual character of occurring on the day of the new moon. Similarly, the final spawning at the full moon in April fell on the specific day. The data from this year will be examined in greater detail below and compared with the data for 1962.
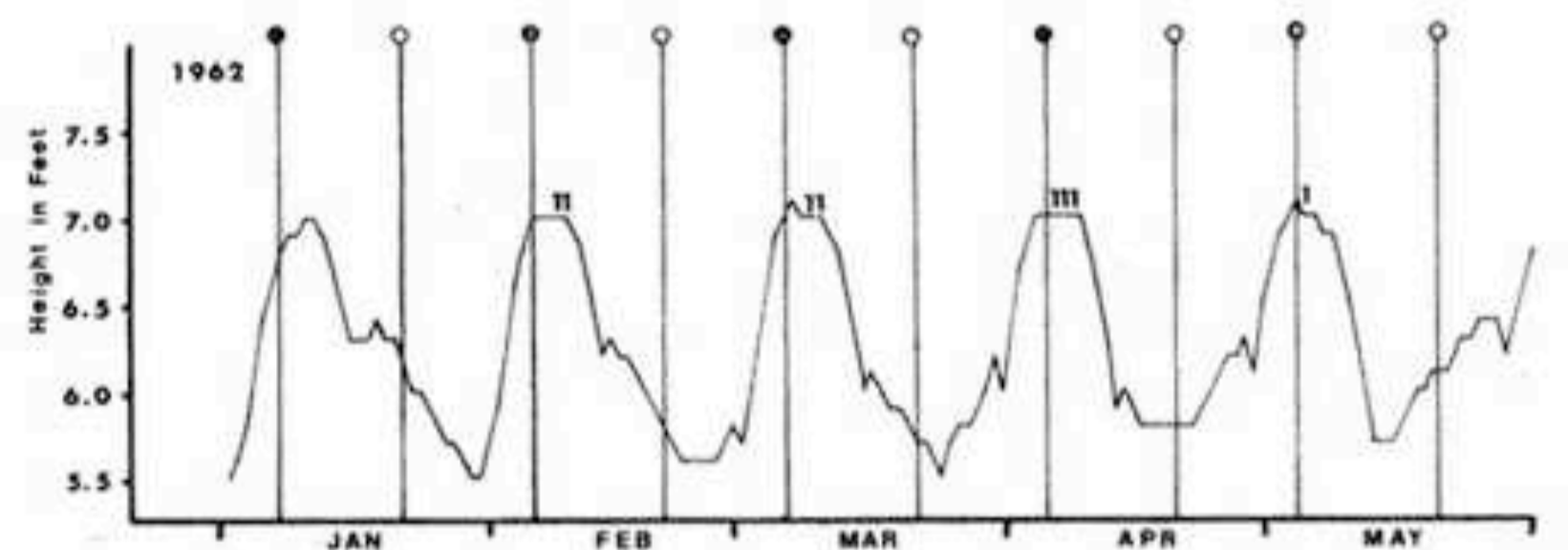


FIGURE 5. *Saltwater Creek. Predicted tides and actual spawning dates, 1962.*

In general, peak spawning appeared to occur as the tide began to fall. The whole school moved into the pasture grass and the fish spawned in such a depth of water that while their bellies touched the substrate their backs just broke the surface. The extent of spawning could be assessed because the eggs from individual females were clustered in a restricted area. If spawning was light these masses were easily recognisable; if it was heavy the distinction broke down and there was a heavy cover

of adhering eggs. The eggs, which are just over 1 mm. in diameter, adhere to the lower parts of the vegetation, especially in the rather fibrous grass roots found above ground level. As spawning occurs on successive tides which may be of different heights, the end result may be a deep horizontal band of eggs, up to three or four feet wide, on the spawning ground. There is no evidence for any male-female pairing in this spawning, rather it is a communal phenomenon. All the fish move in to the area together and as the sex ratio in spawning shoals varies from month to month it is very unlikely that a pair bond is formed. Each female sheds all her eggs in a short series of abdominal contractions associated with a lateral lash of the tail. The males shed their milt and in the disturbance it is spread so that the whole area of water over the shoal looks milky.
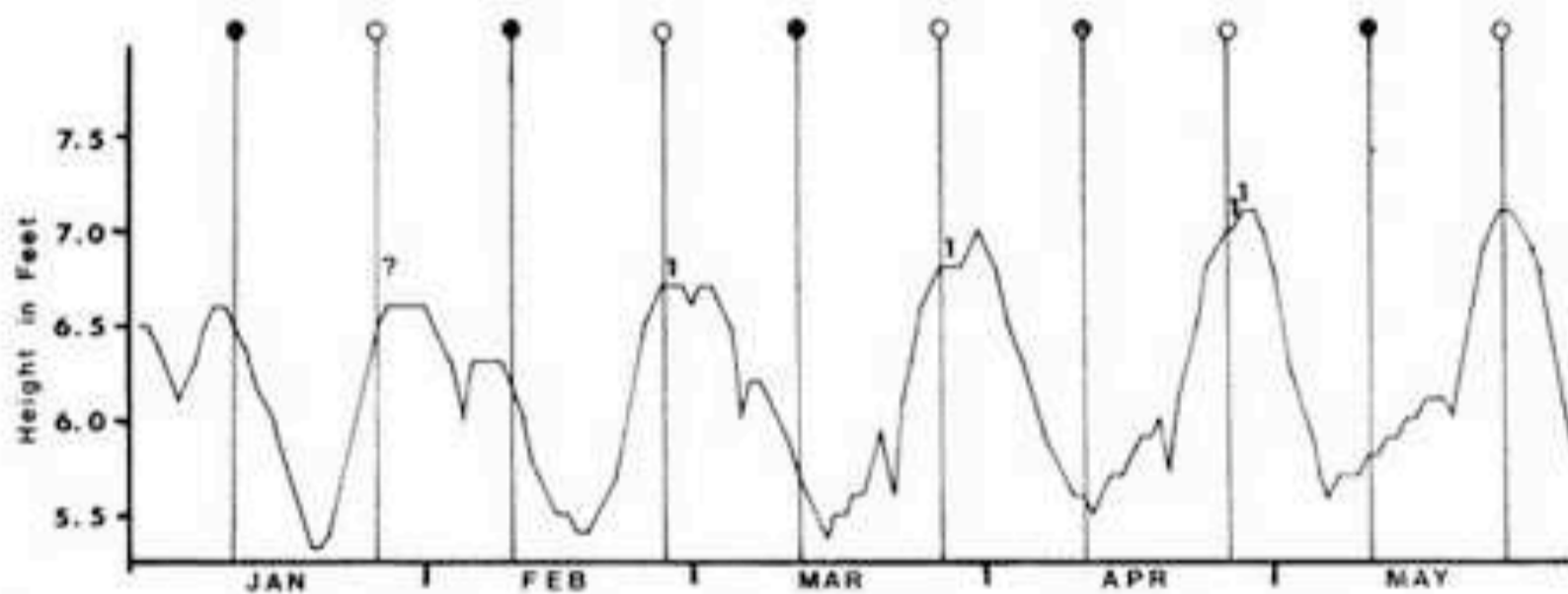


FIGURE 6. *Saltwater Creek. Predicted tides and actual spawning dates, 1967.*

In addition, I kept a watch on the controlled outlet from Horseshoe Lake, which empties into Kerr's Reach of the Avon River, Christchurch. Several large schools of ripe *G. m. attenuatus* were netted there but they were caught only on days immediately preceding the spawnings at Saltwater Creek. Presumably they were about to spawn in the lower reaches of the Avon River.

While this study was in progress Burnet (1965) had begun observations on the downstream migrations of adult *G. m. attenuatus* by observing catches at a trap built to span a small tributary of the Waimakariri River, the main river south of the Ashley River. Burnet placed juvenile *G. m. attenuatus* above the trap early in the summers of 1959–60 and 1962–63. In 1958 the fish which entered the trap were those which had entered that water unimpeded during the summer preceding the building of the trap. Figure 7 shows Burnet's catches for 1958, plotted against the predicted tide for the same period. These fish would probably have spawned on the next spring tides if they had behaved in the same way as the fish observed in the later seasons.
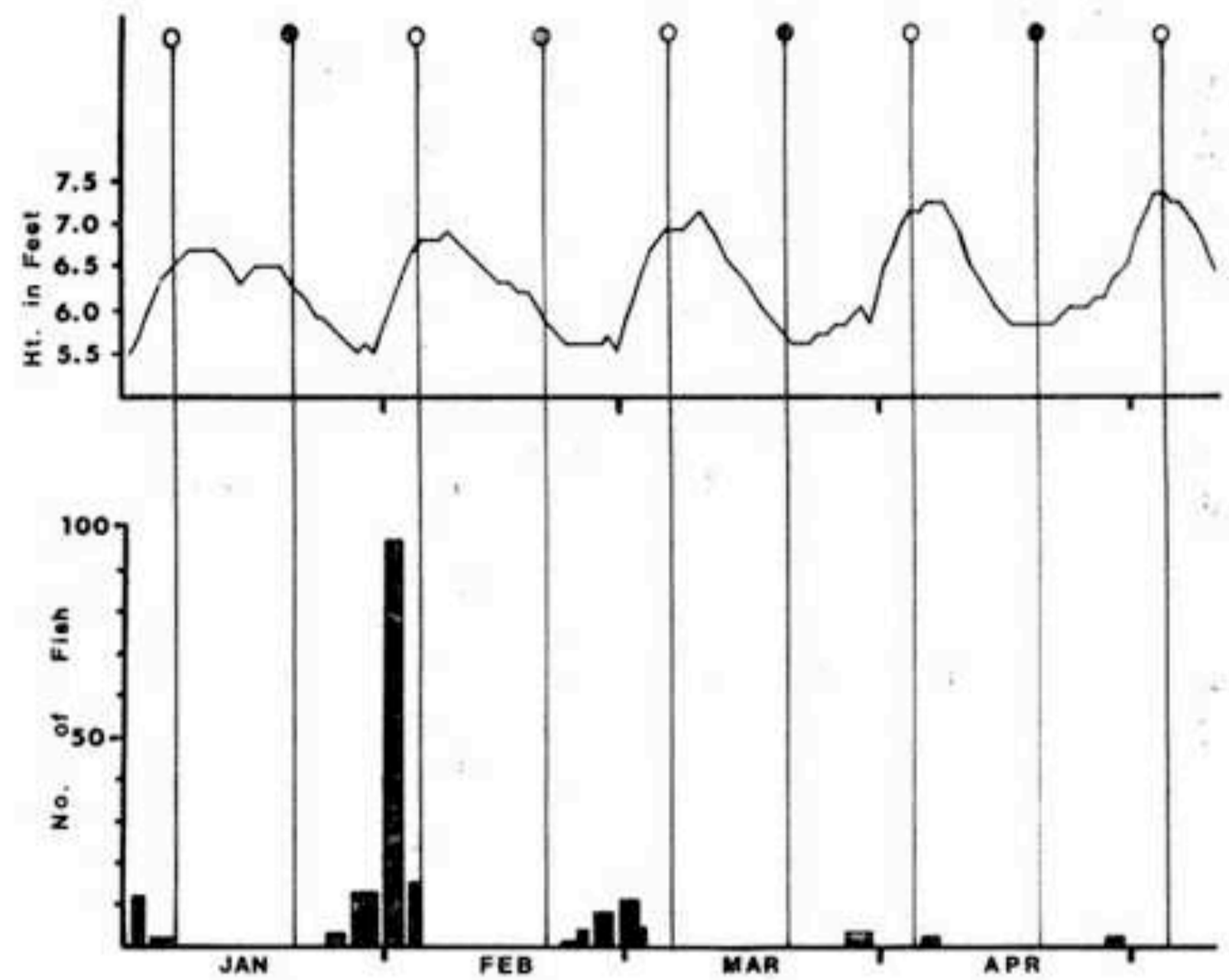


FIGURE 7. *Adult* G. m. attenuatus *caught in South Branch Trap, 1958 (after Burnet).*

The combined data from all sources are shown in Figure 8 which represents in detail the 1960 breeding season. Burnet's data are given as black histograms. The migrations of mature fish at Kerr's Reach clearly followed the same temporal pattern as elsewhere but differed in the relative numbers.
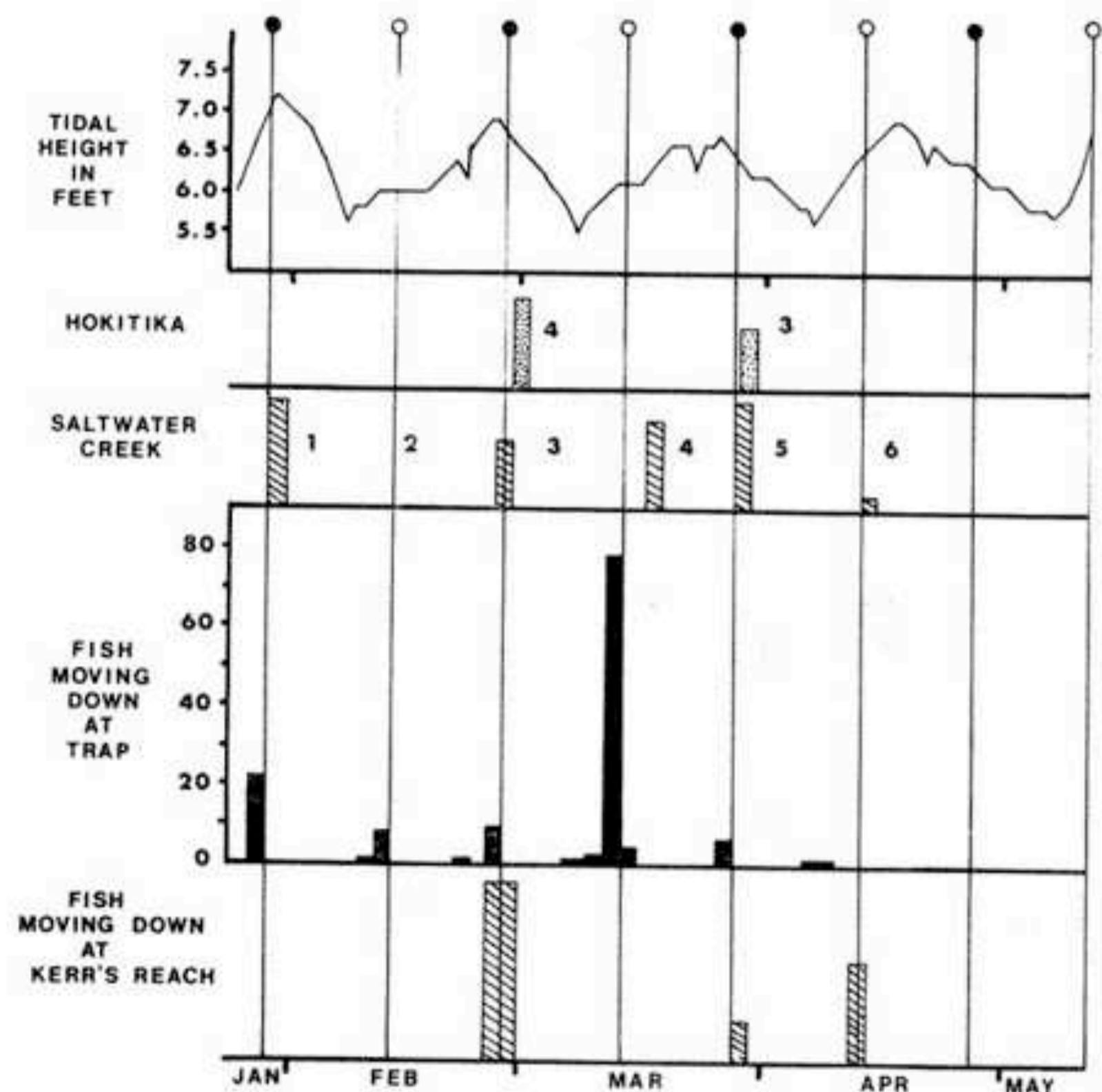


FIGURE 8. *Combined data for 1960 breeding season.*
N.B. *Subjective data in diagonal lines (own observations) or dotted.*

KEY
1, 5. Very extensive spawning.
2. No spawning.
3. Some spawning.
4. Quite extensive spawning.
6. A few egg masses.

The absence of fish at any particular time at this site may merely be because they were not noticed, but Burnet's data show conclusively that the migration of mature fish can be correlated with the tides (or moon).

Although the assessment of intensity of spawning is subjective it provides some scale of reference and the dates are exact. Data from spawnings at the mouth of the Hokitika River (A. Cutbush, pers. comm.) are included.

A comparable figure for 1962 is given in Figure 9. The peak migrations of mature fish at Burnet's trap once again preceded the observed spawnings at Saltwater Creek, although the picture is much clearer because the tides were not then complicated, as they were in 1960.
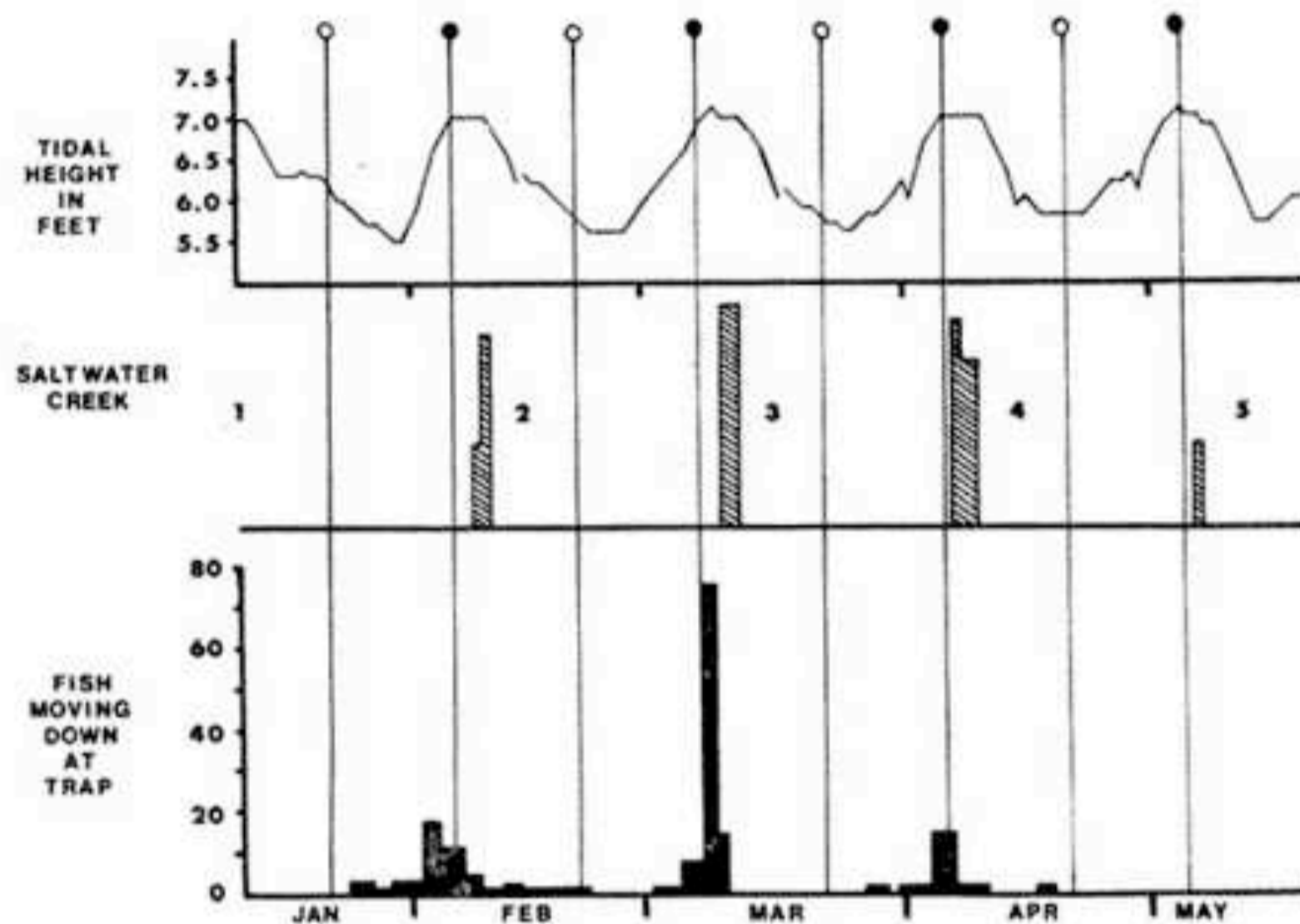


FIGURE 9. *Combined data for 1962 breeding season.*
*N.B. Subjective data in diagonal lines.*
KEY
1. No spawning.
2. Quite extensive spawning on three tides.
3. Very extensive spawning on three tides.
4. Quite extensive spawning on five tides.
5. A few batches spawned on one tide.

*Discussion*

The data presented in Figures 2–9 inclusive show that sexually mature *G. m. attenuatus* migrate downstream at the phase of the moon appropriate to the nearest spring tide.

Burnet (1965) analysed his trap results and found that although they were clearly cyclic, and therefore independent of climatic factors such as rainfall, their cyclic nature could be expressed in terms of lunar, lunar plus tidal or tidal effects in different years. The additional data supplied to the present study from Burnet's invaluable records at the fish-trap (Figs. 8, 9) show that the fish migrated in large numbers just before the days on which spawning was observed at Saltwater Creek.

The only inference which may be drawn from this is that the phase of the moon immediately associated with the spawning tides cannot be correlated directly with these migrations since they actually precede the moon-phase. The assumption had previously been that the simplest stimulus the freshwater fish living up to twelve and more miles inland could respond to is either moonlight or its absence. That this is too naive an explanation is clear because overcast weather has apparently had no effect on the overall pattern. It is tempting to suggest that the phase of the moon (full or new) immediately preceding the "spawning" phase (new or full) acts as a trigger to set off the downstream migration but, in the absence of any further evidence, it would be folly to be satisfied by this hypothesis. An examination of Captain Hayes' data presented in Figures 10 and 11, shows that
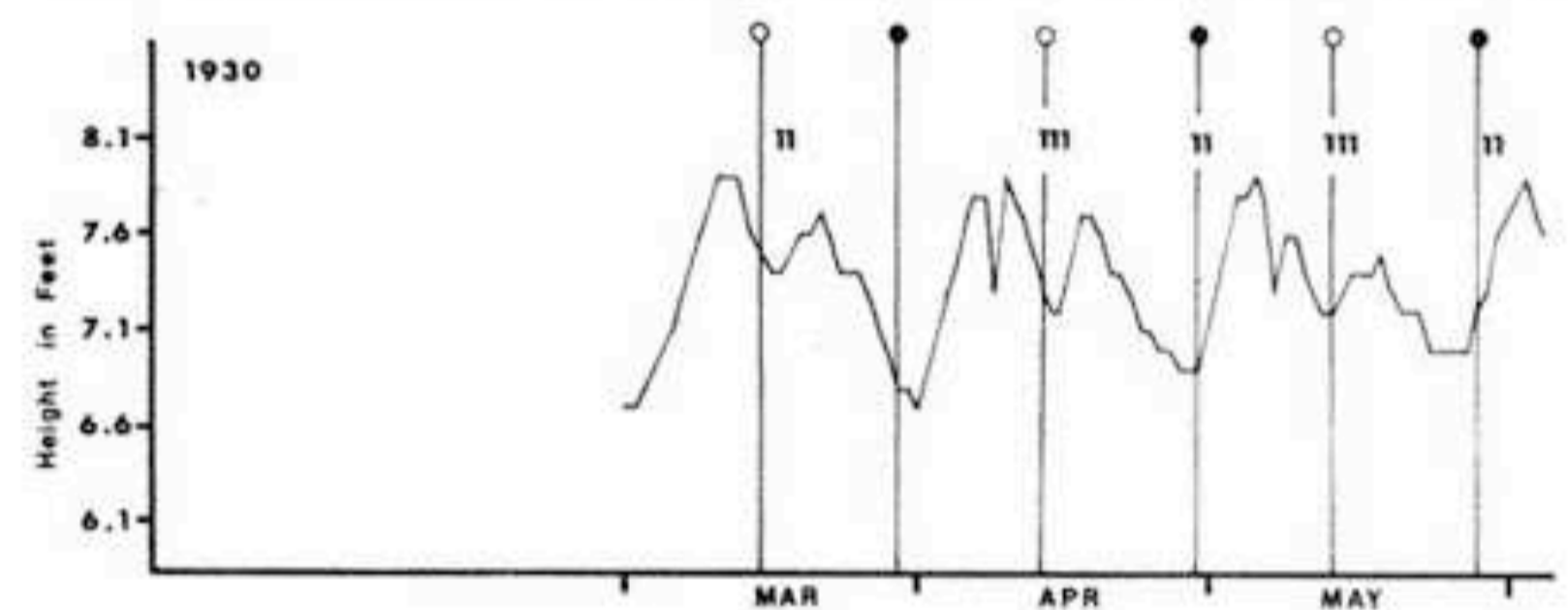


FIGURE 10. *Manawatu River. Predicted tides and spawning dates, 1930.*

spawning appeared to occur after and on either the full or the new moon in each year but there appears to be no correlation with the tides in 1930 and only a partial correlation in 1931. These results are presented as an indication that conditions for spawning may be very different in other areas. Other factors such as barometric pressure (Deelder 1954) may also affect fish migrations; Burnet (1965) mentions these in the analysis of his results.
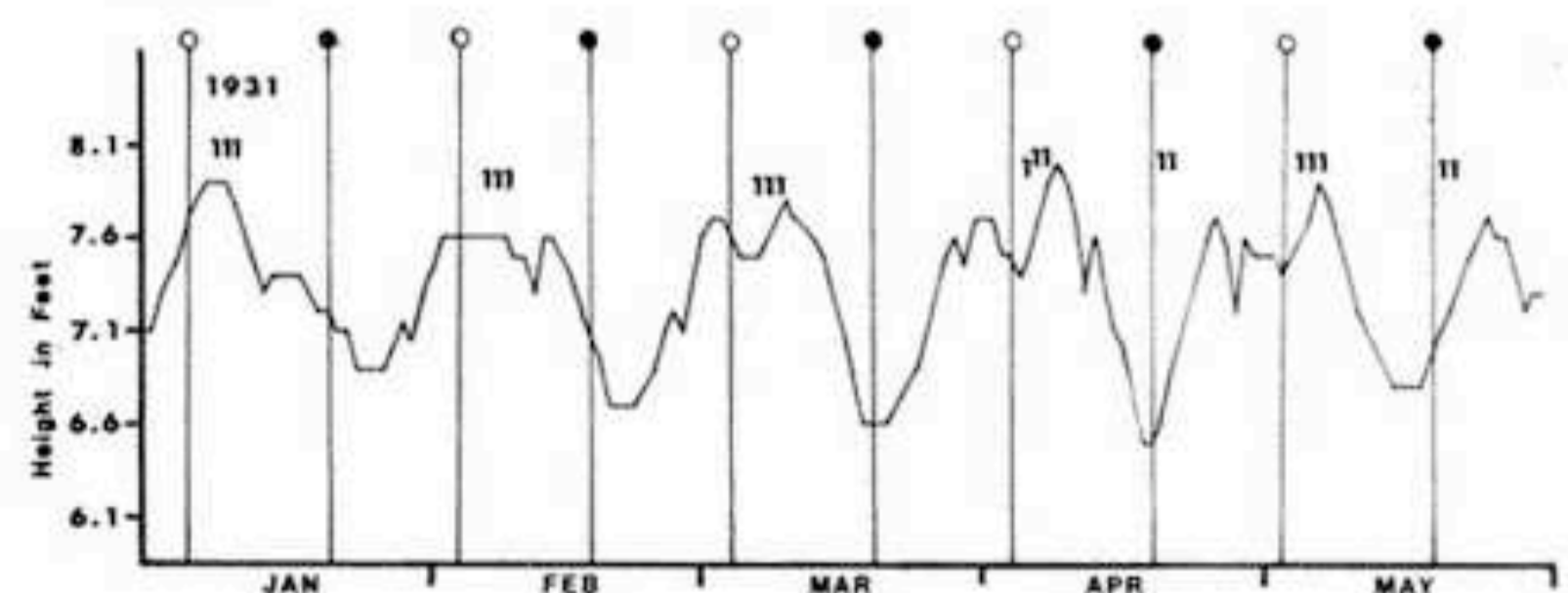


FIGURE 11. *Manawatu River. Predicted tides and spawning dates, 1931.*

Without a detailed study of all climatic factors no further conclusions may be made, but it may be possible to test for the initiation, by the appropriate lunar phase, of downstream migration.

## FACTORS INVOLVED IN THE CHOICE OF SPAWNING SITE

A careful examination of the spawning area on many occasions made it clear that spawning had occurred only in certain places (marked in Fig. 1) but that it is restricted to far fewer of these places than expected is, in itself, interesting.

Several theories may be put forward to explain these apparent anomalies but almost all can be refuted. The first set of hypotheses are concerned only with the characteristics of the spawning ground:

1. *The areas are too deeply submerged at the appropriate time:* This is not true as they have the same slope as the areas which are used and are immersed to the same extent.

2. *There is not enough water at spring tides to cover the area:* This is not true of the area indicated.

3. *There is salt water influence at the spawning level:* This is not true.

4. *The vegetation is not suitable:* The vegetation in all areas indicated is the same grass-clover mixture as in the areas which are reached by freshwater only. The same small *Scirpus* sp. vegetation occurs in the areas contaminated by saltwater.

5. *The areas are not accessible to the fish:* All such areas were equally accessible.

6. *The areas may be too far upstream:* This could be true of the areas upstream of the footbridge but the study was downstream from this bridge and the spawning ground used regularly is one of the most upstream "bays" of the river bank.

Other hypotheses which take into account the behaviour of the fish may also be put forward:

1. *There may be some chemical factor involved, or some other such feature not detected by a human observer:* This is obviously possible and it could be that the precise balance between the saltwater welling in from the estuary below and the overlying freshwater flowing down the stream determines the spawning place. If so, it is difficult to reconcile the two different places in which spawning occurs or has occurred, i.e., above and below the road bridge. This hypothesis will have to remain open, in the absence of any conclusive evidence for or against.

2. *It is possible that the communal spawning habit requires a concentration of fish in one area:* As evidence for this there is the fact that the fish collect in the area before spawning begins, which suggests that final maturation may be facilitated by schooling. Further supporting evidence is supplied by the 1967 spawning results. Very different numbers of eggs were laid on successive spawnings, even between successive tides, yet each month all eggs were laid in the same area. Other evidence for the importance of schooling behaviour is deduced from the fact that with these relatively light spawnings it was possible to see that eggs were concentrated in the areas easiest of access even though the tides were different in the different months so that these areas varied. More evidence in favour comes from the observations made during the abnormally high tides of 1960. Then, eggs were laid in a large hollow in the pasture itself, high above the usual spawning areas which would have been submerged.

During the years of this study all the eggs collected were taken from the pasture grass-clover vegetation. Assiduous searches of sedge beds further downstream, in which the dominant plants were the tall *Leptocarpus simplex* and *Scirpus americanus*, never uncovered any eggs. This is particularly surprising as they have been collected there in past years (Mrs. F. R. Allison, pers. comm.) and Hayes (1930, 1931, 1932) mentions sedges and rushes as spawning areas.

## THE ECOLOGY OF THE EGGS

During the spawning season the range of the ambient temperature from January to May varies considerably and daily fluctuations are also very great, especially in late April to May when the nights are cold. The nearest meteorological station measuring similar climatic conditions is at Christchurch. The results for the appropriate years (1959–62) have been averaged in Table 1 (N.Z. Meteorological Service, 1962–64).

TABLE 1. *Averages of meteorological data for Christchurch, 1959–62.*

| Temperature in °C. | Jan. | Feb. | Mar. | Apr. | May |
|---|---|---|---|---|---|
| Mean daily grass minimum | 17.3 | 16.8 | 14.2 | 12.0 | 9.0 |
| Mean daily maximum | 22.5 | 21.6 | 18.9 | 17.4 | 13.6 |
| Mean daily minimum | 12.1 | 11.3 | 10.1 | 8.2 | 4.9 |
| Mean daily grass minimum | 10.6 | 9.6 | 7.9 | 5.0 | 2.4 |
| Mean days of ground frost | — | — | 1.0 | 4.2 | 11.0 |

These data were compared with the summary of observations at Christchurch from 1905–60 (N.Z. Meteorological Service, 1966). The latter have lower values but all the monthly trends are the same. The significant features in Table 1 are that the mean daily grass minimum, which would correspond with the temperature at which *G. m. attenuatus* eggs would be developing, is lower than the minimum air temperatures each month; and in May, which marks the end of the spawning

season, frosts have become prevalent (they are equally prevalent in the 1905–60 summary of means).

It is all the more surprising that laying occurs in areas which are apparently high and dry for over two weeks out of four, when the relative stability of the temperature of water over such a period is considered. Maximum-minimum thermometer readings taken in these areas showed that a single batch of eggs may be exposed to a range between 5°C. to 18°C. in one day; yet no abnormalities in development were seen and egg mortality was very low. Not only eggs collected in the field but also those fertilised artificially were used for studies of the influence of temperature and water on development.

During these studies I found that even although eggs will develop in fresh water, salt water, on moist cottonwool or on damp turf, the success of artificially fertilised eggs was far below that of naturally-spawned eggs. This was true even of eggs spontaneously shed and fertilised by captured fish, when such eggs were gently pipetted into the container or on to the substrate. Stripping and fertilisation were easy but these eggs proved very susceptible to the attack of *Saprolegnia*, as did those eggs exuded spontaneously into a collecting bucket.

A search for an explanation for this susceptibility to infection led to the idea that the adhesive layer which attaches the eggs to the grass and the soil actually protects them against infections. This idea was supported by the fact that when eggs were removed from these masses with a fine paintbrush and stored separately in water they succumbed to *Saprolegnia* quickly and their adhesive layer could be seen to be incomplete. Undisturbed eggs on turfs immersed in water came to no harm. It must be important for eggs to be attached as soon as they are laid, so that this layer is undisturbed; but an antibiotic effect from the soil cannot be ruled out, at least as an additional factor. In natural conditions the few eggs which die do so in the first few days of development, so that their deaths may be attributed to a failure in development rather than to an attack from outside.

The various requirements of the eggs during development may be summarised as protection, supply of water and facilities for gaseous exchange. Protection is provided by the vegetation which is about 6–8 in. high. Water is provided by the tidal cover twice daily for the first few days; it is then conserved by the vegetation. The spawning ground and all similar areas are well sheltered from direct sun by overhanging willow trees and by the close cover of low vegetation. The eggs are laid in the

lower levels of this vegetation, from soil level to about an inch above it. The microclimate in such an environment is very stable, with less extreme temperatures than the air above and a very high relative humidity and water vapour pressure (Geiger 1965). When the grass was undisturbed such an area was very close to an aquatic medium and the eggs developed normally, according to the temperature. Their turgidity was maintained unless the grass was cropped short by cattle, when desiccation occurred unless soil moisture was high. It was only during the very hottest periods that eggs were killed in this way.

Gaseous exchange probably occurs by diffusion across the moist chorion. Towards the end of embryonic development more complex wastes accumulate inside the eggs so that eggs ready to hatch often appear yellow.

It had previously been found that in hot summers the eggs were ready to hatch 14–16 days after laying (temp. max. 18°C., min. 11°C.); and that if eggs were kept cool in the laboratory the rate of development was slowed. In 1967 constant temperature cabinets were available at 4.4°C. and 17°C. Sample turfs in plastic bags were kept at these temperatures and checked daily by the
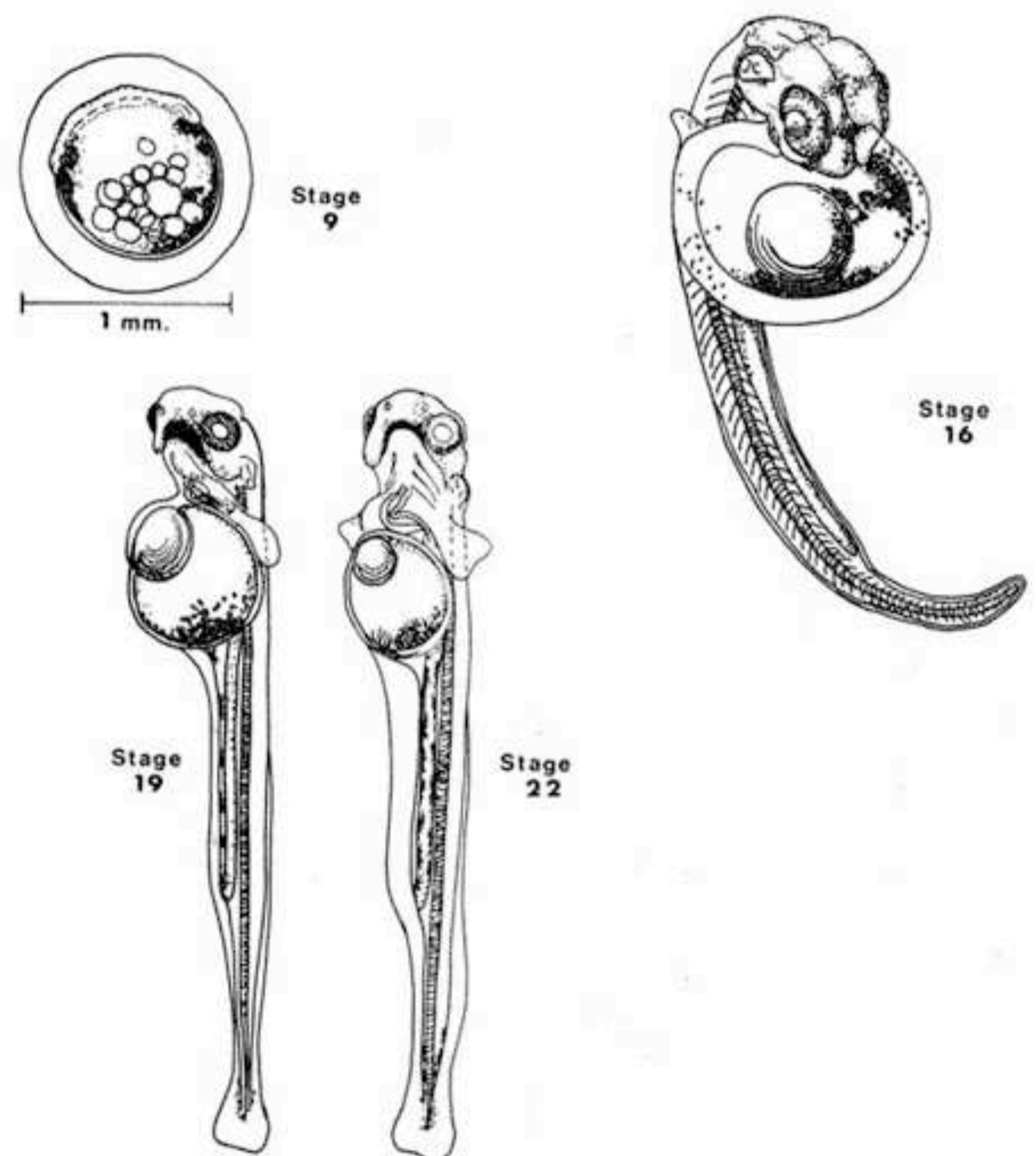


FIGURE 12. *Stages in the embryonic development of G. m. attenuatus.*

removal of a number of eggs. As far as could be determined each turf carried eggs from a single female.

Several stages of development are given in Figure 12. (The details of embryonic development are to be the subject of another paper.) These stages are also indicated on the growth graphs in Figure 13 and show the relative effects of the two temperatures. All eggs developed at the same rate at a constant temperature, but whereas embryos were ready to hatch after 10 days at 17°C., it took 31 days at 4.4°C. The four stages of development of Figure 12 are marked on Figure 13. As the anatomy changes very little during the last days and the amount of yolk present varies a little with the temperature of development, readiness to hatch is recognised by the softening of the chorion.
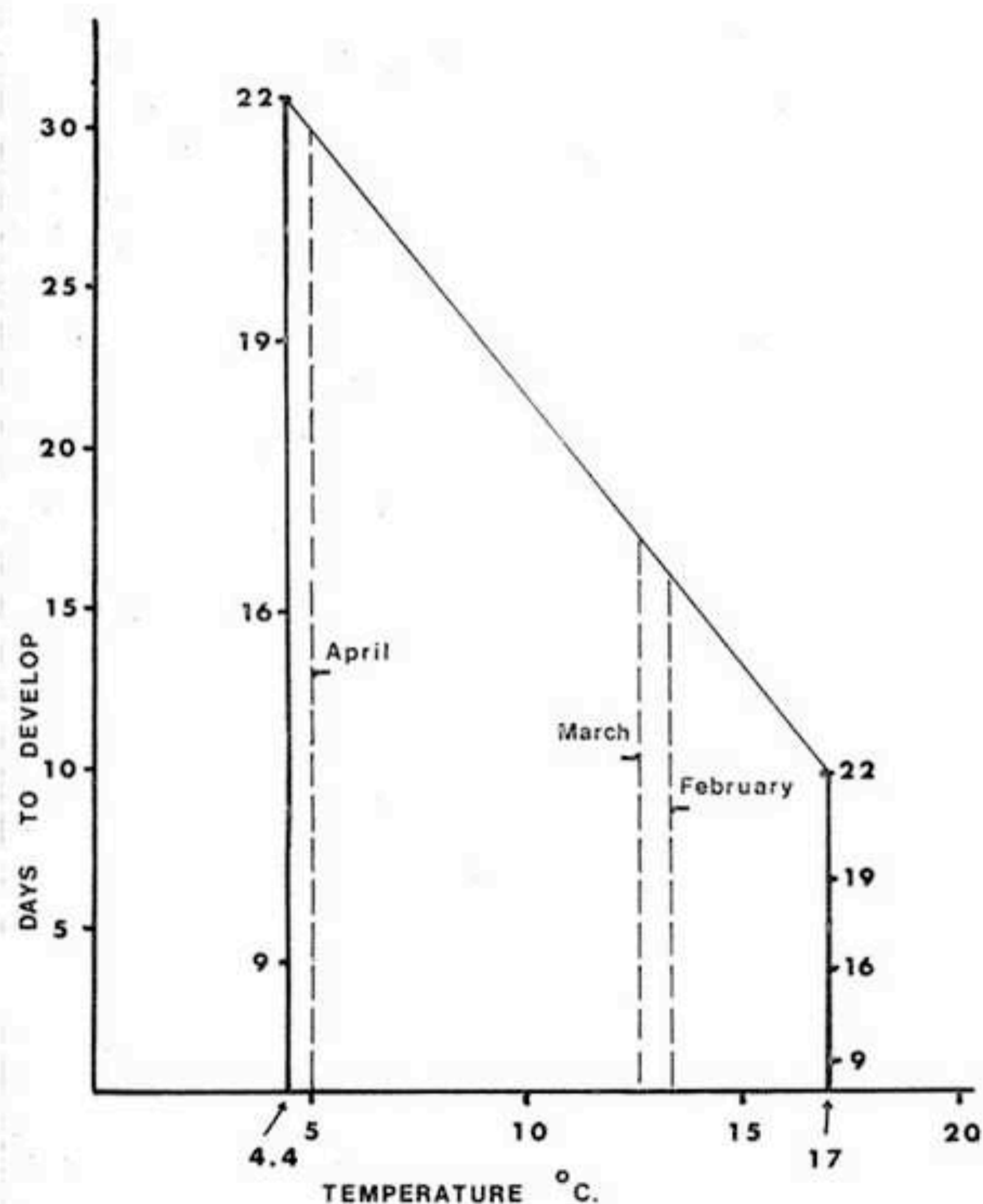


FIGURE 13. *Rate of development of* G. m. *attenuatus at different temperatures, with field data added. Numbers in body of graph are development stages, as shown in Fig. 12.*

The fact that this remarkable temperature lability is actually called upon in development is shown in Figure 13, by the interrupted lines showing the field data for 1967. Whereas the February and March eggs were ready to hatch after sixteen and seventeen days respectively, the April eggs

developed during cold weather and took twenty-nine days to hatch. Figure 6 indicates that whereas the February and March eggs would have had to survive for about thirteen days before hatching, the April eggs had already been immersed for at least seven days before the first were ready to hatch and they hatched over three days. In every other year of the study the periods of development in the different months were comparable with the results for 1967.

Hatching involves two processes:
 (i) The softening of the chorion by Stage 22.
 (ii) Immersion of the egg in cold water. The embryo performs rapid coiling movements which rupture the chorion and so the young fish escapes.
Embryos may hatch spontaneously at Stage 22, but may take up to three more days (April eggs, 1967).

How did the experimental embryos really fare at these diverse but constant temperatures, and how do these findings correlate with observed field data? First, the experimentally-reared eggs experienced more difficulty in hatching than those reared at less extreme temperatures. In fact, 4°C. and 17°C. represent near-critical limits for normal development at constant temperature. Yet in the field, with wide daily fluctuations, eggs develop normally. Although below the grass cover the eggs remain moist they may occasionally become quite dry. When the egg loses its turgidity, so that the chorion collapses upon the embryo, it is still viable if it regains moisture in a day or two. This loss and gain occurs occasionally before, and often after, the softening of the chorion; but if loss of water has occurred immediately before the eggs are immersed by a tide (or artificially), they hatch on the subsequent tide (or over half an hour later). Turgid eggs hatch in up to ten minutes after immersion.

Tides high enough for hatching may not occur soon after the spring tide on which the eggs were laid. In 1962 one entire spawning had to wait six weeks before immersion. These young had little yolk left and did not survive when hatched in the laboratory. In 1960 the flood tide which immersed part of the paddock resulted in the total loss of the eggs which had been laid over the entire flooded area, as none were ever submerged again.

Normally, the rising tides cover the spawning ground about three to three and a half weeks after the eggs are laid. The young hatch and swim up towards the light and swim together as if schooling. These responses are easily demonstrated experimentally, but at this stage in the life-history the

"schooling" response is only a reaction to a current. (Almost all larvae face into an artificially induced current.) They are then swept down immediately as the tide falls. The river water banked up by the spring tide rushes out to sea, so that the flow through the estuary is a maximum at this time. (Captain Hayes netted newly-hatched young at the mouth of a river as the tide fell.) These young vanish out to sea and reappear as an important component of our commercial whitebait catch about six months later.

## CONCLUSIONS

It is clear that, in the area studied, adult G. m. attenuatus migrate downstream at such a time that they spawn on the spring tides during mid- to late summer. This spawning usually occurs just after the new or full moon, whichever is associated with these tides at any particular time.

When combined data for the years 1960 (Fig. 8) and 1962 (Fig. 9) are compared it is clear that migration downstream precedes the phase of the moon with which spawning is apparently associated. The year 1962 is especially interesting because fish spawned at the tidal changeover. Burnet's data suggest that although a large quantity of fish migrated at the appropriate time in March, very few moved before the additional spawning a fortnight later. At Saltwater Creek an extensive spawning occurred when the ground was first covered, but after the new moon (the appropriate phase in January and February) there was a very extensive spawning despite the fact that the tides were falling. This is the only clear evidence adduced during the seasons of the study of both lunar and tidal effects operating in the determination of spawning time. Apart from this, the tidal level seemed to be the dominant factor, although how it is perceived inland is not known.

The fact that there was this discrepancy in 1960 lends support to the idea that the aggregation of fish in the spawning area facilitates completion of their maturation and suggests that they subsequently spawn in an area chosen as suitable once the tides are high enough for the banks to be sufficiently submerged by freshwater.

The basic differences in the data for 1930 and 1931 (Figs. 10 and 11) cannot be explained in terms of this section of the present study.

The spawning season for G. m. attenuatus studied in Canterbury ranged between January and May, peak spawnings occurred usually in February and March. The only information available on the spawning habits of the Tasmanian form is the suggestion by Scott (1937, p. 127) that "sexually mature fish normally emigrate from creeks and headwaters of rivers, descending to brackish or saltwater to spawn about April, and are absent until about June or July".

The observations of Pollard (1967 and pers. comm.) are of great interest, since he studied a landlocked form of G. maculatus in Lake Modewarre, Victoria. The lake is slightly saline and adult fish migrate up intermittently in-flowing creeks to spawn in late winter and spring. Spawning occurs when creeks are swollen after heavy rain so that eggs are laid in flat flooded vegetation by the water's edge. These eggs are stranded as the water subsides, develop out of the water, and hatch on the first flood after development is complete (about two weeks after spawning). Hatching may be delayed up to at least a month after spawning. This description shows that the population studied by Pollard had the same overall behaviour sequence in its spawning pattern as the species I have studied, except that the fish spawned in the later winter and spring (interpreted as July to September or October in the absence of any other indication). There is no report of spawning occurring in the New Zealand population of G. m. attenuatus other than in mid- to late summer. The publication of the description of two new species of Galaxias from New Zealand, each very similar to G. m. attenuatus (Jenyns) and each collected from small land-locked coastal dune lakes in North Auckland (McDowall 1967) is of interest, as in fact these species seem very like Pollard's population of G. maculatus. However, details of their life histories would clarify their position. McDowall (1966) questions the identity of the fish studied by Pollard. Details given by Pollard (pers. comm.) suggest that the fish he studied is more like G. maculatus than any other species.

These investigations emphasise the necessity for an overall study of the life histories of the Galaxiids. The spawning habits of the annually migrating populations of G. m. attenuatus in the Canterbury area have been very regular; but the divergence of the data from those of Hayes for the seasons of 1930 and 1931 for the Manawatu River, and the entirely different seasonal emphasis found by Pollard, suggest that generalisation may be dangerous. The ecological conditions for the development of the eggs are in all instances similar, in that the eggs are laid in vegetation which is left apparently out of water for part of the life cycle, so that the same effect has been achieved in different ways. This suggests that the spawning

cycle is primarily concerned with access to suitable areas for embryonic development to occur. Subsequent growth to the whitebait stage takes about six months in all instances.

The breeding cycle of Pollard's fish, with its reliance on flooding on several occasions so that the grassy spawning areas are covered, may seem more hazardous than that of the fish spawning at Saltwater Creek. The relative danger is increased by fluctuations in the height of spring tides from month to month in the latter area. Occasionally this has resulted in the stranding of large numbers of eggs. In addition, the peak of the Saltwater Creek spawning is in the February–March early April period when temperatures are high and a proportion of eggs is lost through desiccation if they are not immersed within the month. At very high temperatures the yolk reserves are severely depleted so that the hatching young may often be less fit than those of Pollard's fish, which develop and hatch in cooler months.

Almost all breeding *G. m. attenuatus* in the Canterbury study area are in their first year (Burnet 1965); that is, are up to six months older than whitebait. Therefore it is remarkable that in every year of the Saltwater Creek study the same small spawning area was used provided the tides were normal. There is no evidence to suggest that the fish had visited that spawning area before (the presence of unripe fish in the school would have provided such evidence). Any homing hypothesis, involving the return of the young to the area in which the eggs were laid, their migration upstream to feed and mature and their migration down again at spawning time, must take into account one important factor: The eggs hatch and are swept out of the spawning area to sea within a few hours of hatching, so that the idea that a firm association with the area is formed should be regarded very sceptically until it is demonstrated that such a short time will suffice. The homing of salmon occurs after up to two years on the nursery site and has been shown to be effected in the last stages by olfactory cues (Hasler 1960).

We are left with a spawning cycle in which the adult fish, living inland, migrate to estuaries so that their arrival just precedes the peak of the spring tides. The eggs are laid at and after the peak. Each fish sheds all its products at one spawning. The eggs develop in grass and the larvae hatch when next immersed by the tides.

## ACKNOWLEDGMENTS

## SUMMARY

A spawning locality for *Galaxias maculatus attenuatus* (Jenyns) is described. Details are given of spawning movements and dates for 1959–62 and 1967. The complex relationship which must exist for a freshwater fish (albeit with a marine larval phase) to move downstream only at such times that it will reach estuarine areas at spring tides is examined.

Spawning habits and the conditions under which the eggs develop and the rate of development at different temperatures are described. An attempt is made to co-ordinate three studies of the spawning behaviour of this species.

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