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845

The Life History of *Neochanna apoda* Günther (Pisces: Galaxiidae)

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New Zealand Ministry of Agriculture and Fisheries

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Frontispiece: Natural habitat of the brown mudfish.

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FOREWORD

MANY of New Zealand's native freshwater fishes are small and inconspicuous and until recently little was known of their detailed distribution, biology, and behaviour.

In recent years our knowledge of them has steadily increased as a result of the work and interest of various members of staff of Fisheries Research Division. Tony Eldon has ably contributed to our understanding of the biology and environmental requirements of the brown mudfish. This species, though still common, is seldom seen because it inhabits swamps and drainage ditches in which it can survive, even during dry seasons, provided it can hide in a damp atmosphere in holes or under forest debris.

One point to stress is that species such as this, which are seldom seen and little known, can easily be eliminated from an area by thoughtless environmental changes such as swamp reclamation.

G. DUNCAN WAUGH,
Director, Fisheries Research Division

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INTRODUCTION

The brown mudfish (*Neochanna apoda*) is one of three species of *Neochanna* (Galaxiidae), all of which are indigenous to New Zealand. Each species has its own distinct range of distribution, that of *N. apoda* being the greatest (Skrzynski 1968). *Neochanna apoda* was first described in 1867 by Günther from a single fish found at Kaniere, near Hokitika on the west coast of the South Island, and sent to him by Sir James Hector at the request of Sir George Grey. Since then *N. apoda* has been recorded from much of the west coast north of the Whataroa River in the South Island and from Wellington, Wairarapa, Manawatu, and, rarely, Taranaki in the North Island.

Neochanna apoda does not usually exceed 150 mm in length, but occasional specimens of about 200 mm are recorded (Phillipps 1923; present study see Table 6). The fish has a brown, cylindrical, cigar-shaped body (Fig. 1). It has no pelvic fins and the dorsal and anal fins are fleshy. It has adapted to swamp habitats unsuitable for other species of fish except short-finned eels (*Anguilla australis* Richardson) (Eldon 1968). The adult mudfish is nocturnal and secretive in its habits and therefore is difficult to observe.

The populations used for this study were located in the Wairarapa, a once heavily forested region, which lies to the east of the Rimutaka and Tararua Ranges and is largely drained by one main river system—the Ruamahanga (Fig. 2).

Much of the Wairarapa was swampy, but the swamps have been drained after the felling of the forest. This swamp drainage has had an unknown effect on the distribution and abundance of *N. apoda*, but judging from the number of small remnant habitats in isolated places, and from the large numbers of individuals within some of these habitats, the extent and overall numbers of the fish in the Wairarapa may once have been large. It seems likely that their potential habitat in the Wairarapa was spread over an area exceeding 2000 km ^{2}.

This study was mostly a spare-time pursuit carried out from 1969 to 1973 and directed at learning something of the life history and ecology of *N. apoda*. It was followed as opportunity permitted. Few data were collected at regular intervals and much of the information is fragmentary. The study began spontaneously with the bogging of a vehicle in a ditch close to a field station being used on another project. Mudfish were found when the vehicle was being dug out. The habitats in this area were frequently disrupted or even destroyed by farm improvement and ditch-clearing operations, and so a further study area in a remnant patch of forest was used to try to complete the work.

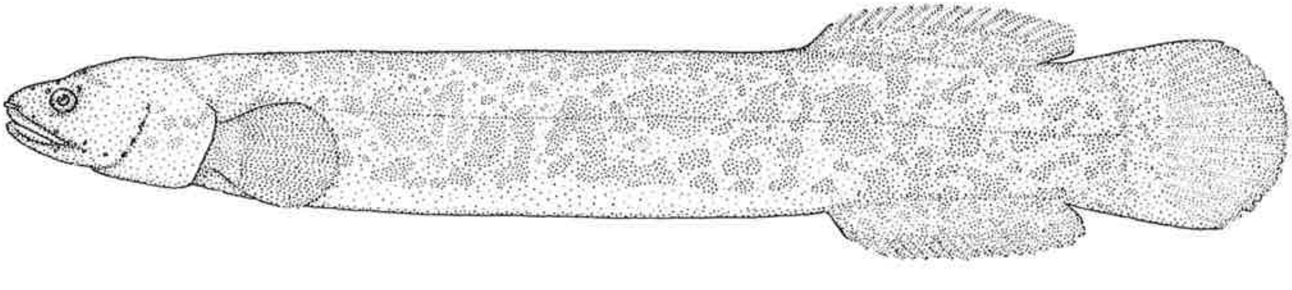


Fig. 1: Adult *N. apoda* (R. M. McDowall).

DESCRIPTION OF THE STUDY AREAS

There were three study areas within a few kilometres of each other (Fig. 2), and each included a number of different habitat types. Two areas were used extensively, the third being used mainly for comparison of feeding habits.

AREA 1

This area, referred to as Hinau, is part of the lower Hinau Valley (Fig. 2). The valley is formed by one main semi-permanent stream, but is criss-crossed by a network of drains, ditches, and natural watercourses,

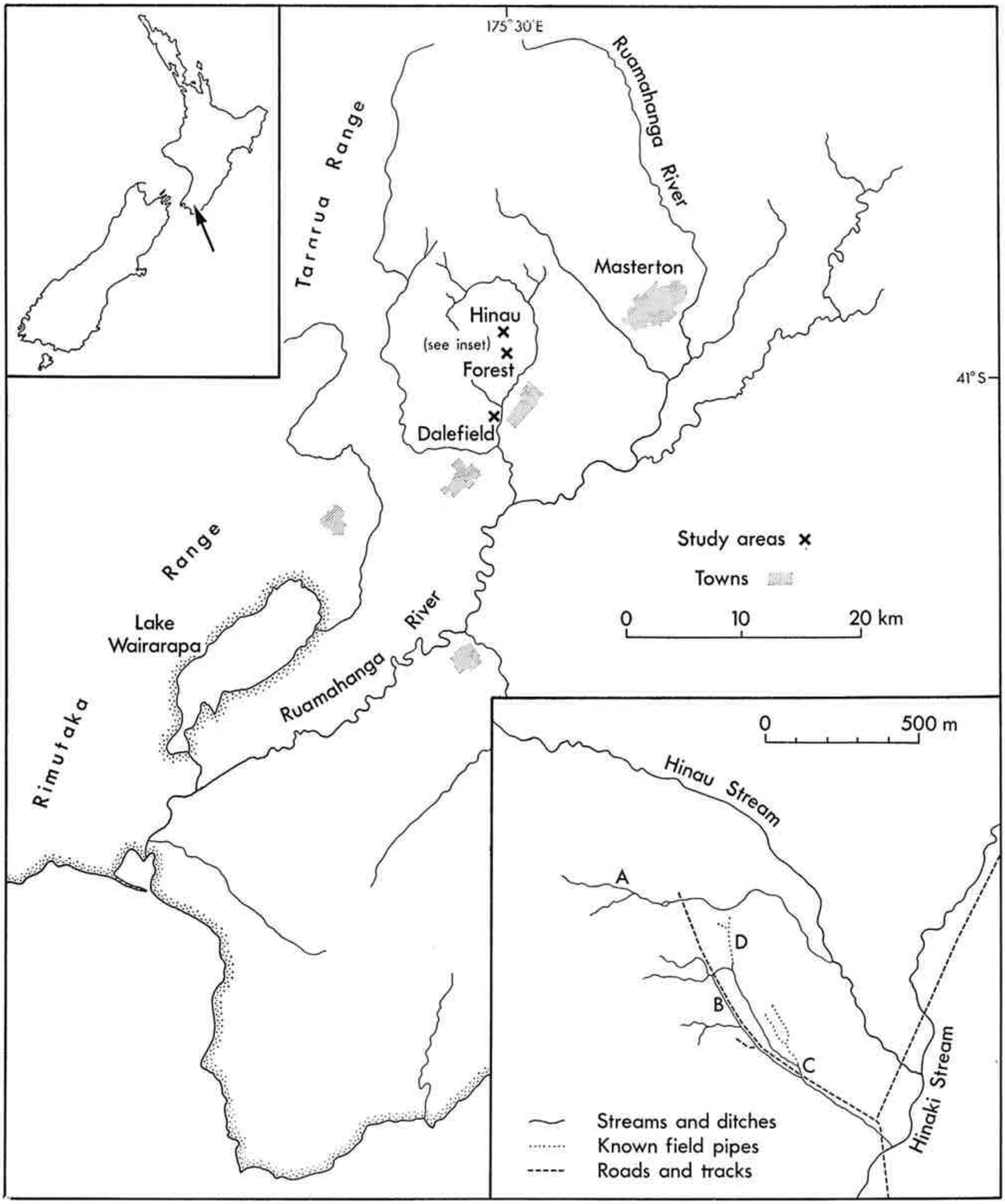


Fig. 2: Map of the Wairarapa, with the locations of the three study areas marked by crosses. Inset: Lower Hinau Valley, showing the places where *N. apoda* was found. A: An impermanent rapid stream in a pine plantation. B: A ditch alongside the road (Fig. 3). C: A very short ditch which connects subterranean pipes to a rapid watercourse confined to a regime channel. D: Site where fish were present before the watercourse was piped and filled in (see pages 21 and 39).

some of which are now confined to subterranean drainage pipes. Many of these watercourses have a permanent flow of water, but those featured in Fig. 2, with the exception of the Hinaki Stream, normally dry up from late January or early February to late April. The original forest cover has gone and, with the exception of habitat A, which is a stream running through an exotic pine (*Pinus radiata*) plantation, the watercourses are open. They run through fields or alongside roads, but with one or both sides protected by banks 1 m or more high.

Habitat A, "Cretney's Creek", is a stony-bedded impermanent creek less than 1 m wide which falls down a hillside at the rate of 6.7 m per 100 m of stream course. It contains pools of up to 0.4 m^2 in area and 0.2 m in depth formed by pine tree roots and fallen branches, where mud and pine needles collect to form a soft bottom. It runs through two man-made ponds and the lower and larger of these (400 m^2) appears to act as a barrier to the mudfish, which is not found in or below this pond. The steepness and fairly rapid flow (10 m per minute at normal levels) of this creek make it an atypical mudfish habitat.

Habitat B is a very narrow ditch (Fig. 3) which runs in two directions from a rise beside a road and breaks down into an area of wet turf of 25 m^2 (Fig. 4) at one point. The ditch is bounded on one side by gravel road and on the other by a steep grass bank about 1.5 m high. It is choked with pasture grasses and floating sweet grass (*Glyceria fluitans*). Unfortunately, the ditch was cleared by a road grader during the study and up to the time of writing the population of mudfish had not recovered to its former numbers.

Habitat C is a 5-m-long ditch 0.5 m wide which carries water from field pipes to the same watercourse (originally a natural stream, but now a regime channel) as habitat B above. This ditch contained 100 mm of mud supporting water starwort (*Callitriche stagnalis*) when first studied, but as it was cleared by a farmer soon after the study began, it was abandoned as a regular sampling area.

AREA 2

This is an area of private podocarp forest reserve (hereafter referred to as the Forest) which is 5 ha in extent and surrounded by fields on three sides and a scrub-covered hill on the fourth. Water drains from the Forest in three directions, providing habitats for three separate populations of *N. apoda*, one of which was outside the reserve and separated from the others by a stock water race which bisects the reserve. This population was used only for the collection of a few aestivating fish.

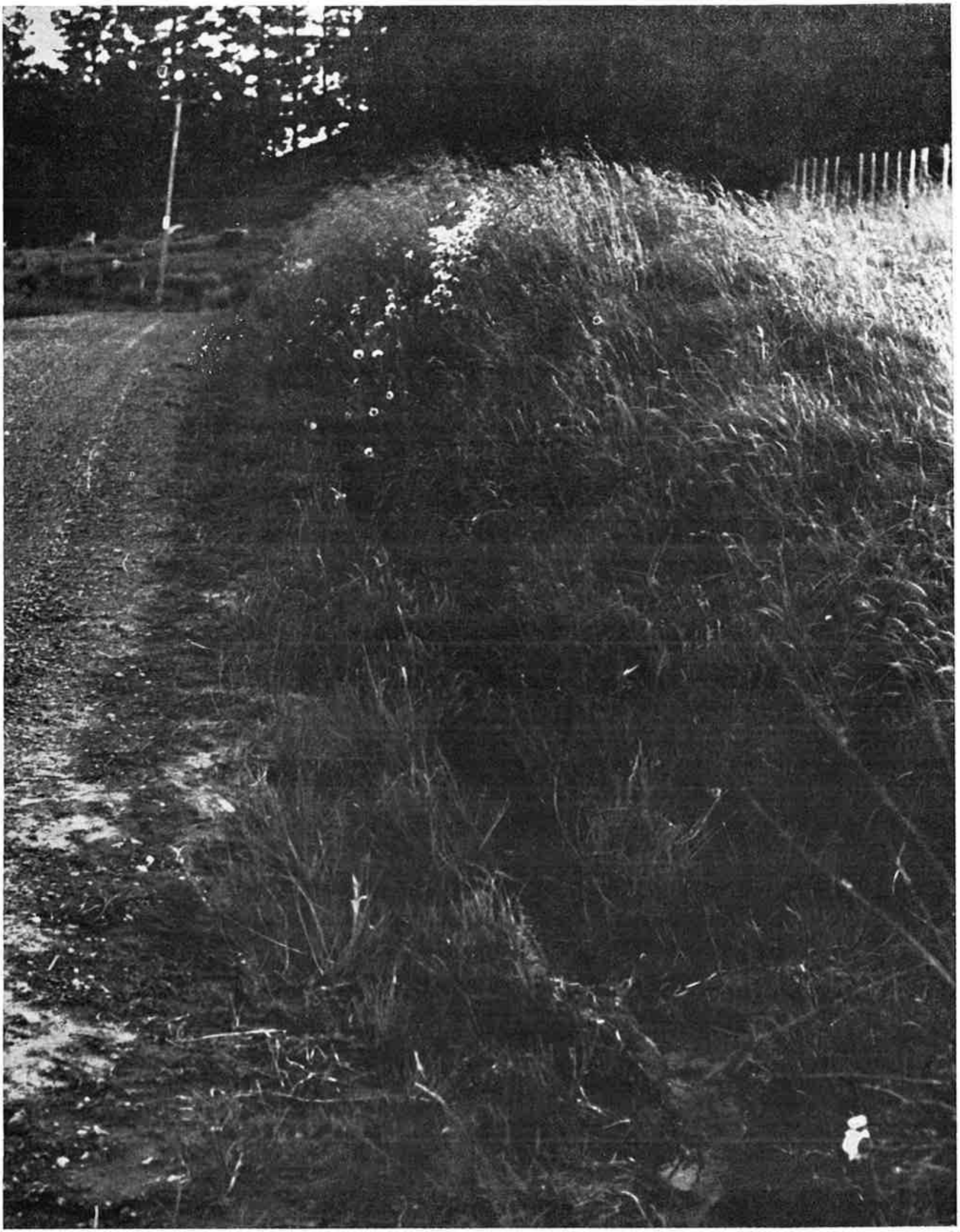
All the Forest waters begin to dry up in summer. The period of total drought (no surface water at all) is usually from mid February to mid April, but the effective drought (insufficient water to allow free movement of adult mudfish) is longer and may extend from late January to late April.

Habitat A is a shallow trough up to 0.5 m deep, with a low wet area around it which extends from the trees into an open pasture and which gradually narrows down to an artificially confined drainage channel. The demarcation between the wet area (about 450–500 m^2) among the trees and the boggy part (350–400 m^2) of the pasture is abrupt (Fig. 5). However, it is lessened partially by the presence of floating duckweed (*Lemna minor*), which extends among the trees for a few metres (the distance varying with the wind speed and direction) and provides cover in the pasture, and also by the presence of a few old logs in the boggy area of the pasture.

Habitat B is an extensive area of winter pondage with a total area of about 5000 m^2. It is on the opposite side of the Forest to habitat A, from which it is separated by a low rise. This area also extends into open ground, but the water is much deeper and more pond-like than at A, and *N. apoda* inhabits only the fringes of the shallow water (less than 0.5 m deep) among the trees, where cover is provided by tree roots, branches, and detritus (Fig. 6) and where aquatic vegetation is absent.

AREA 3

This is an area of pasture land at Dalefield, where *N. apoda* is found in both permanent and impermanent waters. A major semi-permanent spring forms a well-defined stream with a series of lesser springs rising on the gravel terraces on either bank. One of these springs rises in and fills a swampy depression, which is covered by spongy turf. The other springs have a cover of grasses and watercress (*Rorippa* sp.), the density of which varies considerably, depending on whether or not cattle are grazing the pasture. Area 3 differs from both Hinau and Forest in that water is normally present in the main stream throughout the year. Only in the exceptionally dry weeks of February 1973 did the top 200–300 m of the main course dry up.



[*K. F. Maynard photograph.*

Fig. 3: Hinau 1B; the ditch is 300–400 mm wide and 400 mm deep.

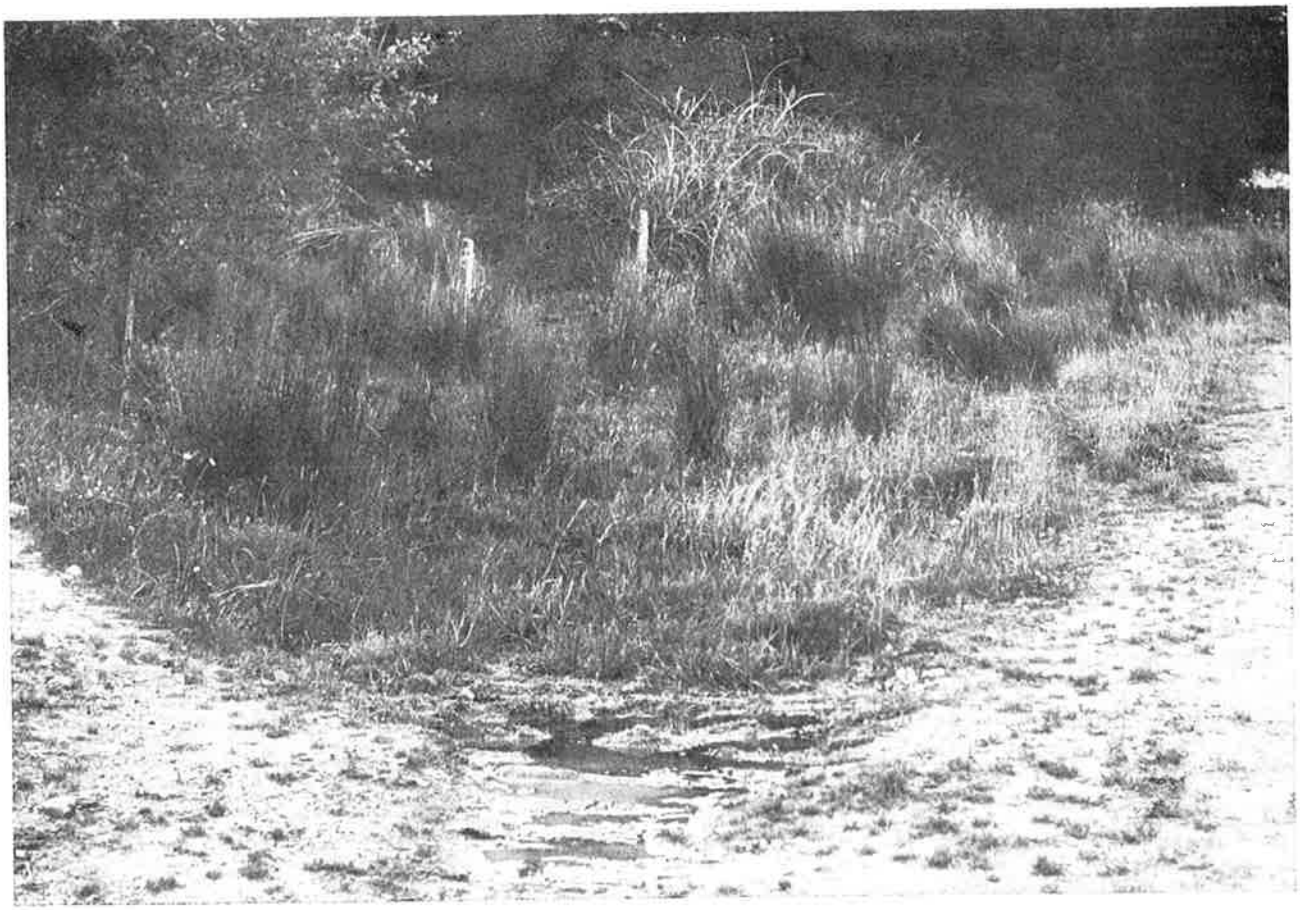


Fig. 4: Hinau 1B where the ditch breaks down into a small area of wet turf with a few clumps of rushes.

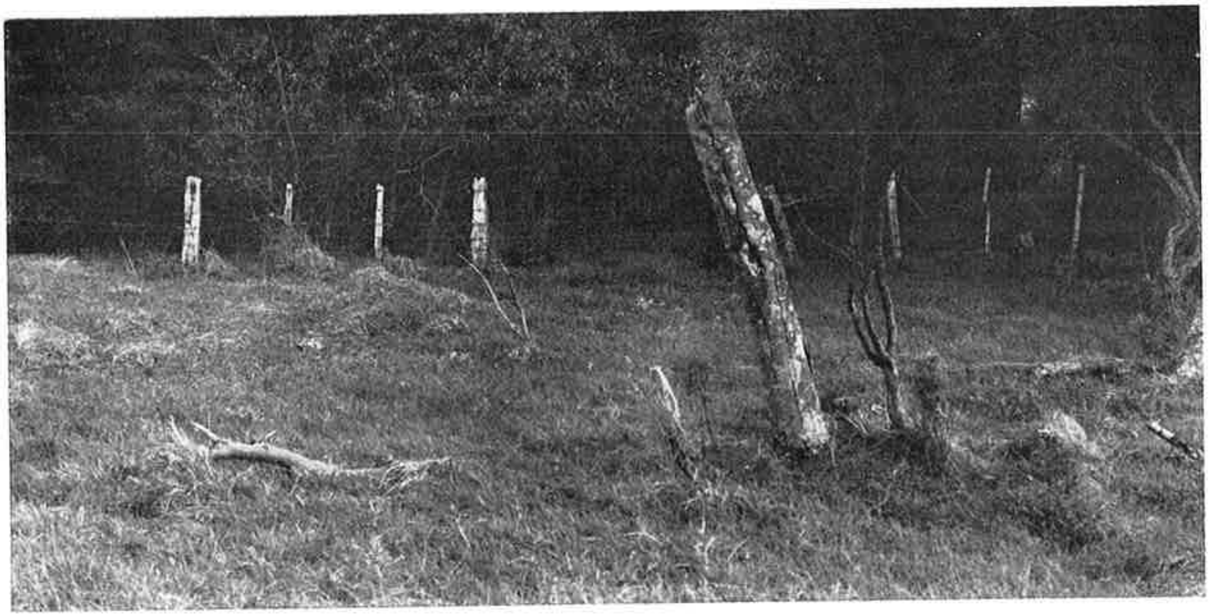


Fig. 5: Forest 2A, showing the boundary between forest and pasture.

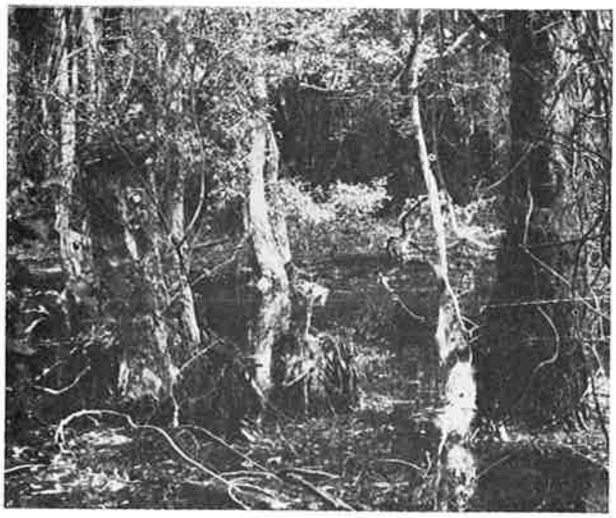


Fig. 6: Forest 2B, showing the shallower area of winter pondage (*N. apoda* habitat).

Habitat A is the main watercourse at Dalefield. It is 4.5 m wide and normally has dense cress cover lining the margins. The bed is gravel, but the marginal vegetation traps much mud and detritus and this results in a swift gravel stream less than 1 m wide which flows at 10 m per minute. It is bordered by spongy cushions of cress and grasses in which *N. apoda* is present. Only when cattle are short of feed in late summer may this vegetation be depleted seriously.

Habitat B is a swampy depression 60 m in circumference, where there is permanent water, but very little flow.

Habitat C consists of a number of small gravelly shallow side springs which are inhabited by *N. apoda* only when watercress provides some cover. They are dry in summer.

Habitat D is a watercourse issuing from two sets of field drainage pipes. The bed is firm, since it is a shallow depression of turf, well trampled by farm stock, on gravel. Cover is composed of lush grass and water starwort. The course is dry in summer (Fig. 7) and joins up with the main watercourse A by a serpentine route of over 500 m. *Neochanna apoda* is present only within the first 50 m below the drainage pipes.

Fig. 7: Dalefield 3D, the hard-bottomed watercourse which, unlike other Dalefield habitats, regularly dries up. *Neochanna apoda* survives the drought in the field pipes from which the course emerges.

METHODS

Most fishing for adult *N. apoda* was done with a battery-powered portable D.C. electric fishing machine carried on the operator's back or used from a fixed point with the aid of a cable reel. Although large numbers of fish often were caught by this method, it was inconsistent and had severe limitations when used in swamp conditions (Eldon 1968, Cadwallader 1975b). Two examples which occurred in the present study illustrate the difficulties: electric fishing was carried out by two experienced operators in a swampy paddock ahead of an excavator, and though no fish were seen by the operators, many were revealed subsequently by the excavator; on several occasions the numbers of fish caught on the first run through a station were equalled by a subsequent, equally intensive run.

Normally fishing was done in daylight, but some night fishing was carried out with the aid of electric torches. The results of night fishings were usually better than those done by day, probably because fish were not concealed in their daytime cover.

Small plastic traps made from lunch boxes were used to a limited extent, but were not very successful.

Fry were caught with an aquarium net of 1-mm stretch mesh mounted on a plastic-coated wire frame. The fry were netted from open water where they could be seen or were caught when the net was blindly pushed into vegetation as quickly as possible. Both methods were satisfactory and often the latter revealed the presence of fry where none were observed otherwise.

Fish to be retained were anaesthetised in chlorbutol before being preserved in 10% formalin, or they were deep frozen if they were required for otolith studies or for weighing.

Adult total lengths (TL)—length from snout to tip of caudal fin—were read to the nearest 1 mm on a measuring board. Fry were measured to the nearest 0.1 mm with a stage micrometer on a binocular microscope.

Cadwallader (1974) found that both length and weight of *Galaxias vulgaris* Stokell were affected by preservation in formalin, the length shrinking and the weight increasing. The greatest effect was within the first day, shrinkage continuing at a decreased rate thereafter and weight decreasing towards its initial

TABLE 1: Shrinkage of *N. apoda* in preservative. The data are from 10 different samples kept for various periods of time

Live length (mm)	Preserved length (mm)	% shrinkage
19	18	5.3
19	18.5	2.6
33	32	3.0
36	35	2.8
38	37	2.6
38	36.5	3.9
38	36	5.3
38	37	2.6
39	38	2.6
41	40	2.4
42	40	4.8
42	41	2.4
44	43	2.3
50	48	4.0
52	49.5	4.8
58	56.5	2.6
59	57	3.4
61	59	3.3
62	60	3.2
62	60	3.2
62	60	3.2
65	63	3.1
65	63	3.1
66	64	3.0
66	65	1.5
67	64	4.5
67	63	6.0
68	66	2.9
68	66	2.9
68	64	5.9
70	67	4.3
70	68	2.9
70	68	2.9
71	69	2.8
74	71	4.1
77	75	2.6
77	75	2.6
78	76	2.6
79	76	3.8
79	76	3.8
79	77	2.5
81	80	1.2
81	79	2.5
83	82	1.2
85	83	2.4
86	84	2.3
87	84	3.4
87	84	3.4
97	94	3.1
111	107	3.6
114	110	3.5
115	114	0.9
117	116	0.9
119	117	1.7
125	120	4.0
126	121	4.0
126	123	2.4
129	125	3.1
133	125	6.0
135	133	1.5
138	133	3.6
142	139	2.1
144	140	2.8
146	142	2.7
151	147	2.6
169	160	5.3

Mean shrinkage = 3.2% n = 66

value. Other workers (Hoar 1939, Parker 1963, Stobo 1972) have had similar results with other species of fish.

In this study no allowance was made for the length of time the specimens were kept in formalin, but an adjustment of 3.2% was made in lengths of all preserved fish, based on the data in Table 1. All condition factors (length-weight relationships) were derived from actual live lengths. Weights were obtained from fish which had been frozen and later thawed. They were weighed to the nearest 0.1 g on a Metler balance.

Many of the fish used for length-frequency analysis and all those used for marking were anaesthetised with MS 222, measured, and returned to the capture site.

Some fish were marked by injecting dyes. Cadmium sulphide (Hansen and Stauffer 1964) and National Fast Turquoise P.T. (National Fast Blue 8 G.X.M.) (Kelly 1967) were injected under the skin with a hypodermic needle. Six body positions were used for the injections (three on each side)—above the pectoral fin, mid lateral, and above the anal fin. Different combinations of these positions made it possible to mark many fish individually. For instance, 41 combinations could be achieved by use of only 1 colour in not more than 3 positions on any one fish. The first batches of dye-marked fish were retained overnight to determine whether there were any ill effects from the injections. None were recorded.

In addition to individual dye marking, some batch marking was done by clipping off the top or the bottom of the caudal fin.

Because mudfish have no scales, attempts were made to determine age from the otoliths. Two methods of treating the otoliths were tried. Firstly, the otoliths were mildly scorched on a knife blade held over a low flame and then examined, either whole or split across the centre, against various backgrounds under a binocular microscope. Secondly, the whole fresh otolith was viewed in glycerine against a mat black background.

Each otolith comprised a central dark area surrounded by alternating wide white opaque zones and narrow dark translucent (hyaline) zones (Fig. 8). These zones were assumed to represent periods of fast and slow growth respectively, and the age of the fish was determined by counting the number of hyaline zones. The number of hyaline zones recorded in separate counts of one otolith did not always agree. When this occurred, a third examination was made without reference to the first two and the results were compared again. If two of the readings agreed, that figure was taken as the zone count, but if none agreed, as occasionally happened when numerous fine rings were present, the data were discarded.

At first none of the results obtained from the examination of otoliths appeared satisfactory, but later analysis of the data showed that the age determinations were probably valid.

The condition factor (CF) was derived from the expression

$$CF = \frac{10^7 W}{L^3}$$

where W is weight in grams and L is length in millimetres.

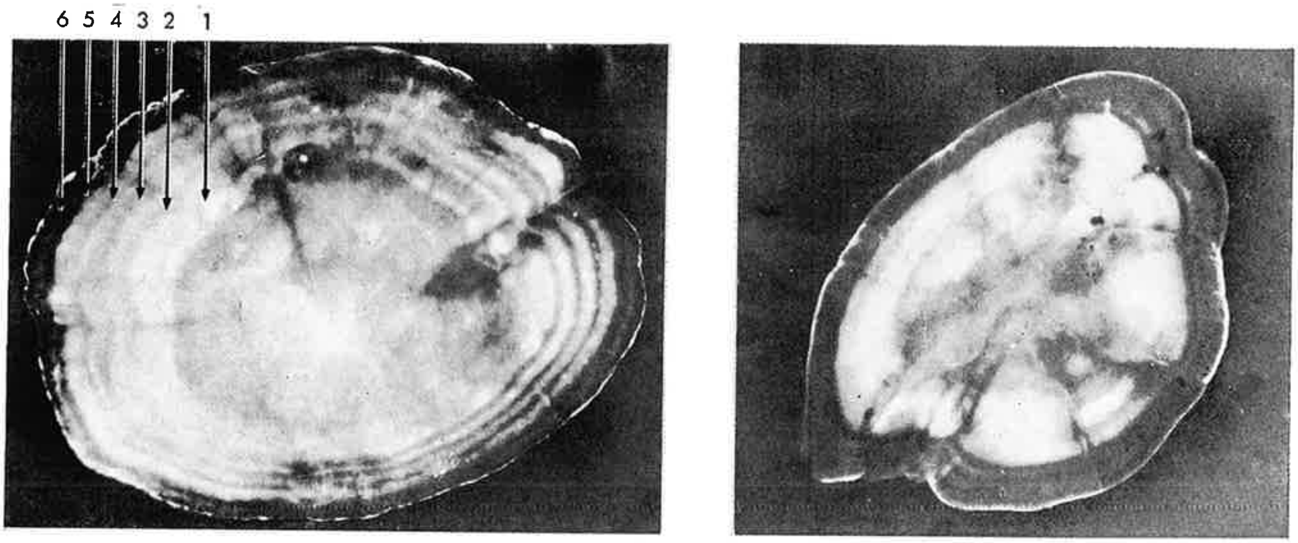


Fig. 8: Hyaline zones in otoliths. Left: Otolith measuring 2.7 by 2.1 mm, taken from Hinau fish of TL 138 mm and age 6+ recaptured nearly 4 years after being marked at TL 112 mm. Right: Otolith measuring 1.8 by 1.3 mm, taken from Dalefield fish of TL 75 mm and age 3+.

The degree of sexual development was assessed arbitrarily from the appearance of the testes or the size of the eggs:

Stage 0: No development obvious to the naked eye.

Stage 1: Sex of dissected fish obvious to the naked eye.

Stage 2: Testes fattening; eggs 0.9–1.4 mm in diameter.

Stage 3: Advanced or ripe. Milt running; eggs 1.5–2.6 mm in diameter.

Stage 4: Spent.

In ripe females the following year's eggs were already recognisable. Stage 4 females therefore progressed directly to Stage 1.

Two methods were used to assess stomach contents: the numerical method, in which the numbers of each food organism were calculated as a percentage of the total number of organisms, and the occurrence method, in which the numbers of fish containing each organism were calculated as a percentage of the total number of fish examined.

Temperature records were obtained from Hinau 1B with maximum-minimum thermometers, from other field localities by spot checks, and in the laboratory with maximum-minimum thermometers and a probe connected to a strip chart recorder.

Brief tests were made on the reaction of *N. apoda* to depleted oxygen levels. Air lines from sealed flasks half filled with water were connected by T junctions to a hose from a running tap. This reduced the dissolved oxygen, the level of which was recorded with an oxygen meter. Individual fish were placed in the flasks, and control fish were placed in similar flasks containing water at the same temperature, but not de-oxygenated.

HABITAT

Although *N. apoda* is primarily a swamp dweller, it was found in clean water, and a feature of its habitats was that usually there was some water movement, albeit very slight. This movement may not be permanent, as the water may become stagnant and dry up completely at times. Fish were found in clean fresh spring water (as at Dalefield), and they formed dense populations in small weed-choked ditches and less dense populations in shallow forest puddles and troughs littered with debris. However, they were found rarely in foul-smelling water.

The type of cover used by *N. apoda* was related to fish size, especially in the Forest habitats, where leaves, twigs, and sticks on the forest floor provided cover for small fish, whereas larger fish occupied holes under roots of standing trees. Neither large nor small fish were normally present where the depth of water above the detritus exceeded about 0.3-0.5 m. Where deep water occurred the fish were always caught in the shallows around the margins, their number depending on the amount of cover. If there were no shallows, *N. apoda* was absent, even if cover was available.

The only other species of fish to be found frequently in the same waters as *N. apoda* was the short-finned eel (*Anguilla australis*). Eels were found rarely in *Neochanna* habitats at Hinau, regularly though sparsely at Forest, and abundantly at Dalefield. The eleotrid *Gobiomorphus breviceps* (Stokell), which migrates locally (Hopkins 1970), and *Galaxias divergens* Stokell both occurred in the lower Hinau

TABLE 2: Water temperatures (°c) **in the study areas in 1969**

Month	Hinau Maximum-minimum thermometers Min.	 Max.	Forest Spot checks Min.	 Max.	Dalefield Spot checks Min.	 Max.
Jan						
Feb					13.0	20.0
Mar					13.5	16.5
Apr	15.0 (spot check)				9.0	14.0
May	6.0	15.0				
Jun	4.0	9.5	6.0	9.0	12.0	13.0
Jul	4.0	10.0			5.5	11.5
Aug	5.5	9.0			12.0	12.5
Sep	6.5	10.5			12.0	12.0
Oct	8.5	12.5				
Nov	10.0	21.5			12.0	15.0
Dec			16.5	21.5	13.0	13.0

Valley. *Galaxias divergens* was confined to a permanent spring where *N. apoda* did not occur and *Gobiomorphus breviceps*, though it sometimes migrated into temporary water, did not appear to invade the *Neochanna* habitat.

The temperature range recorded at Hinau was from 4° to 21.5°c, at Forest from 6° to 21.5°c (in the open field), and at Dalefield from 5.5° to 20°c, but the Dalefield temperature was usually fairly constant at 12°–15°c (Table 2).

GENERAL BEHAVIOUR

Adult mudfish are nocturnal (Eldon 1968). However, fry are active both by day and night and were observed to be free swimming; they may be found congregated in groups near the point of hatching when very small, but there is no evidence of shoaling behaviour in the groups. As the fry grow they disperse if there is sufficient water to allow this, and they gradually become more cryptic and nocturnal until all the daylight hours are spent under cover. This usually occurs when the fish are about 30 mm long. Cadwallader (1975a) reported a similar behaviour change from juvenile to adult for *N. burrowsius* and showed that this was reflected in the brain structure. The relative sizes of the optic lobes and the forebrain were shown to change, the former decreasing in importance and the latter increasing in adult fish as compared with juveniles.

In open water during the day both young and adult fish buried themselves deeply among the roots of whatever vegetation was available; if old logs or broken fence posts were present, fish could always be found congregated under some of them.

The habit of many large mudfish of living under tree roots in the Forest resulted in the period of activity of these fish ceasing in summer earlier than might be expected from the appearance of the water level. This was because standing trees did not occur in the wettest places, but grew around the margins of troughs and depressions subject to regular flooding. As the water level dropped these hiding places under trees were cut off from the main body of water. Many smaller fish, however, continued to feed and grow for as long as there was sufficient detritus to give them cover and sufficient water to allow them mobility. At Forest 2B all *Neochanna* activity ceased before the last of the water was gone from the deeper parts. The fish did not inhabit deep water, and they did not move into it when their marginal habitats dried out.

In early January before the water level dropped far enough to inhibit movement of adult fish, the numbers of fish caught in the open pasture part of Forest 2A declined considerably, and it seems likely that fish had moved back into the forest before their access to the tree roots was blocked. Some fish were later found aestivating under the few old logs which lay in the pasture section of the habitat, but they were few compared with the numbers recorded during winter and spring. It is not known what may have prompted any movement from pasture to forest, but possibly it was temperature motivated.

Although active during winter immediately after aestivation, *N. apoda* was more active in water warmer than 10°c. Fish kept in captivity showed reduced activity at lower temperatures. This is surprising, because maximum-minimum thermometers left at Hinau 1B showed that the temperature never rose above 10°c from June to early September.

AESTIVATION

The first *N. apoda* described was found, reportedly, under 4 ft of clay (Hector, quoted by Günther 1867). Several early reports describe the fish being discovered in similar conditions (Fitzgerald 1873, Vollams 1873) and claims were made that some were torpid when found (Vollams 1873). Of the 98 *N. apoda* which I have found in conditions of dormancy (that is, in a state of inactivity) because of drought, none have been torpid.

About 50 fish found in the Forest were buried singly from 30 to 400 mm deep in damp vegetable detritus (leaves, twigs, seed pods, etc.) which lay on an impervious base of blue clay. Only a few of these fish had recognisable holes leading through the detritus to their hiding places. There were no holes in the clay.

Other fish found aestivating in man-modified habitats, for example, the pasture part of Forest 2A and the open part of Hinau 1B, were all hiding under objects lying on the surface of the ground. When surface objects such as logs, planks, and discarded cardboard boxes were lying on earth or clay, the fish under them were always on the surface and immediately obvious when the object was removed. Only when the object lay on vegetation, such as matted grass roots, were the fish sometimes in holes or burrows. Only one fish gave the impression of being torpid, in that it did not immediately react to its exposure, but this fish instantly became active when water was poured on to the ground.

At Dalefield 3D (Fig. 7) there were no trees, logs, or rubbish, and the bed of the impermanent watercourse was hard, compacted earth up to 200 mm deep lying on gravel. In late summer this topsoil and underlying gravel retained no moisture and it did not seem conceivable that *N. apoda* could survive there, yet each autumn small numbers of both adults and fry were found. These fish occurred only at the head of the course and did not extend down through the open fields; so it was unlikely that the fish were migrants from other Dalefield habitats. During the summer drought fine gauze bags were clamped over the outlets of the two sets of field pipes feeding this watercourse, and after the drought broke, the place was visited as soon as possible and the bags were removed; one was empty, but the other contained three adult *N. apoda*.

It was not always possible to identify aestivation sites in completely modified habitats. A drainage contractor collected 27 specimens from one of two "pockets" of fish exposed by an excavator in a boggy section of a grass field. Unfortunately, when these fish were found the habitat was completely destroyed by the excavator and no useful examination of the locality was possible.

Several observations indicate that mudfish sometimes do not find a suitable place to aestivate, even when burrowing would appear to be possible. Two dead fish were found on matted damp grass beneath a sheet of corrugated iron, where they had presumably died from heat, as the iron was fully exposed to the sun. The skeleton of a fish was found on bare earth beneath a plank in a ditch which retained no moisture at all.

On another occasion a mudfish was found dead and fully exposed on damp mud in a saucer-like depression in the bed of the stream at Hinau 1A. The mud was soft and there was no indication that the fish had made any attempt to burrow. The stream was still flowing and the fish had been feeding shortly before death, for its stomach contained 14 recognisable animals; so it is unlikely that sickness or injury were the causes of its failing to burrow.

In the Forest, as already indicated, small mudfish spend the summer dry season in the detritus of the forest floor, but few of the large fish are found there. They spend the season in holes under the roots of standing trees (Fig. 9). Many of the holes lead into broad open caverns and, though only one of these was opened up (a minor one under the roots of a sapling, where there were three fish), physical contact sometimes could be made by thrusting a hand into a hole. The fish were lying on the floor, and they wriggled out of reach when touched.

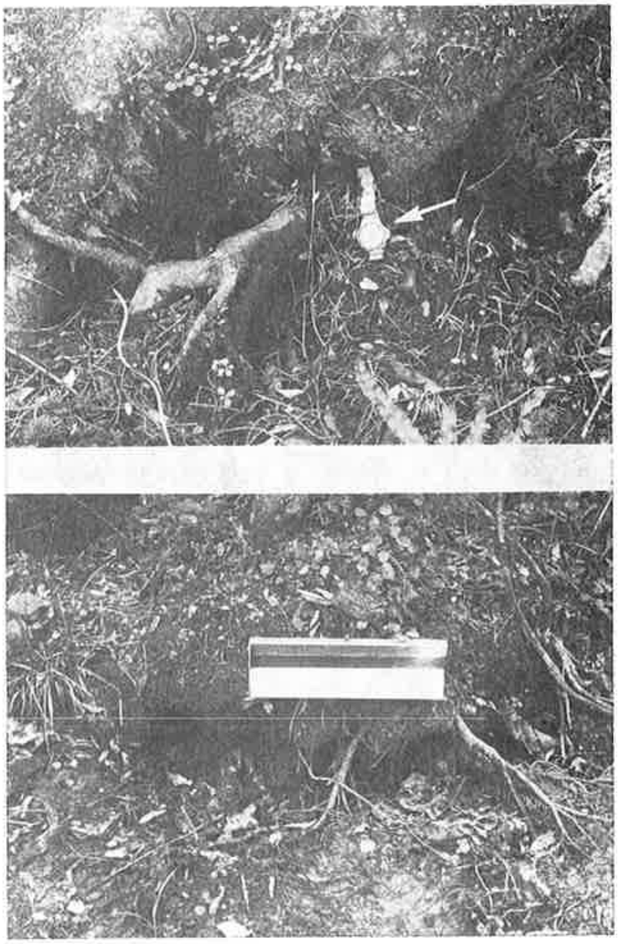


Fig. 9: Holes under trees where *N. apoda* aestivates and breeds. The wrist watch (arrowed) indicates scale. The measuring board is 300 mm long.

On four occasions artificial drought conditions were imposed on captive adult fish by slowly siphoning the water out of a tank and leaving no surface water on the substratum. Although the substratum normally was harder than it would be in the natural habitat, a fish trying to burrow could be expected to make some impression. When there were stones or wood under which the fish could hide, they curled up out of sight. When there were no hiding places, the fish remained on the surface of the sand or mud, sometimes lying on their backs.

Fry appear to be able to survive short recurrences of drought which may occur after eggs have hatched. In late April 1973 fry were known to be present in a small side pool of Forest 2A. Because there was a delay before further rain fell, the pool dried up and no surface water remained by 11 May. On 14 May, after heavy rain, 52 fry were collected from this pool. Their size range was 9.1–10.9 mm, mean 9.87 mm (preserved lengths). This is larger than the size of newly hatched fry (8–9 mm live lengths) and indicates that the fish had survived from an earlier period.

To determine if fry can survive drought conditions, a tank with a false base of stainless steel mesh on a wooden frame was set up with 30 mm of mud and detritus covering a layer of sand (Fig. 10). Three control tanks without substrata were also used. Fourteen *N. apoda* fry were placed in each tank and given 7 days to settle down. The water level of the experimental tank was lowered over a 2-day period until it was level with the bottom of the false base. The mud and detritus were thus kept moist but not waterlogged.

At this time the control tanks contained 6, 10, and 13 fry respectively. It is not known how many were surviving in the experimental tank because of the amount of cover present.

Ten days later the water level was raised and after the detritus had softened and broken up four live fry were recovered. All but one of the control fish still survived.

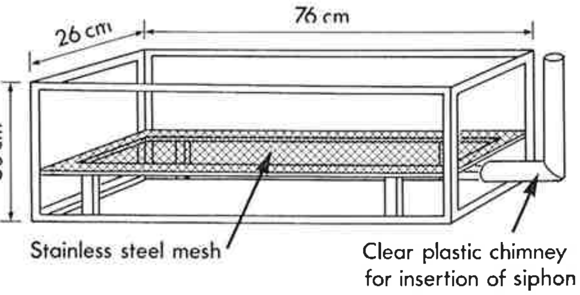


Fig. 10: Tank used in some aestivation experiments.

WEIGHT LOSS AND LOSS OF CONDITION DURING AESTIVATION

Weight loss varied under simulated aestivation conditions and there was also reduction in body length of all fish (Table 3). Similarly, body shrinkage during aestivation has been recorded in the African lungfish (*Protopterus* sp.) (Herald 1961) and has also been recorded for New Zealand eels during hibernation (Burnet 1969).

One group of six fish was subjected for 68 days to conditions which would induce aestivation. They were kept in a tank in a dimly lit and seldom visited basement. Humidity was maintained in the tank

TABLE 3: Shrinkage, weight loss, and loss of condition in two groups of *N. apoda* during laboratory aestivation

	Before aestivation			After aestivation			Mean % reduction
	Range	Mean	S.D.	Range	Mean	S.D.	
First group, 68 days							
Weight (g)	11.2–15.5	13.6	1.7	10.3–14.2	12.6	1.7	7.8
Length (mm)	126–140	132	6.5	125–138	131.2	6.3	0.9
CF	54.1–64.5	58.6	4.0	52.9–61.2	55.5	3.3	5.2
Second group, 63 days							
Weight (g)	5.8–11	9.1	1.85	4.8–9.1	7.6	1.5	16.2
Length (mm)	94–117	111	8.6	92–115	109	8.5	1.8
CF	61.2–70.5	66.1	3.3	53.4–62.4	58.5	3.0	11.5

TABLE 4: Condition factors of fish at various reproductive stages and percentage of weight contributed by ovaries and testes

	Condition factor			% of total weight contributed by testes or ovaries		
Category	Mean	Range	S.D.	Mean	Range	S.D.
Juveniles						
Before aestivation (n = 14)	55.5	45.0–67.2	5.3			
End of aestivation (n = 15)	51.1	41.3–69.2	8.1			
Adults						
Before aestivation (n = 10)	62.0	55.6–67.2	3.5	7.05	3.8–14.5	3.3
Aestivation about to end or just ended						
Males (n = 5)	51.7	48.6–57.9	3.7	9.1	8.7–9.7	0.4
Females (n = 5)	57.7	52.4–61.7	4.0	21.6	16.5–26.0	4.7
Aestivation ended						
Ripe and part spent males (n = 15)	51.8	39.0–65.0	7.6	5.1	3.3–7.0	1.3
Spent females (n = 7)	42.3	36.7–50.8	4.7	Negligible		
Juveniles and adults recovering						
April-May (n = 24)	59.4	47.4–70.3	5.8	4.8	3.9–5.4	0.6
Juveniles and adults						
June (n = 25)	65.3	49.5–81.9	7.4	0.64	0.12–1.46	0.2

by sealing it with plastic sheeting after the water had been siphoned out. The fish hid under stones, but apparently made no attempt to bury themselves in the fine gravel and sand which formed the bottom material. One fish entered a length of 12-mm diameter pipe set into the sand; this fish died. The remaining five survived. Temperatures inside the tank ranged from 10° to 21°C.

A second group of six fish was subjected to aestivation conditions for 63 days in the tank with a false base (Fig. 10). Fine gravel and sand were placed on the mesh with stones for cover. The water was siphoned out of the tank so that enough remained to permeate through the sand and gravel. The fish were known to move about from cover to cover during the period. All six survived, and at the end of the experiment one fish was lying on its back. The tank air temperature during aestivation ranged from 14.5° to 25.5°C.

Figure 11 shows the loss in weight and length of this second group of fish and their subsequent recovery. Table 4 shows the condition factors of fish taken from the wild before aestivation, towards the end of aestivation before spawning, and after spawning.

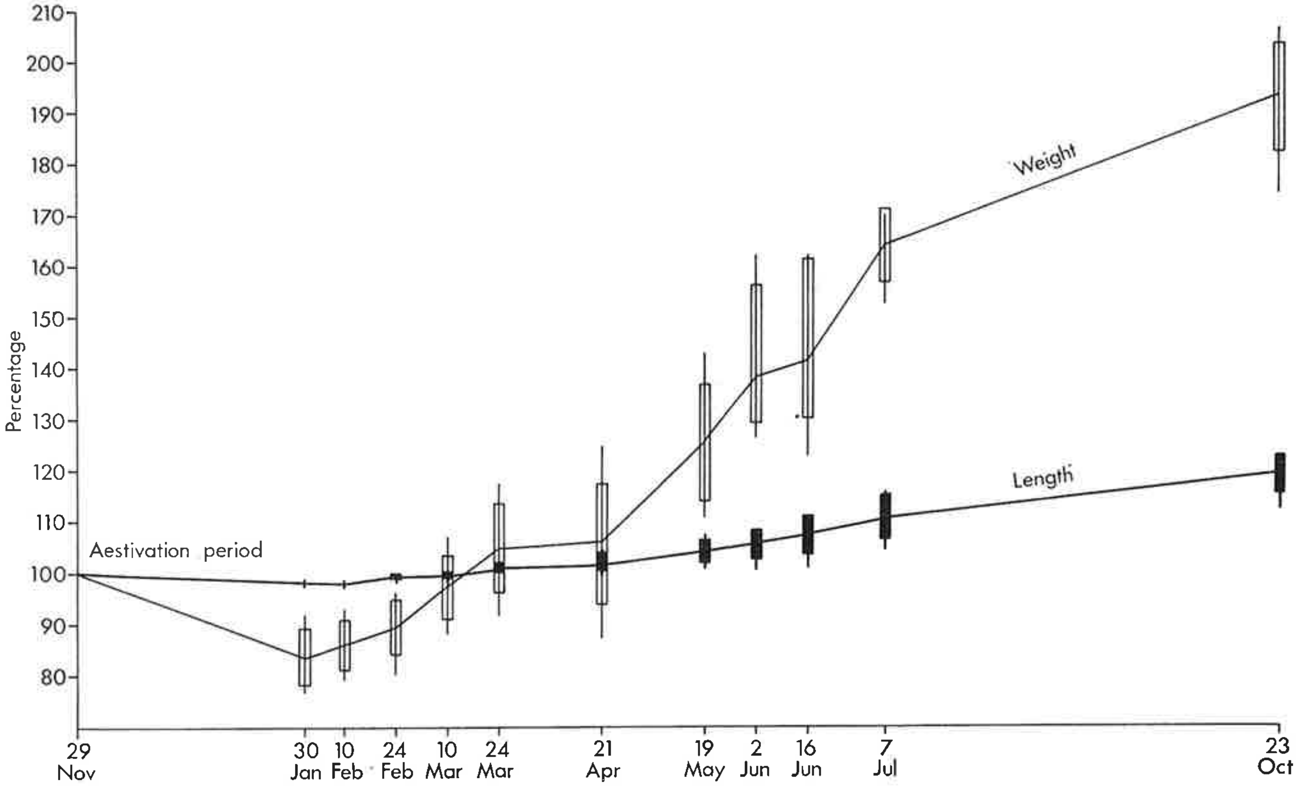


Fig. 11: Loss of weight and length (mean, range, and standard deviation) during aestivation and the subsequent recovery and growth of six fish kept in captivity.

REPRODUCTION

When mature, small females may have fewer than 200 eggs, large ones more than 1000 (Fig. 12). Preserved eggs measured from 2.4 to 2.6 mm in diameter when ripe and formed from 16% to 26% of the body weight of the fish. The gonads of males formed about 9% of the body weight. Spawning, at the end of aestivation, therefore greatly increases the overall loss of condition of the fish.

By late summer, before aestivation occurs, most adults are well developed sexually (Fig. 13), but large females caught in the Forest immediately after the return of surface water in autumn were spent. Males were partly spent, their testes contributing just over 5% of body weight (Table 4).

At times free-swimming fry with yolk sacs were captured from pockets of water beneath the roots of trees many days before any surface water had collected and fry were recorded in surface water as soon as it appeared.

From this evidence it is believed that spawning in the Forest occurred at the aestivation sites. This helps to account for the fact that repeated searches for the eggs of *N. apoda* were unsuccessful.

An experiment was devised to try to ascertain the spawning areas in the Forest. During the drought period a number of 18-litre tins, with the tops and bottoms cut out, were placed upright on the forest floor and driven into the ground (Fig. 14). They were placed on the bare mud in the deepest parts of the ponding areas, in the detritus in the shallows of these areas, in the forest beyond the normal margins of the water, and among the grass at the forest edge. No fry were found in any of the tins after the return of surface water, and the tins were resited at random in the ponding areas. A single fry was obtained from the resited tins. This was from a tin set close to an earth bank with two saplings growing on the margin. It was noted that fry were present in the vicinity of certain trees.

Since the trees seemed to be significant, the experiment was repeated the next year. Eleven tins were placed deliberately to prevent the dispersal of any fry which hatched in the holes under trees. Thirteen other tins were set at random on the forest floor as previously. As soon as enough water had collected to allow movement of fry the tins were examined and six of those around trees were found to contain fry. From 1 to 12 fry were seen in these tins, but the exact number could not always be determined because the fry still had access to the holes. No fry were found in any of the randomly placed tins.

These observations suggest that spawning had taken place when the first rains partially flooded the hollows in the holes under the tree roots and that the eggs hatched as soon as the holes were fully flooded. However, not all spawning in the Forest takes place at the first breaking of the drought. The retention of milt by mature males suggests this, and the continued recruitment of newly hatched fry for the first few weeks of winter confirms it (Fig. 15).

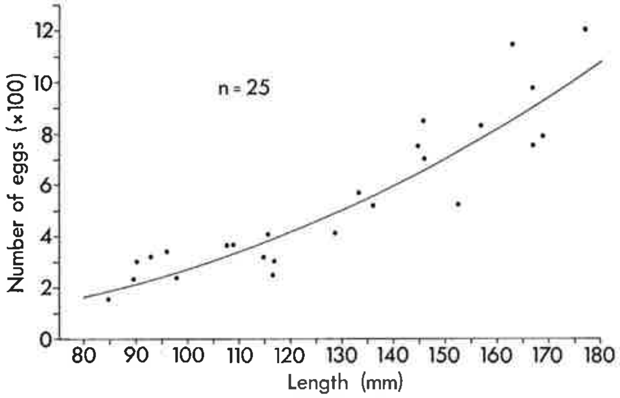


Fig. 12: Fecundity of stage 3 females. The line is drawn from a log-log regression.

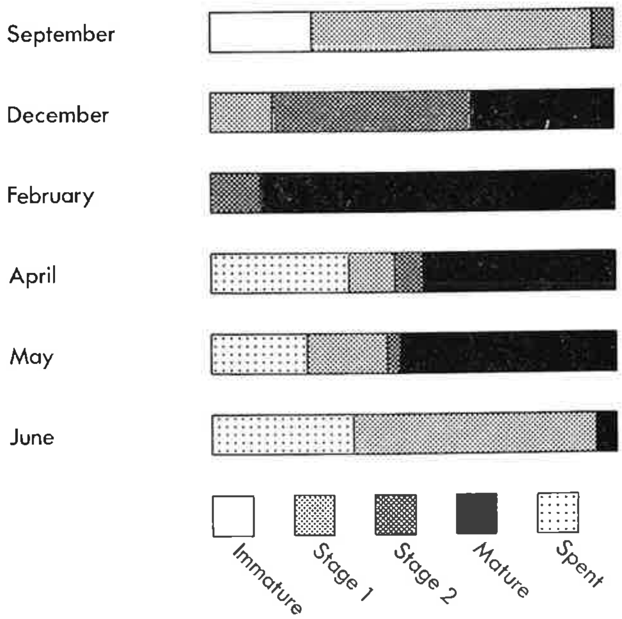


Fig. 13: Proportions of adult fish at various stages of maturity at different times of the year.

Of the smaller adults, under about 100 mm long, only a few males become mature at aestivation, but a few females are at development stages 1 or 2 at that

Fig. 14: Tins used to determine the location of spawning of *N. apoda*.

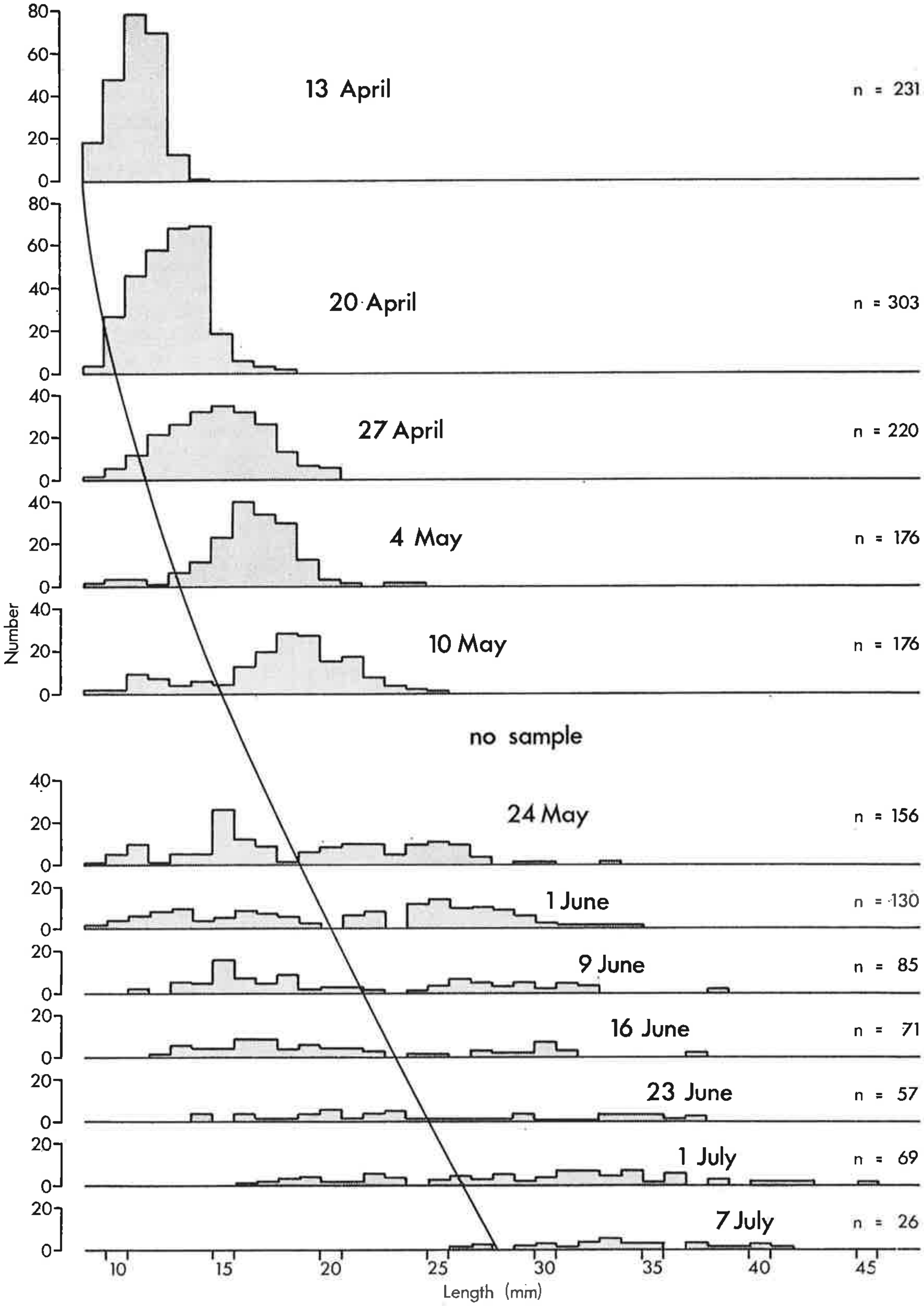


Fig. 15: Growth of Forest fry during first few weeks of life and continued recruitment over 2 months. The curved line separates the original fry (to the right) from later hatchings.

time and become mature in late winter or spring. Spawning therefore occurs spasmodically for several months and newly hatched fry have been recorded as late as August at Forest and September at Hinau. Where these later Forest spawnings occur is not known. Nor is there much information on the spawning at Hinau or at Dalefield, where the habitat is different and newly hatched fry are found in small numbers throughout most of the year (Fig. 16). At Hinau the whole of habitat B was searched carefully but unsuccessfully for eggs on many occasions in two successive years.

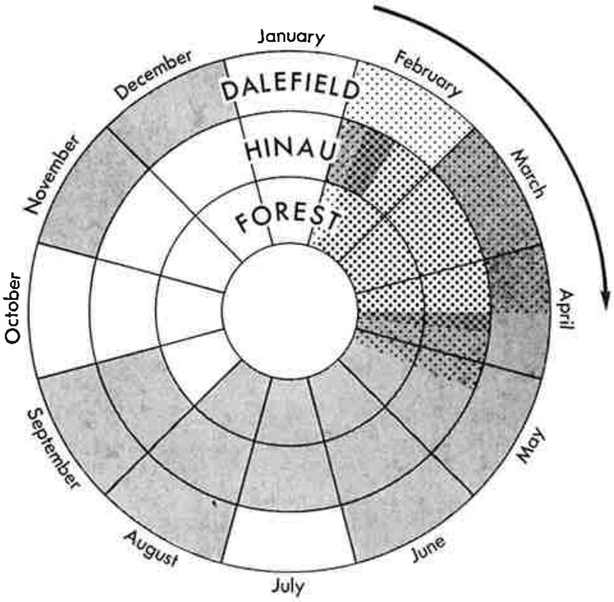


Fig. 16: Months (shaded) during which newly hatched fry have been found in the three areas. Heavy stipple shows period of normal drought. Light stipple shows period of occasional extension of drought.

At the time these concentrated searches for eggs were made at Hinau, the population of *N. apoda* there was much smaller than it had been formerly, but some large fish inhabited the open part of the habitat, and fry were recorded there each year.

On 26 April 1972, within 24 hours of the drought breaking, 11 adults were caught, none of which appeared to have spawned. Four of these fish—three females and one male—were examined and found to be fully mature. The remaining seven were fin-clipped and released at the capture site. Three days later, eight fish were caught at the same place, including six of those previously marked. Two unclipped and one clipped fish were examined; all were spent females. This suggests that spawning had not occurred when the fish were first active after aestivation, but that it took place within the first 3 or 4 days of surface flooding.

In the rest of Hinau Valley that year the habitats were partly flooded earlier than the open section of 1B, and *N. apoda* caught on 26 April were a mixture of unspawned and spent or immature fish. Twenty-eight *N. apoda* eggs with well-developed embryos were found in the stomach of one fish (see Table 8).

At Dalefield, also, searches for *N. apoda* eggs were made and on one occasion 10 eggs in various stages of development were sieved from gritty mud in a water-filled hollow about 300 mm in diameter formed by cattle tracks near the head of one of the side springs (Fig. 17). This spring was about 1.5 m above the level of the main watercourse and 8 m from it. Small fry were also present in the hollow, and fry had been observed there in a previous year. On other occasions fry were found in vegetation on the margins of the main course and in small pockets in the peaty turf of the swampy depression, and once they were found in a shallow gravelly spring head. Fry have also been observed in the gravel spring heads by R. M. McDowall (pers. comm.).

From the above evidence it appeared that breeding in the Forest took place before the drought had fully broken. Probably the first rains which soak the forest floor and raise the water table sufficiently to cause partial flooding of the hollows beneath the trees stimulate spawning, and later rains which totally flood the holes trigger off hatching. At Hinau spawning occurred within a few days of the drought breaking. This is because, unlike the situation at Forest, there is no gradual raising of the water table within the modified habitat. At Dalefield it appeared, from the locations at which fry were found, that spawning may occur in any shallow water at most times of the year.

Fig. 17: The pool in which *N. apoda* eggs were found at Dalefield. The thermometer spanning the pool is 300 mm long.

DEVELOPMENT AND GROWTH

After fish in an aquarium had deposited eggs over the glass sides of a tank above the waterline (Eldon 1971), several unsuccessful attempts were made to induce spawning under controlled conditions. Two eggs found in an aquarium took 21 to 28 days to hatch at temperatures ranging from 11° to 18°C (mean 14°C). The exact number of days taken to hatch is not known, because the time lapse between spawning and the discovery of the eggs may have been up to 7 days.

Of the 10 eggs found at Dalefield, only 2 hatched. Two days after being found they were judged to correspond in appearance with the description of stages 12 and 15 for *Galaxias vulgaris* (Benzie 1968). If development times and stages are roughly equivalent to those of *G. vulgaris*, these eggs would be at least 3 and 6 days old when found on 26 April, and their hatching on 18 and 14 May respectively would make their total hatching time about 26 days each. The temperature of the water in which they were found was 9°C and they were later kept at about 10°C. The hatching time for *G. vulgaris* at 14°C is 18 days (Benzie 1968).

Fry less than 9 mm in length were seldom caught, but those fry that were caught were suspected of being several days old. Therefore, by inference and from a few laboratory observations, it appears that they hatch at 8–9 mm in length. In an aquarium newly hatched fry sought the darkest corner for the first week or two and did not move about much, though they started to feed within 2 days of hatching. In the wild some fry of 9.5–10 mm, which had yolk sacs, had food in their stomachs.

The stomachs of a sample of 51 fry with a mean preserved length of 9.9 mm (range 9.1–10.8 mm) caught in May 1973 were examined. Twenty-one with a mean length of 9.7 mm (range 9.1–10.3 mm) had yolk sacs, but the stomachs were empty, and 30 fry with a mean of 10.1 mm (range 9.2–10.8 mm) had been eating.

Very small fry have a median fin fold which starts about 3 mm from the tip of the snout on the dorsal surface and slightly forward of this on the ventral surface (Fig. 18). The fin fold shrinks in both height and length as the fry grows and, on the dorsal surface, only the dorsal fin remains by the time the fry is 17–20 mm long. The ventral fold lasts much longer, until the fish is 34–38 mm long, when the anal fin alone remains. This is similar to the development of *N. burrowsius* fry (Cadwallader 1975b).

The growth rate of *N. apoda* is extremely variable, as may be expected in a fish which is subjected to variable periods of dormancy in a changeable habitat. When early ponding of water has permitted the build-up of small aquatic fauna such as copepods and chironomid larvae, growth is rapid, but it is much slower when prolonged semi-drought conditions confine a large number of fry to a limited pocket of water. Both favourable and unfavourable conditions for early growth may affect different groups of fry within the same population. Sometimes a return of drought conditions will force the premature aestivation of fry in one part of an area, whereas enough water remains in another part to allow other fry continued activity.

The variation which occurs in growth under different conditions was demonstrated experimentally by dividing a sample of fry of 9–10 mm in length into two groups. The first group, of 14 fry, was placed in a previously established tank 600 mm long by 300 mm wide, which contained natural food organisms, but only 3.5 l of water. The second group, of 50, was placed in a large trough containing about 40 l of water, and the fish were fed regularly with small aquatic invertebrates. After 21 weeks 36% of the fish in the first group were still alive, but they measured only 16.5–24 mm (mean 19.5 mm). Forty-eight percent of the second group survived and the fish measured 44–55 mm (mean 49.4 mm).

Because of the variation in growth rate, the prolonged spawning season, and the varying periods of aestivation, interpretation of length-frequency distribution data is difficult. There were few samples from Hinau which were adequate for interpretation, but data from the Forest fish were more useful. Mean lengths, range, and standard deviation were derived for most months during the first 3 years of life (Fig. 19A).

Although sample numbers from Hinau were generally too small to obtain adequate length-frequency distribution data, there were sufficient marked fish returns (Table 5) to provide some indication of growth. The method used was to

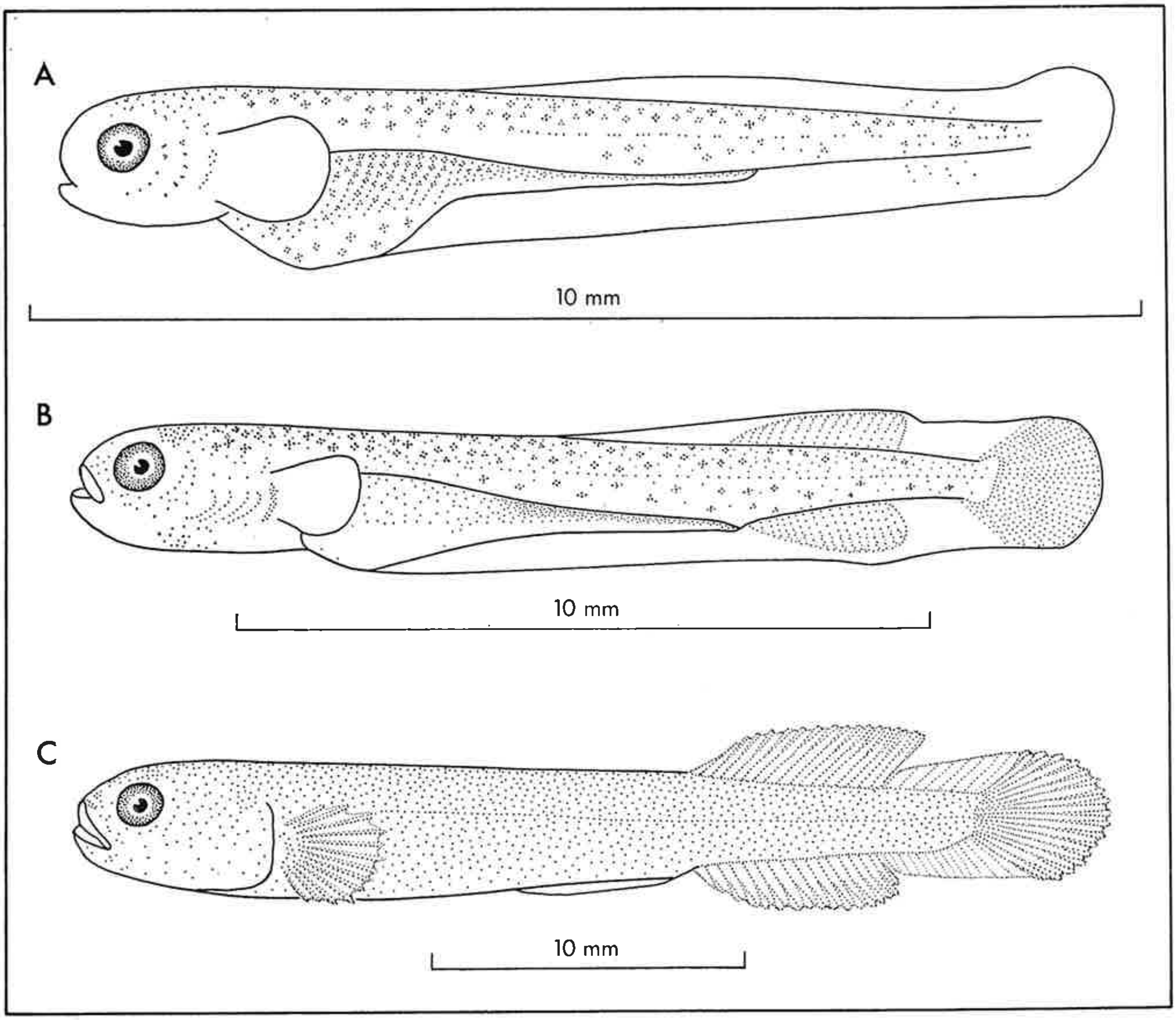


Fig. 18: Juvenile development of *N. apoda*. A: Recently hatched fry. B: Development of fins. C: Disappearance of fin folds.

determine the total growth of marked fish and divide the increment by the number of days at large. If the time between marking and recapture included an aestivation period, the number of days at large was reduced by 110. This figure was an estimate of the period of non-growth based on the usual aestivation period (about 12 weeks for adults) and the recovery time (as observed in the laboratory) between the end of aestivation and resumption of growth at the point reached before aestivation. This multiplied by 30 gave the monthly increment for growth months.

If aestivation had occurred the formula was

$$\frac{\text{Increment}}{\text{No. of days free } (-110)} \times 30$$

and if aestivation had not occurred the formula was

$$\frac{\text{Increment}}{\text{No. of days free}} \times 30$$

Monthly increment was then plotted against length

TABLE 5: Marked fish returns from Hinau

Length when marked*	Date	Length at first recapture	No. of days since last captured	No. of aestivations†	Increment per growth month	Length at second recapture	No. of days since last captured	No. of aestivations	Increment per growth month	Length at third recapture	No. of days since last captured	No. of aestivations	Increment per growth month	Length at fourth recapture	No. of days since last captured	No. of aestivations	Increment per growth month
50	3/9/68	69	93	0	6.3												
50	5/12/68	56	183	1	2.7												
62	5/12/68	84	183	1	9.3												
91	27/9/71	119	220	1	7.8												
93	15/2/68	113	165	1	11.1	119	32	0	5.7	122	28	0	3.3	135	73	0	5.3
99	1/8/68	101	126	0	0.6												
99	1/8/68	116	179	0	3.0												
112	5/12/68	112	53	0	0												
116	1/8/68	116	126	0	0												
118	5/12/68	118	183	0	0												
104	6/6/69	105	47	0	0.9												
106	1/8/68	115	61	0	4.5	127	77	0	4.8								
106	5/12/68	109	183	1	1.5												
109	1/8/68	122	126	0	3.3	122	78	0	0	129	193	1	2.7				
111	1/7/68	117	31	0	6.0												
111	5/12/68	115	183	1	1.8												
112	1/7/68	125	159	0	2.7												
112	1/8/68	129	126	0	4.2												
112	1/8/68	138	1366	4	0.8												
112	5/12/68	117	53	0	3.0												
113	1/8/68	120	126	0	1.8												
113	5/12/68	115	53	0	1.2												
118	1/8/68	122	33	0	3.9	129	93	0	2.4	129	271	1	0				
122	5/12/68	122	53	0	0												
129	5/12/68	129	53	0	0												
123	1/7/68	138	212	0	2.1												
127	1/8/68	142	126	0	3.6	145	53	0	1.8								
124	5/12/68	127	53	0	1.8	127	130	1	0	128	47	0	0.9				
129	5/12/68	132	271	1	0.6												
128	1/7/68	131	31	0	3.0	134	33	0	2.7								
133	5/12/68	133	271	1	0												
135	5/12/68	135	53	0	0	135	25	0	0	136	152	1	0.9	136	41	0	0
131	5/12/68	132	271	1	0.3												
130	1/7/68	141	159	0	2.1	142	271	1	0.3								
131	1/8/68	133	33	0	1.8	142	93	0	3.0								
141	27/9/71	143	220	1	0.6												
142	5/12/68	143	271	1	0.3												
159	1/7/68	163	31	0	4.2	167	33	0	3.9								
159	5/12/68	160	53	0	0.6												
155	5/12/68	155	230	1	0												

*Lengths and increments are in millimetres.
†110 days are deducted for each aestivation to obtain increment per growth month.

at time of marking. This gave a wide dispersal of points (Fig. 20).

Growth curves calculated from Forest length-frequency distribution data and from a simple linear regression of the Hinau marked fish returns were drawn (Fig. 19A). The length-frequency distribution data were plotted first, and the calculated growth rate of Hinau fish was then drawn in by use of material derived from the regression made with lata from Fig. 20, but this curve is clearly too low when the overall size of Hinau fish is considered (Hinau fish were in fact larger than Forest fish (Table 6)). This discrepancy may result from growth being adversely affected by the marking procedure, as indicated by the large number of zero growth returns which occurred over a considerable portion of the size range. A number of other factors may also affect its accuracy, particularly the varying time periods between release and recapture. Figure 19A suggests that growth will probably not be linear

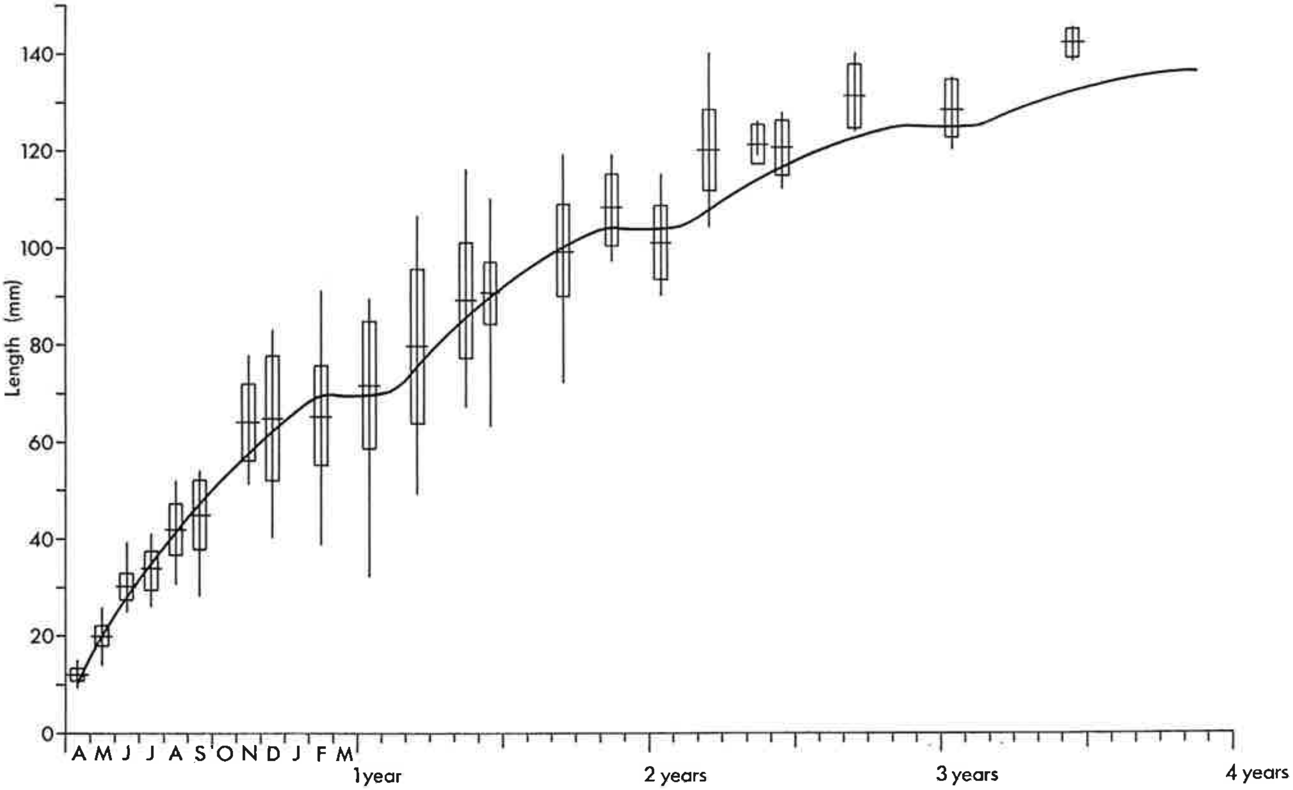


Fig. 19A: Growth curve showing length range, standard deviation, and mean length of Forest fish and calculated growth curve (continuous centre line) of marked Hinau fish. The latter curve may be over-flattened (see text).

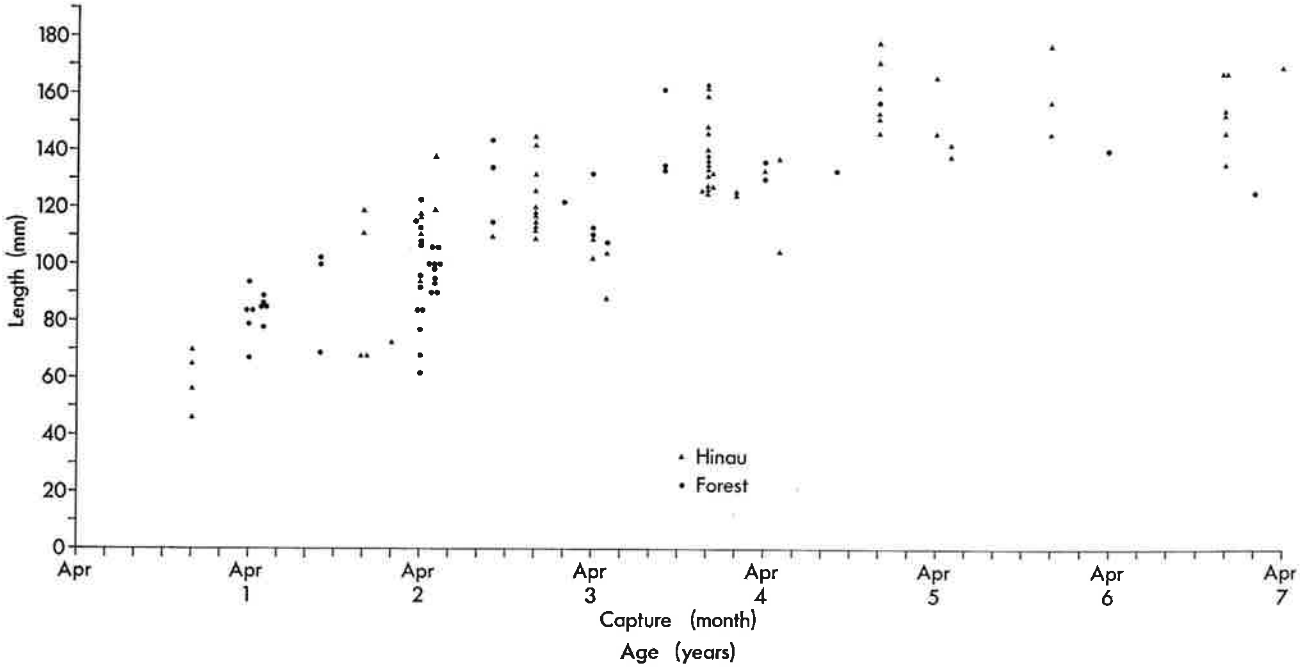


Fig. 19B: Month of capture and age in years determined from otolith readings plotted against total length.

TABLE 6: Mean size, standard deviation, and maximum size of post-fry (over 40 mm) from the three areas, with sex ratio and *t* value for comparison of the means

Data by area	Male	Female	Released unsexed	Combined	*t* statistic	Test inference	Sex ratio male : female
Hinau							
No. of fish	62	65	445	572	1.132	not significant at 5% level, accept H_0	1:1
Mean size (mm)	115.3	122.0	104.6	107.8			
S.D.	32.6	32.4	34.8	34.6			
Maximum size (mm)	178	177	194	194			
Forest							
No. of fish	71	89	1204	1364	0.191	not significant at 5% level, accept H_0	1:1.3
Mean size (mm)	100.7	101.3	88.0	89.5			
S.D.	20.6	21.7	22.9	22.9			
Maximum size (mm)	148	161	167	167			
Dalefield							
No. of fish	42	74	27	143	2.474	significant at 5% level reject H_0	1:1.8
Mean size (mm)	94.9	86.9	83.5	88.6			
S.D.	18.1	15.6	33.7	21.3			
Maximum size (mm)	138	125	132	138			

The *t* statistic hypotheses are: H_0 mean female size is equal to mean male size; H_A mean female size is not equal to mean male size.

even in ideal conditions. There is also reason to believe that the calculated "monthly" increments derived from marked fish returns will be lower than they actually were. This could lower the regression line and flatten the growth curve (see Appendix).

At Forest fish caught in the pasture were usually larger than those caught among the trees (Fig. 21) and had a higher condition factor (mean CF 68.5 and 61.8 respectively) in June. Application of a one-sided *t* test indicated a significant difference at the 5% level ($t = 2.1$; d.f. = 19). This may be partly a reflection of the difficulty of retrieving small fish from the thick grass cover of the pasture, or it may show a difference in preferred habitats at different ages, but it seems possible that the larger size of fish in the open ground could be due to the different food items available. It has been noted at other times that some fish in open grassy habitats were larger than those in forest habitats. Both the maximum and average sizes of Hinau fish were greater than those of Forest fish (Table 6), and Hinau habitats were mainly in open pasture land. The largest mudfish recorded among 24 from west coast (South Island) forest habitats was 118 mm, and the largest of 23 from west coast open habitats was 160 mm. As these fish were collected on different dates, the fact that the mean size of open habitat fish was also greater is not significant.

One hundred and thirty-six pairs of otoliths were examined (124 from Hinau and Forest) to see if the ages of individual fish could be determined. There was great variation in the hyaline zones of different otoliths, both in their clarity and in their breadth, some being very broad bands and others fine, sharp rings. It is not known when hyaline zones are laid down, but a 112-mm fish which was marked in August 1968, when probably it would have been between 2 and 3 years old (age 2+), was recaptured in May 1972, nearly 4 years later, and its otoliths showed six hyaline zones (Fig. 8), which suggests that only one hyaline zone forms for each year of life. When the otolith zone counts were compared with the length-frequency distribution data they agreed (Fig. 19B).

Mean lengths at age 1+ appear to be 65–70 mm, at 2+ 100–105 mm, at 3+ 120–125 mm, and at 4+ 130–135 mm. Length at maturity varies between 80 and 105 mm, and spawning probably occurs at 2 years of age, males usually maturing at a smaller size than females. According to otolith readings (Table 7) the maximum age is 7 years. However, some of the largest fish recorded were returned to the water alive, and it is possible that a greater age may be attained.

Hinau fish grew larger and apparently lived longer than Forest fish (Tables 6 and 7). However, the data from the two stations are not comparable, because Forest otolith data were collected from a cross section of the adult population, whereas Hinau material had to be gathered from whatever fish could be caught, with a bias towards large fish.

At Hinau and Forest application of the *t* test detected no significant difference at the 5% level in the size of the sexes, but at Dalefield males were significantly larger than females, and the sex ratio at Dalefield was also distinctly different from those at the other two stations. Females always tended to outnumber males, but the margin of difference was substantial at Dalefield (Table 6).

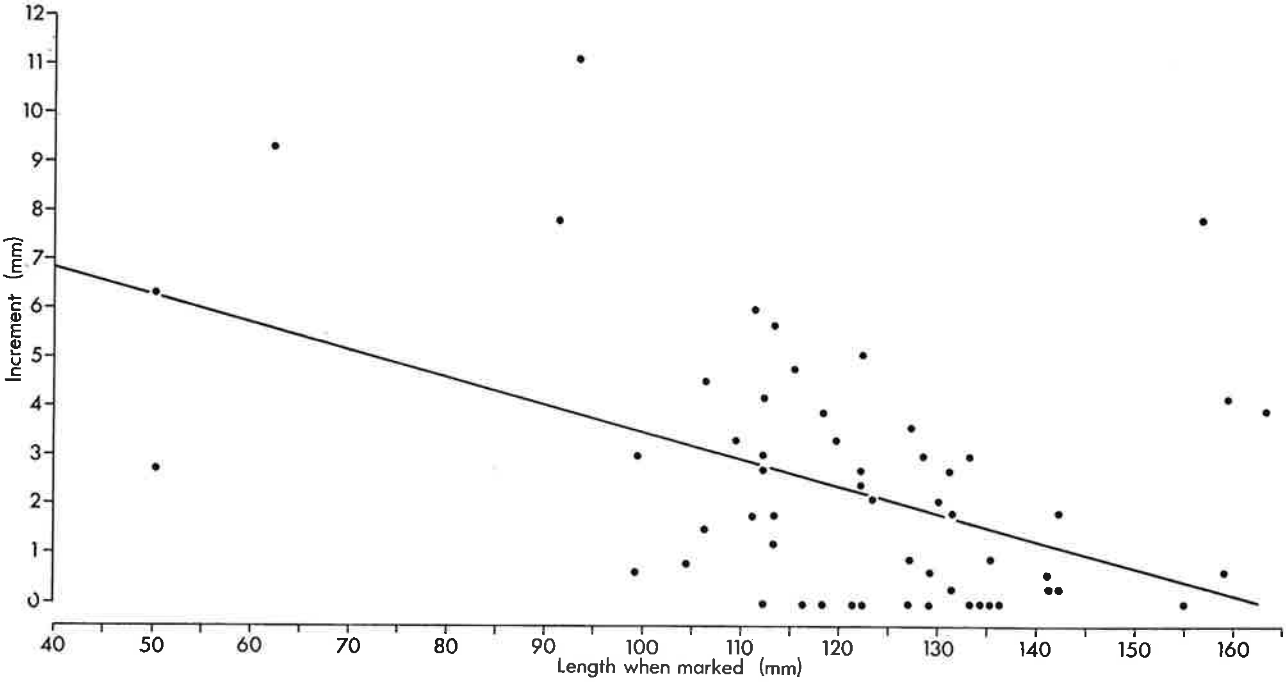


Fig. 20: Monthly growth plotted against length from marked fish data. The equation for the line is $y = 9.036 - 0.0555x$, where y is monthly growth increment (mm) and x is length (mm) at the start of the month; n = 56. (These data are presented in the belief that they are at least indicative of growth, but it is recognised that there may be serious defects; see Appendix.)

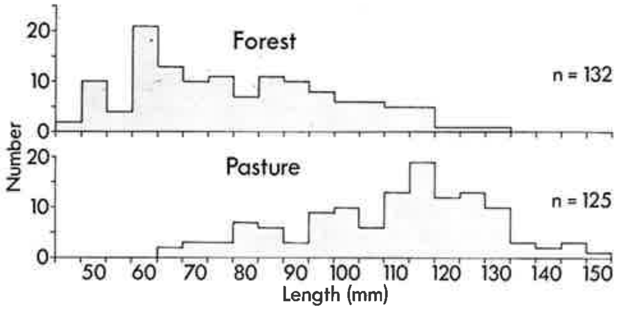


Fig. 21: Length-frequency distributions of two samples of fish taken on the same day from Forest 2A to show the larger size of fish taken in the pasture.

TABLE 7: Number of fish recorded in different age groups from otolith readings

Age (years)	Hinau	Forest	Dalefield
0	4	0	0
1	5	13	0
2	20	24	2
3	23	7	4
4	9	3	4
5	7	0	2
6	6	2	0
7	1	0	0
Total	75	49	12

MOVEMENT

Only 32% of fish (40 of 126) marked at Hinau 1B were recaptured. This is a low figure in view of the small area of the habitat (200–300 m^2) and suggests that fish had moved out of the area. Seven recaptures were made between 50 and 100 m from the point of release, all the fish having moved up one side of an incline, over the "saddle", and on to the other slope. Had they continued for another 50 to 100 m, they would have left the sample area and entered a swiftly flowing stream. However, one fish recaptured nearly 4 years after marking was still at the original capture site, though movement both up and down the road had been possible at times of heavy rain.

K. F. Maynard (pers. comm.) saw many mudfish at Hinau 1B "splashing about all over the road" during a period of heavy rain when the ditch was overflowing and spreading across the road. There can be little doubt that some fish would be lost at such times because rapid run-off would strand some fish and carry others away.

It was noted at Forest 2A that fry spread steadily down the drainage channel through the pasture during the first few weeks of life. For example, in 1971 fry were observed in the forest on 12 April and none were observed outside. The following spread was observed:

20 April, fry present for 2 to 3 m on the pasture side of the fence at the boundary of the forest;
4 May, fry present for up to 150 m from the fence;
10 May, fry plentiful to 250 m from the fence and present for up to 350 m;
24 May, fry plentiful to 350 m.

Probably few of these fry would survive to adulthood because the drain had little suitable cover for aestivation and a return to the forest against the current seems unlikely. However, at one point about 200 m from the forest was an old log which generally provided cover for a few adults, and newly hatched fry were found in this area at about the same time that the larger fry arrived from the forest. Newly hatched fry also occurred at a point where the drain ran under the road through a culvert, and it is believed that some adults may have found cover, not in the culvert, which was open and dry during the drought, but under it.

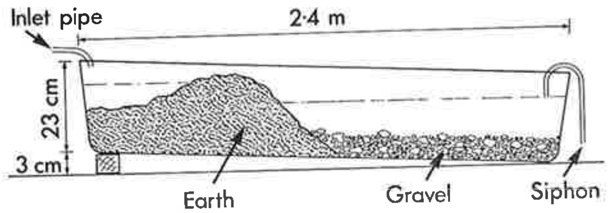


Fig. 22: Trough used in experiment to demonstrate overland movement.

In the laboratory an attempt was made to determine whether *N. apoda* would move overland when stranded. A trough 2.4 m long by 230 mm deep and 320 mm wide at the base was set up so that one end was lower than the other by 30 mm. A bank of earth planted with grasses and weeds divided the trough into two sections (Fig. 22). The investigation was carried out in three parts.

In the first part two fish were placed in the higher section of the trough, which contained 120 mm of fine earth. Over a period of 36 hours most of the water was siphoned from the lower end so that the higher section gradually became dry as the water filtered through the earth bank.

One fish moved over the bank and into the lower section, where water was still present (a distance of 0.8 m). The second fish was found under a tuft of grass on the bank at the edge of the higher section. The trough was refilled and a trickle of water allowed to flow over the bank at the rate of 100 ml per minute. The distance over the bank was reduced to 0.6 m by the increased depth of water. On the third night after filling, the second fish moved over to the lower section.

In the second part three fish were placed in the higher section 2 hours before dark. The water flow was turned off, but the trough was not emptied. Overnight one of the fish moved over the bank.

The water level was then dropped to expose the earth bottom of the higher section. The remaining fish did not attempt to move or to bury themselves, but remained curled up on the earth for 7 hours until this part of the experiment was terminated.

In the final part a glass tube too small to allow the passage of a fish was pushed through the bank to enable both sections to be kept full and a flow of water to be maintained without any surface flow over the bank. The distance between sections was 400 mm. Four fish were placed in the higher section at 1700 hours, and by 0800 hours next day all four had migrated to the lower end.

This experiment showed that *N. apoda* is able to move overland for at least short distances and that it may do so even when still provided with water. Its reluctance or inability to bury itself is again demonstrated if it fails to move when stranded.

FOOD

Neochanna apoda is a carnivore which feeds on a wide variety of small invertebrates, and its intestine is a simple straight one typical of carnivorous fish.

The food varies according to the habitat. Vegetation was sometimes found in the stomachs, particularly of aestivating fish, but was probably taken in accidentally when the fish were foraging.

Aquarium observations indicate that mudfish are able to see small active animals. However, if an animal moves quickly, the fish are unable visually to follow the movement and may strike abortively at the place where the quarry was before it moved away. Brain morphology (Cadwallader 1975a) and the behaviour of the fish suggest that both smell and touch play a part in their feeding, though the fish do not react to bodily contact with a prey animal with the same rapid response as I have seen in eels.

Copepods formed the bulk of food eaten by fry, and they were the first items to occur in the stomachs of fry in all three areas (Fig. 23). Other important animals in the diet of fry were Cladocera (at Hinau); Cladocera and chironomid larvae (at Forest); chironomid larvae and *Paracalliope fluviatilis* (at Dalefield).

Copepods also formed part of the adult diet at both Hinau and Forest, but disappeared from the diet at Dalefield as the fish grew. The small bulk of copepods would have been unimportant to adults, though nearly all food items were small (Tables 8 to 11) in comparison with some of the more common food animals of stream-dwelling fish (mayfly larvae and caddis-fly larvae).

At Dalefield the diet of adults consisted almost entirely of *P. fluviatilis* and the larvae of *Austrosimulium*, but in both the other areas a wide variety of food was taken. The most common large food items were earthworms (*Lumbricus*), which were taken in large numbers immediately after aestivation. For several days after fish first became active at Hinau, every stomach examined was full of earthworms. This was true also of the open pasture portion of Forest 2A, for though other animals were eaten, earthworms formed by far the greatest bulk of the food taken (Fig. 24). Tables 8, 9, and 10 list the food items found in the stomachs of fry and adults at the three study areas.

Larvae of damselflies (Odonata) were the largest invertebrates commonly found in the Forest area, but they were never found in the stomachs of *N. apoda* taken from there, though they did occur in some fish from Marsden, on the west coast of the South Island.

Sixteen fish collected in October from a forest habitat near Harihari, on the west coast of the South Island, contained large numbers of Cladocera. These animals were taken mainly by the smaller fish (Table 11), which had been feeding intensively, but they also formed 50% (by numbers) of organisms eaten by larger fish (60–101 mm). A wide variety of other items was eaten also; in one stomach were the remains of a crayfish, *Paranephrops planifrons* (White), with an estimated carapace length of 20 mm.

TABLE 8: Food composition in Hinau fish at times other than immediately after aestivation

		Fry under 30 mm (n = 50)			Adults over 50 mm (n = 54)		
Type of animal		No. found	% of total animals	% occurrence*	No. found	% of total animals	% occurrence
Ph. Arthropoda							
Cl. Insecta	Chironomid larvae	50	4.3	36.0	31	7.9	20.4
	Austrosimulium larvae	7	0.6	10.0	8	2.0	3.7
	Tipulid larvae	0	0	0	7	1.8	13.0
Cl. Crustacea	Copepoda	608	52.5	82.0	73	18.6	16.7
	Ostracoda	47	4.1	46.0	118	30.0	64.8
	Cladocera	441	38.1	40.0	3	0.8	3.7
	Paracalliope	1	0.1	2.0	16	4.0	11.1
Ph. Mollusca							
Cl. Gastropoda	*Potamopyrgus*	0	0	0	29	7.4	14.8
Ph. Annelida							
Cl. Oligochaeta	*Lumbricus*	0	0	0	25	6.4	35.2
	Others	3	0.2	6.0	18	4.6	13.0
Miscellaneous terrestrial animals		1	0.1	2.0	12	3.0	10.5
Miscellaneous aquatic animals		0	0	0	5	1.3	7.4
Eggs of *N. apoda*		0	0	0	42	10.7	3.7
Unidentified		0	0	0	6	1.5	3.7
	Total animals	1158			393		

*Percentage of fish in which food organism was found.

TABLE 9: Food composition in Forest fish at times other than immediately after aestivation

		Fry under 30 mm (n = 30)			Adults over 50 mm (n = 34)		
Type of animal		No. found	% of total animals	% occurrence	No. found	% of total animals	% occurrence
Ph. Arthropoda							
Cl. Insecta	Chironomid larvae	105	23.9	50.0	389	44.1	44.1
	Austrosimulium larvae	1	0.2	3.3	3	0.3	5.9
	Tipulid larvae	0	0	0	7	0.8	17.6
	Trichoptera larvae	5	1.1	10.0	4	0.5	11.8
	Coleoptera	0	0	0	5	0.6	11.8
	Coleoptera larvae	1	0.2	3.3	106	12.0	8.8
Cl. Crustacea	Copepoda	248	56.4	76.7	50	5.7	29.4
	Ostracoda	26	5.9	36.7	172	19.5	61.8
	Cladocera	49	11.1	20.0	3	0.3	5.9
	Paracalliope	0	0	0	28	3.2	20.6
Ph. Mollusca							
Cl. Gastropoda	*Potamopyrgus*	0	0	0	16	1.8	3.0
Cl. Lamellibranchiata	Sphaeriidae	0	0	0	13	1.5	11.8
Ph. Annelida							
Cl. Oligochaeta	*Lumbricus*	0	0	0	4	0.5	11.8
	Others	5	1.1	6.7	54	6.1	11.8
Miscellaneous terrestrial animals		0	0	0	11	1.2	20.6
Miscellaneous aquatic animals		0	0	0	13	1.5	17.6
Unidentified		0	0	0	4	0.5	5.9
	Total animals	440			882		

TABLE 10: Food composition in Dalefield fish

		Fry under 30 mm (n = 30)			Adults over 50 mm (n = 50)		
Type of animal		No. found	% of total animals	% occurrence	No. found	% of total animals	% occurrence
Ph. Arthropoda							
Cl. Insecta	Chironomid larvae	63	23.6	46.7	16	3.5	21.0
	Austrosimulium larvae	0	0	0	81	17.5	81.0
	Tipulid larvae	0	0	0	2	0.4	5.3
	Trichoptera larvae	1	0.4	3.3	5	1.1	7.9
	Deleatidium larvae	0	0	0	3	0.6	5.3
	Dixid larvae	2	0.7	6.7	0	0	0
Cl. Crustacea	Copepoda	123	46.1	53.3	1	0.2	2.6
	Ostracoda	24	9.0	40.0	17	3.7	21.0
	Cladocera	7	2.6	10.0	0	0	0
	Paracalliope	39	14.6	56.7	323	69.8	73.7
Ph. Mollusca							
Cl. Gastropoda	*Potamopyrgus*	0	0	0	10	2.2	15.8
Ph. Annelida							
Cl. Oligochaeta	*Lumbricus*	0	0	0	3	0.6	2.6
	Others	4	1.5	6.7	0	0	0
Others		4	1.5	13.3	2	0.4	5.3
	Total animals	267			463		

TABLE 11: Food composition in Harihari fish

		Fish 33–48 mm (n = 8)			Fish 60–101 mm (n = 8)		
Type of animal		No. found	% of total animals	% occurrence	No. found	% of total animals	% occurrence
Ph. Arthropoda							
Cl. Insecta	Chironomid larvae	54	2.8	87.5	43	17.5	87.5
Cl. Acari		22	1.1	75.0	6	2.4	50.0
Cl. Crustacea	Copepoda	40	2.1	100.0	2	0.8	25.0
	Ostracoda	12	0.6	37.5	11	4.5	25.0
	Cladocera	1746	91.7	100.0	119	48.4	75.0
	Paracalliope	9	0.5	62.5	9	3.6	62.5
Miscellaneous terrestrial animals		11	0.6	50.0	11	4.5	75.0
Miscellaneous aquatic animals		11	0.6	75.0	15	6.1	25.0
Unidentified eggs		1	0.05	12.5	30	12.2	37.5
	Total animals	1906			246		

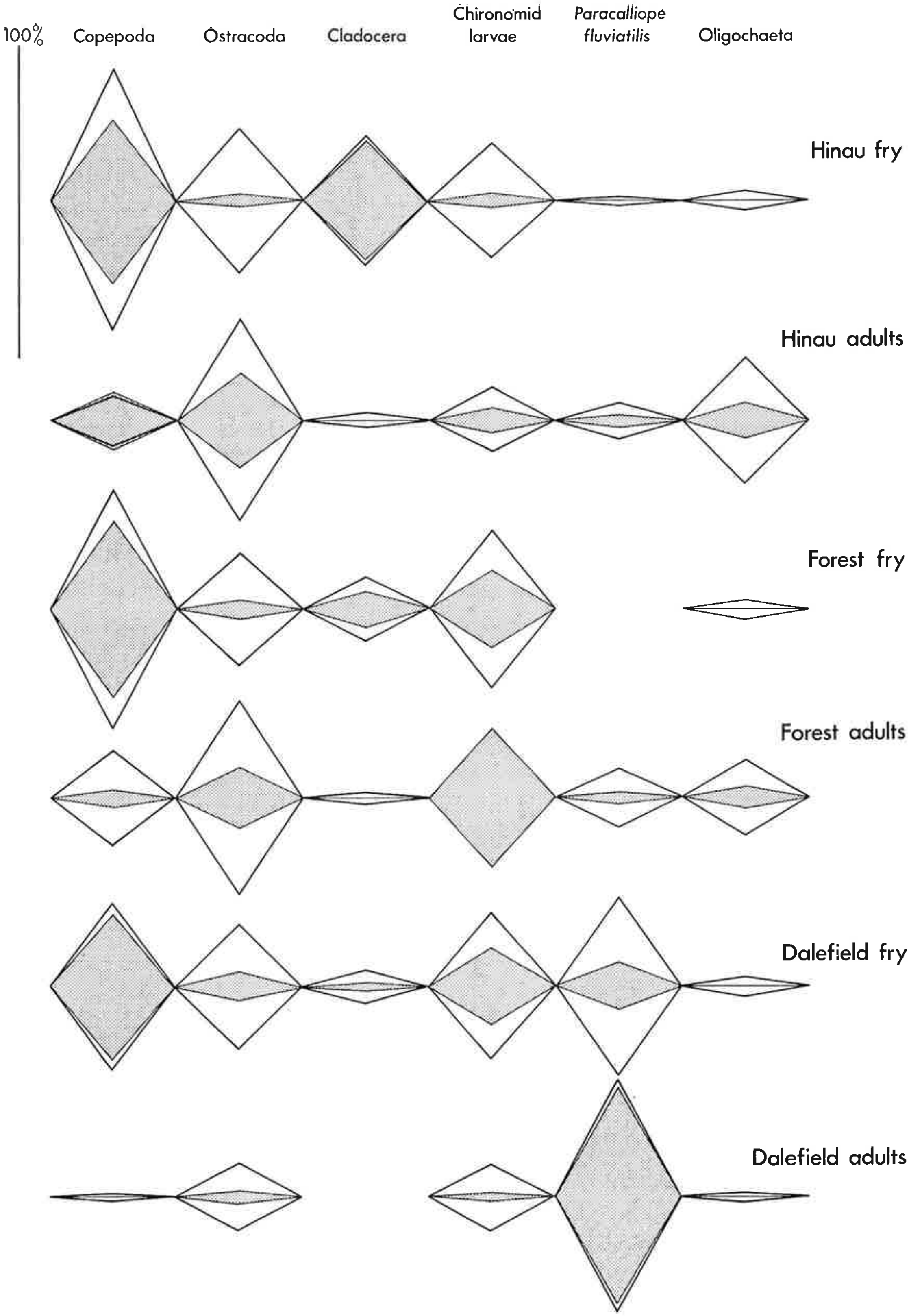


Fig. 23: Food items found in fry and adults from the three study areas. Shaded portions show each type of food animal as percentage of total animals; unshaded portions show percentage of fish in which food type occurred. See Tables 8, 9, and 10 for further data.

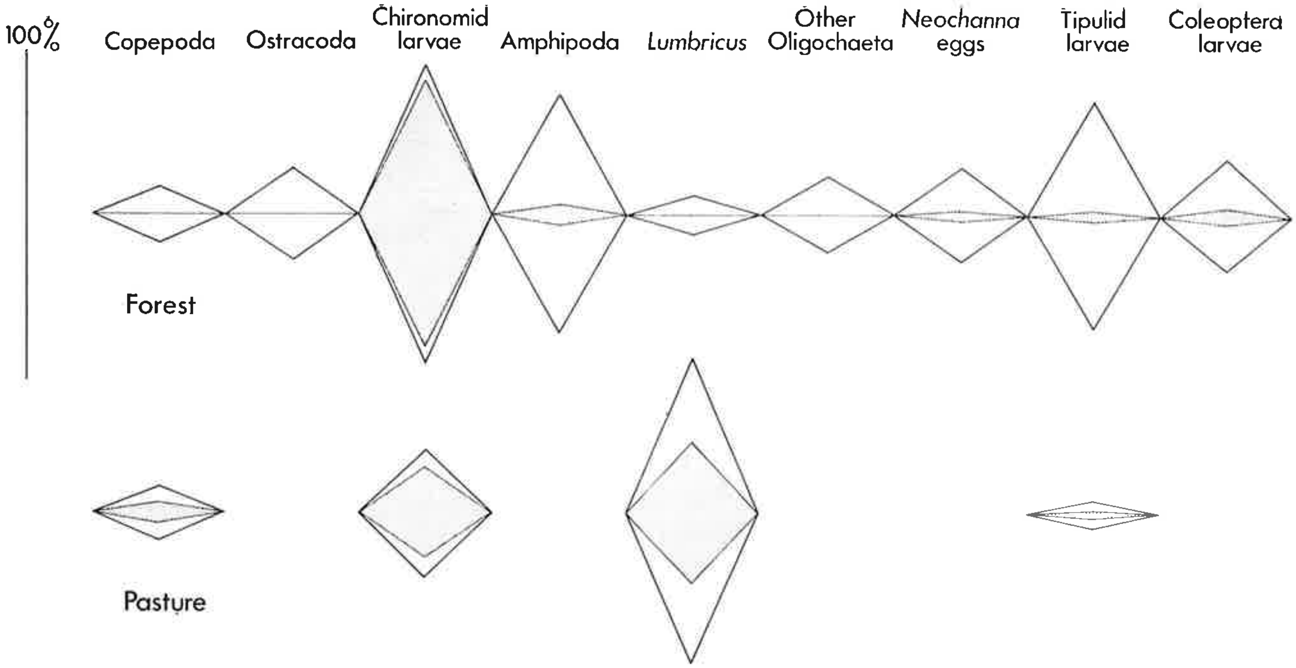


Fig. 24: Food items eaten at Forest 2A immediately after the breaking of the drought. This illustrates the difference in food eaten in the forest and in the open pasture. Shaded portions show each type of food animal as percentage of total animals; unshaded portions show percentage of fish in which food type occurred.

Eggs of *N. apoda* were commonly found in the stomachs of Hinau and Forest fish during April, but only one fry was found in a stomach.

Phillipps (1930) suggested that in New Zealand *N. apoda* probably is one of "the chief fish enemies of the mosquito", but he gave no data to support this statement. In an aquarium mudfish ate mosquito larvae as readily as they ate any other small invertebrates and caught them easily, engulfing them at the surface. However, mosquito larvae were found rarely in the stomachs of *N. apoda* in the wild. This is of interest because though mosquitoes occur in swampy habitats, their presence generally indicates an absence of *N. apoda.* It may be that mosquito larvae prefer water too foul or stagnant for mudfish, or possibly the larvae are eaten as soon as they hatch if *N. apoda* are present.

There seemed to be a connection between size of the food items eaten by *N. apoda* and the size of adults. At Dalefield, where all the food items were small, the size of the mudfish seldom exceeded 125 mm despite the fact that normally there was no aestivation period. At Forest, where some food items were larger, the fish commonly reached lengths of up to 130 mm, but seldom exceeded 140 mm. At Hinau, where much of the diet consisted of large earthworms, many fish reached 150 to 160 mm.

PARASITES, DISEASE, AND PREDATION

PARASITES AND DISEASE

In the examination of stomach contents and gonads a record was kept of any parasites found. No examination of the intestines was made.

The nematode *Hedruris spinigera* Baylis was the only parasite found in the stomach, with the single exception of ten rhabditoid nematodes in a fish from Forest.

The smallest *N. apoda* found to be infected with *H. spinigera* was only 20 mm long, but this was exceptional and generally infection occurred only in fish of over 60 mm (33 or 36 occurrences). The following percentage of infection figures refer only to fish over 60 mm long. Dalefield showed by far the highest incidence of infection, with 63% of fish having *H. spinigera* in their stomachs. The mean worm burden was 4.2, with a maximum of 14. At Forest and at Hinau incidences of infection were 3.7% and 2.7% respectively, with only three (seven *H. spinigera*) and two (two *H. spinigera*) fish parasitised.

The infection incidence agrees well with the abundance of *Paracalliope* in the diet of *N. apoda* in the three areas and this accords with the findings of McDowall (1968), who recognised a similar agreement between the feeding of *Galaxias maculatus* (Jenyns) on aquatic amphipods and the infection of the fish with *H. spinigera* in the Waikanae River and the Waimeha Stream. *Paracalliope fluviatilis* is known to be infested with larval *H. spinigera* in the Waimeha Stream at Waikanae (P. M. Hine, pers. comm.).

Stomach contents of 38 fish from various parts of the west coast of the South Island were examined, but no nematodes were found. Twenty-six of these fish were 60 mm or more in length. Two fish from Masterton in the Wairarapa were examined; only one was over 60 mm in length and it contained four *H. spinigera*.

The metacercarial cysts of *Telogaster opisthorchis* Macfarlane, a digenean fluke (Trematoda), were often found attached to, or embedded in, the gonads of *N. apoda*, but unless a very careful examination was made, they were easily missed because they resembled eggs. Infection rates of 15.8% at Dalefield, 15.7% at Forest, and 20.7% at Hinau should be regarded as minimal for fish large enough to be sexed, generally about 40 mm. Up to 50 cysts were recorded from a single fish, and 11 were found in a fish 38 mm long. Some males were so heavily infested that at first glance they appeared to be females.

The adult of *T. opisthorchis* is parasitic in the intestine of eels (*Anguilla australis* and *A. dieffenbachii* (Gray)) (Macfarlane 1945). The first intermediate hosts are freshwater gastropods (*Potamopyrgus* spp.), and metacercarial cysts have been recorded from the muscle of several small, sometimes unrelated, species of fish (Macfarlane 1945), but not from their reproductive organs.

The only other parasite I have recorded from *N. apoda* was a single encysted echinostome cercaria on a fish 17 mm long from Dalefield.

Acanthocephala have been recorded in *N. apoda* from Dalefield (R. M. McDowall, pers. comm.).

Few *N. apoda* were caught which showed any outward sign of sickness. One exception was a fish caught at Dalefield shortly after the very dry summer of 1972–73. This fish had a large raw red patch on the body identified as caused by *Pseudomonas* sp. bacteria (P. M. Hine, pers. comm.) and it is the first recorded instance of this infection from a native fish in New Zealand. This localised infection is not unusual in fish which have been damaged or subjected to stress.

PREDATION

Observations suggest that the short-finned eel (*A. australis*) may be the only serious predator of *N. apoda*. The stomach contents of several eels collected at irregular intervals from Forest and Hinau were examined. Generally there was no evidence of fish in the diet, but one eel of 0.62 m in length, caught below a culvert at Hinau, was found to contain three *N. apoda* about 65, 70, and 120 mm long.

The swamp bird pukeko (*Porphyrio melanotus stanleyi*) may also be a predator of *N. apoda*, since it is known to include small fish in its diet (Oliver 1955) and frequents the same habitats as the mudfish.

Eggs of *N. apoda* were often found in the stomachs of adults, but only twice has a small fish been found in the stomach of a larger one (once in the Forest study area and once in a sample of fish from Masterton).

DISCUSSION

An interesting aspect of *N. apoda* behaviour is aestivation. *Neochanna apoda* does not have lungs and does not seal itself in a cocoon; nor does it become torpid in the sense of being benumbed and devoid of the power of locomotion. Davidson (1949) considered that the supplementary oxygen supply of this fish may be obtained by way of oral and branchial epithelia, the skin, and possibly other mechanisms. She found no evidence of an accessory respiratory organ in the gill chamber. The finding of some fish on their backs during aestivation experiments may have some significance with regard to an accessory respiratory system.

The term aestivation is variously defined in biological dictionaries as dormancy or torpor during the summer or dry season. If we accept the definition of dormancy as being a condition of inactivity or quiescence, and that of torpidity as being a condition of deprivation of feeling and power of locomotion, the term aestivation has a wide range of meaning and may be applied to *N. apoda*. However, the term aestivation as usually applied to such animals as African lungfish (*Protopterus*) refers only to a state of torpidity, as used, for example, by Schultz and Stern (1948): "Fishes that estivate (spend the dry season in torpor)". Because *N. apoda* is able to move and reacts to disturbance, it does not become torpid and therefore does not truly aestivate.

Retention of moisture at the aestivation site is necessary for the survival of *N. apoda* in drought conditions, and provided moisture is present it does not seem to matter whether the fish is under a covering log, in a hole, or simply lying on the floor of a cavern under the roots of a standing tree. Therefore survival during drought may create no problems for the mudfish provided its habitat still bears plenty of timber, either standing or fallen, to conserve moisture. It is significant that a Westport farmer, when asked about the mudfish, immediately associated it with wood and remarked that he had seen no mudfish "since all the old wood has gone". Stones large enough to provide potential cover during aestivation rarely occur in *N. apoda* habitats. Where they are present, they tend to be too deeply and firmly embedded for fish to be able to get under them. During this study aestivating fish were never found beneath stones in the natural habitat.

Survival in cleared farmlands may be possible only when drains and ditches are neglected. Mudfish were very abundant at Hinau 1B when first discovered there, with more than three adults per metre along the length of the ditch in December 1968. The ditch was then overgrown, with up to 200 mm of mud and vegetation on the bottom. When it was cleaned out by a road grader, and a gravel bottom was exposed, the population of mudfish was reduced greatly. It did not recover in the next 4 years, though a small population persisted.

Mudfish found when a new drain was being dug (see page 21) were in a depression that crossed a field. Drainage pipes had previously been installed in the field, but they had been neglected and the depression had become boggy. The fish were found in large "pods" and this suggests that they were congregating at places suitable for aestivation, possibly in holes left by rotted logs or in the old drain pipes.

Reid (1886) and Phillipps (1940) state that holes left by rotted wood or roots may account for the presence of *N. apoda* at great depth in the soil. Certainly the fish does not seem to burrow its own holes into clay, as do other aestivating fish such as *Protopterus* and the Indian goby *Pseudapocryptes* (Schultz and Stern 1948).

When it is waterlogged, the forest substratum is loose and easily disturbed by the normal swimming action of fish seeking shelter. This also applies in the pakihi bogs, where mudfish were found in association with burrows (Eldon 1968). In pakihi the mud is low in clay content (Rigg 1962) and is not consolidated by stock or plant roots. In these circumstances the fish would be able to swim into the mud, as into forest litter, and as the surface solidified they would be able to maintain a passage to the open air.

Unlike African lungfish, which Herald (1961) states "survive nicely in the foulest mud imaginable", *N. apoda* was not found in foul conditions, and in captivity it would die if subjected to them.

There is some conflict of evidence between the situation at Forest 2B and that at Dalefield. In the latter area the normal year-round presence of water allows continued activity by the mudfish, yet at the former study area the fish aestivate before the water has all gone. This may be due to the shortage of cover in the deeper parts of this habitat or to the low stagnant water conditions being unsuitable for the fish. Experiments to establish the tolerance of *N. apoda* to very low dissolved oxygen levels were inconclusive, though they did show that fish became distressed at levels as high as 4.8 mg per litre at 22°c. At low oxygen levels the fish reacted by hanging vertically with their heads at the surface.

The suggestion (Eldon 1971) that *N. apoda* may deposit its eggs out of the water appears to be at variance with the evidence given here that the eggs are laid in the aestivation places when the first autumn rains occur. However, it seems likely that the scattering of eggs above the waterline which took place in the aquarium may have simulated what happens in the cavities beneath trees.

If eggs were laid in the water and abandoned, they would almost certainly suffer high losses from predation by parent fish deprived of food for many weeks. If, however, the eggs were splashed up on to the undersides of the tree roots above the water, they could develop undisturbed until further rains raised the water level sufficiently to allow dispersal of the adults. The fact that many of the eggs found in *N. apoda* stomachs were not freshly laid, but contained well-developed embryos, may support this suggestion. The apparent inability of *N. apoda* to catch small quarry capable of rapid movement probably protects the fry when both adults and fry are confined together in a small body of water.

The existence of populations at Dalefield and in other permanent waters suggests that aestivation is not a prerequisite for spawning. The factors which trigger off spawning in permanent water have not been established. Spawning may occur at any time of the year and the presence of small fry in nearly all months at Dalefield, and the occasional appearance of fry during February at Hinau, suggest that neither temperature nor photoperiod are factors which determine time of spawning. Rainfall may stimulate spawning in permanent waters as it does when aestivation has occurred. However, it could not directly have caused the spawning which took place in an indoor aquarium in which the water level had not been altered (Eldon 1971).

The presence of *N. apoda* (sometimes in large numbers) in ditches and pockets of swampy ground of limited dimension is evidence of its ability to survive wherever conditions remain suitable and to recolonise neighbouring areas which may revert to suitable habitat. In some places its continued presence is a result of bad farming practice and it may be quickly eliminated when proper drains are constructed and maintained. Only in exceptional circumstances, such as the private forest reserve described in this study, are populations reasonably safe, but even then the inhabited area may be very small, and slight modification of land usage may jeopardise the population.

Large numbers of mudfish occur in a modified habitat at Dalefield, but the situation there is abnormal in at least two respects. Firstly, *N. apoda* is normally not found in the same habitat as other species of fish except short-finned eels, and permanent running water such as that at Dalefield is usually occupied by other species. However, except on one occasion other species of fish were not recorded there. Secondly, many streams are subject to floods and lack much plant cover. Stable spring-fed streams with extensive shallow water vegetation such as that at Dalefield are rare. These circumstances combined may be the factors which enable *N. apoda* to survive there.

The future of *N. apoda* in the South Island seems assured because of its presence in a number of scenic reserves which are protected from development (Eldon 1968). The situation in the North Island is more precarious.

Mudfish have shown a remarkable ability to maintain themselves in remnant fragments of their original habitat—both natural and modified—provided that other circumstances are favourable; for example, there are flood-drought cycles with periods of standing water and suitable cover for aestivation, or permanent shallow waters with ample cover and an absence of most other species of fish.

However, with the increasing activities of catchment boards and well-equipped drainage contractors, land is being converted which in the past was too difficult for the individual farmer to drain. The remnant patches of swamp or ill-maintained drains which sometimes remain for years on the periphery of reclaimed swamp are being reclaimed also, and as old felled timber gradually rots away the necessary cover for aestivation also vanishes. Where floods still occur, they are brief, and no standing water remains after them. The continued presence of the brown mudfish in the North Island may well depend on the creation of a suitable reserve under the Reserves and Domains Act at a site where a population is still extant.

SUMMARY

The brown mudfish (*Neochanna apoda*) was studied in a remnant of its natural habitat and in two modified habitats in the Wairarapa, in the south of the North Island. Fish spend the summer drought in a dormant, but not torpid, condition under the roots of standing trees, under fallen logs, or in subterranean drains.

In habitats where aestivation occurs most spawning takes place when the first autumn rains fall in April or May, but it takes place in almost any month of the year in populations living where there is permanent water. In the natural habitat the eggs apparently are laid under the roots of trees where adults have been aestivating. In modified habitats the eggs appear to be laid in any shallow water.

The fry are free swimming, but do not shoal. The adults are nocturnal, cryptic, and bottom dwelling in shallow water. Food consists mainly of small aquatic invertebrates, the diet being varied in some places and specialised in others. In some modified habitats earthworms form an important part of the diet and in these places the fish attain a greater size.

Large populations of fish may occur in limited areas if conditions are suitable, but because of land improvement such populations are in a precarious position.

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APPENDIX

SOME COMMENTS ON THE QUANTITATIVE METHODS USED IN THE GROWTH STUDIES

by I. F. West

INTRODUCTION

The problems in the quantitative analysis of data collected in this study are greater than normal because the programme had to fit in with another major project. The time intervals between samples were not uniform and sample size varied widely. The unbalanced nature of the data with such an environment-dependent animal has excluded the satisfactory use of many well-established techniques, such as asymptotic regression. Attempts at fitting a number of growth models to both age-at-length and capture-recapture data were made, but convergence seldom occurred.

The simplistic approach of a regression of "calculated monthly increment" on length of first capture is retained in this bulletin in the belief that the data reduction which accrues displays a pattern that is indicative of the growth behaviour of the animal. It is felt, however, that a statement of the defects of the method is desirable to enable the reader to exercise his own judgment on the results presented and for the guidance of later workers.

A description of the method used for the calculation of the monthly increments from the tag data is given on page 28. See also Figs. 19A and 20.

DEFICIENCIES OF THE METHOD

Regression Model May Not Be Appropriate

The use of the simple linear regression, calculated monthly increment against length when marked, has the effect of proposing a model for *N. apoda* growth: that the monthly increment in growth decreases linearly with increasing length at first capture over all the lengths of observation. Observations suggest that this may not be true at the extremes of the length range. Further, the method yields negative growth increments at only moderate length values.

Use of Monthly Increments

In order to use data based on unequal intervals, reduction to a monthly rate was used. Times between captures vary from 1 to 6 months, not counting time spent aestivating. If the growth increments follow the postulated linear model, and growth is rapid, some of the calculated increments will be smaller than the actual growth increment in the first month after capture. There is a related and more serious consequence of unequal times between captures: A plot of the deviation of the observed values from the regression line against length at first capture indicates the presence of heteroscedasticity, a phenomenon where the variance of the ordinate variable conditional on the abscissa variable may vary over the range of values of the abscissa. The evidence for this is that the deviations at both ends of the length range are much larger than in the mid range. This could arise from the division procedure used to obtain the calculated monthly increments, or it could indicate that the simple linear regression model is inadequate. In either case heteroscedasticity is serious, as it generally invalidates the inference of an expected increment for a given length.

A further problem arises from the size distribution of the fish studied. Most of the observations have an abscissa co-ordinate between 100 mm and 145 mm, and because of the large deviations of observations at the extremes of the length range the line is rather unstable.

CONCLUSIONS

It is not possible to ascertain the true source of the heteroscedasticity, and there are insufficient data to test for a more adequate model. Given that the linear model is an acceptable method in the circumstances, the technique of calculation of growth increments probably means that the displayed line (Fig. 20) has lower valued abscissa and ordinate values than the true curve.

This would tend to flatten the growth curve of Fig. 19A.

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