Rec. West. Aust. Mus. 1989, 14(3): 253-267

Life history aspects of the West Australian Salamanderfish, *Lepidogalaxias salamandroides* Mees

Gerald R. Allen* and Tim M. Berra**

Abstract

A field study of the ecology and general life history of the West Australian salamanderfish, *Lepidogalaxias salamandroides,* was conducted near Northcliffe, Western Australia, during 1986. This species mainly occurs between the Blackwood and Kent rivers, a linear distance of about 180 km. Circumstantial evidence for aestivation including the reappearance of fish in formerly dry pools immediately after a rainfall is presented. Monthly sampling provided data on size-sex composition, population structure, growth rates and diet. Most individuals captured were either juveniles under 25 mm SL (31.6%) or small adults, 25-39 mm SL (55.6%). Most fish probably live two years but a few may reach four years. The largest female was 67 mm and the largest male taken was 53 mm SL. Males could be distinguished from females at 25 mm SL. Females were generally larger than males and the overall sex ratio was approximately 1:1. Length-frequency analysis showed two generations in the population during September-January. The largest fish disappeared from the population in January. New recruits appeared in September-October and were most numerous in November. Juveniles and small adults dominated the population in January-February. Adult females grow about 2.2 mm/month from May-January, and juveniles increase 0.8 mm/month from September-January. The diet consisted mainly of the larval stages of chironomid midges and small crustaceans.

Introduction

The monotypic *Lepidogalaxias salamandroides* Mees is a small freshwater fish endemic to south-western Australia. Since its description by Mees (1961) there has been much controversy about its origin and relationships. A study of the suspensorium and related muscles (Williams 1987) indicated that it is a galaxioid fish related to other Southern Hemisphere salmoniforms.

Until this decade there was little information on its biology. Allen (1982) surmised that "it is apparently capable of surviving drought periods by burrowing in mud or under damp leaves." He was unaware of Pusey's (1981) work in which aestivation was induced in a few laboratory fish. McDowall and Pusey (1983) summarised this experiment and the limited knowledge of its natural history including the description of sexual dimorphism in *Lepidogalaxias* which is characterised especially by the peculiar modification of the male's anal fin (see Figs 29-33 in Rosen 1974). The only other published work, that of Christensen (1982),

* Department of Ichthyology, Western Australian Museum, Francis Street, Perth, Western Australia 6000.
** Department of Zoology, The Ohio State University, Mansfield, Ohio, 44906, U.S.A.

correlated geographic distribution with terrestrial vegetation. The present paper provides additional information about the biology and life cycle. It is based on field work conducted in 1986, although collections and casual observations over the past 14 years by the first author were utilised. Emphasis is on population structure in response to seasonal or climatological factors. Also included is a summary of the geographic distribution of *Lepidogalaxias.*

Study Area

A series of 22 study stations was established at small artificial pools along a 1.6 km stretch of Chesapeake Road situated 9-11 km south of Northcliffe, a small town lying approximately 300 km (370 km by road) south of Perth (Figure 1). The depressions in which the pools were formed date back to the 1960's when roadfill was excavated from them. Stations 15-17 and 19-21 were situated in a creek bed which flows during the wet season, but in late spring becomes a series of isolated pools.

The pools typically had coarse sand bottoms with a thin layer of organic mud and detritus. There was no aquatic vegetation other than algae which forms mainly in spring and summer. However, some encompass heathland vegetation, particularly when water levels were at their winter maxima (Figure 2).

Approximate surface areas and maximum depths of the study pools are given for January, April, July and November (i.e. summer, autumn, winter, and spring) in Table 1. Most of the pools underwent a cycle of summer drying and autumn-winter flooding, although Station 22 contained water throughout the study period because of its large size. However, even this pool dried during the summer of 1987-88. After November evaporation rate was rapid, and some pools were completely dry by mid-January.

The study area and overall range of *Lepidogalaxias* is characterised by hot, dry summers and cool, wet winters. The water is characteristically deeply stained to the colour of dark tea, but it is not turbid. Christensen (1982) reported a pH range of 3.7-6.8 ($\bar{x}$=5.4). Monthly water temperatures and rainfall are summarised in Figure 3. The annual average rainfall for Northcliffe is 1367 mm, but relatively low figures (964 mm in 1986; 868 mm in 1987) were recorded during the study period. *Lepidogalaxias* is able to withstand wide fluctuations in water temperatures. Monthly surface readings ranged from 9^{0}C in winter to 30^{0}C at the end of summer. There were also significant daily fluctuations of between 10^0 to 12^{0}C during summer, particularly during hot spells because of the shallow depths and greatly lowered night temperatures. In deeper pools there was a noticeable gradient of 3-4^{0}C on hot summer days. The bottom-dwelling *Lepidogalaxias* was invariably confined to the cooler layer.

In addition to *Lepidogalaxias,* the study pools contained two species of small (maximum standard length [SL] about 35-40 mm) galaxiid fishes *Galaxiella*

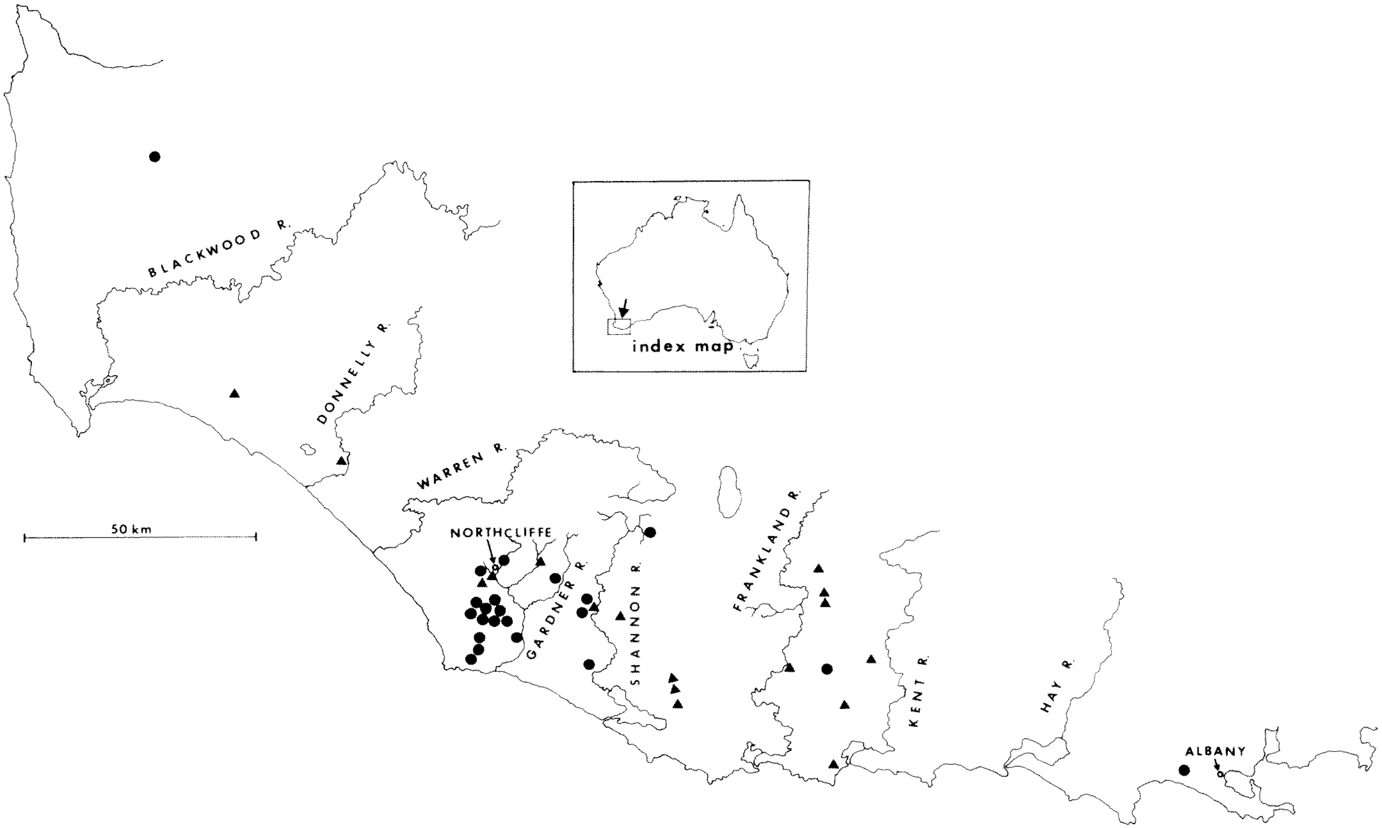

Figure 1. Distribution of *Lepidogalaxias salamandroides*. Circles indicate records based on specimens at WAM. Triangles represent records from Christensen, 1982.

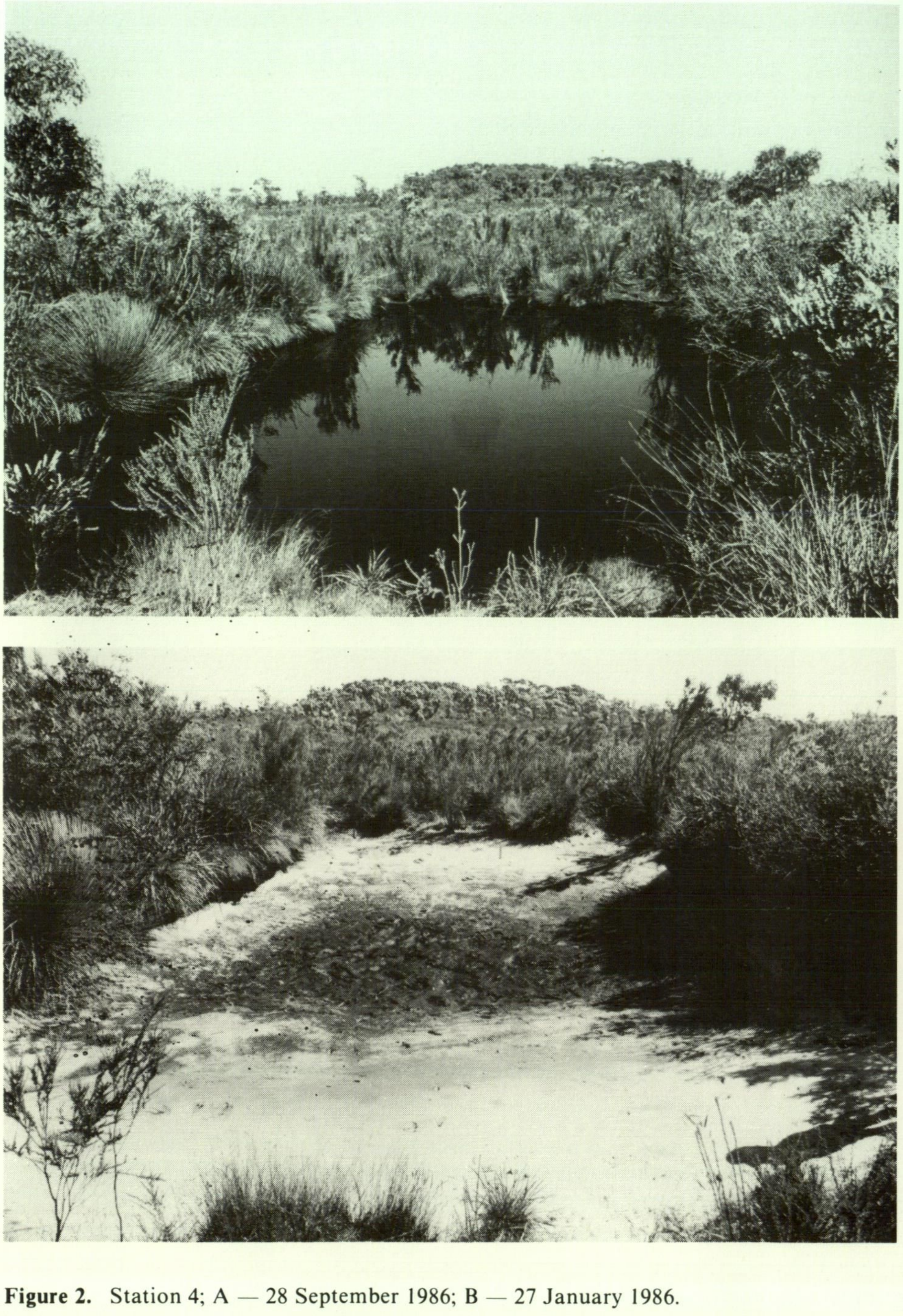

Figure 2. Station 4; A — 28 September 1986; B — 27 January 1986.

nigrostriata (Shipway) which was as abundant or more numerous than *Lepidogalaxias* and the less common *G. munda* (McDowall). Other fishes were absent except for a pair of 35 mm SL *Bostockia porosa* Castelnau (Percicithyidae) captured at Station 22.

Other fauna included the long-necked tortoise (*Chelodina oblonga*), frogs (*Geocrinia leai, Heleioporus inornatus,* and *Ranidella* sp.), crayfish (*Cherax preissii),* and unidentified tadpoles, leeches, and aquatic insects.

Table 1 Approximate surface areas and depths of *Lepidogalaxias* study stations for various months during 1986

	JANUARY		APRIL		JULY		NOVEMBER	
Station	sur. area (m^2)	depth (cm)	sur. area (m^2)	depth (cm)	sur. area (m^2)	depth (cm)	sur. area (m^2)	depth (cm)
1	12	20	dry		128	82	120	62
2	dry		dry		448	82	300	56
3	30	44	dry		128	100	96	70
4	30	29	dry		135	90	112	72
5	20	29	dry		78	60	66	54
6	52	49	11	15	114	95	102	82
7	60	34	1	1	340	95	300	67
8	30	20	dry		252	72	224	59
9	dry		dry		70	69	56	50
10	56	35	11	10	264	100	192	70
11	81	40	24	14	286	100	221	73
12	42	25	dry		440	81	345	60
13	dry		dry		451	32	351	28
14	dry		dry		1092	57	407	35
15	1	6	dry		9	66	7.5	40
16	4.5	29	dry		8	70	8	56
17	1.7	16	dry		12	50	12	39
18	64	17	dry		924	58	576	47
19	3.8	29	dry		6	65	6	60
20	1.3	18	dry		1.7	50	1.7	42
21	1.6	7	dry		2.5	50	2.5	33
22	1800	77	741	40	2894	89	2260	78

Methods

The study sites were visited at least once per month between January 1986 and January 1987, and a total of 14 visits was made. Data recorded for each of the 22 stations included length, width, maximum depth, and surface-bottom temperatures. A 3-metre (1.6 mm mesh) seine and occasionally a one-person Japanese shrimp seine were utilised for fish sampling. Most seining, except at

Station 22, was for the purpose of establishing the presence of *Lepidogalaxias* or *Galaxiella* and the relative abundance of each. A complete census was made of adjacent Stations 6 and 7 on 17 January 1986 with the use of rotenone. Because the two stations were within 10 m of each other and because the samples were taken simultaneously, the data were pooled.

In addition to the sampling methods described above,the largest pool (Station 22) was selected for monthly net sampling of 100 individuals between February 1986 and January 1987. Generally about 2-10 *Lepidogalaxias* were obtained in each 20 m drag of the seine, but 120 fish were netted on one occasion (January 1987). Fish were held in buckets until the required 100 were obtained. The standard length was recorded for each fish before releasing it. Fish under 25 mm SL were defined as juveniles because in the majority of the population the modification to the male's anal fin did not appear on fish less than 25 mm. Prior to May 1986 only "juvenile" and "adult" categories were recorded. In May sex of adult specimens along with the SL was recorded. Flooding occurred in June which prevented collection during that month. In January 1987 an attempt was made to net the entire population of the pool.

Data analyses were conducted using SPSS and SAS (Version 5) and plots were produced via INSTAT and SAS graphics. Volumetric gut content analysis was aided by a binocular dissecting microscope. Rainfall data for Northcliffe were supplied by the Bureau of Meterorology. Representative samples of *Lepidogalaxias* specimens from both within and outside the study sites were deposited in the Western Australian Museum (WAM).

Results and Discussion

Distribution

The known distribution of *Lepidogalaxias* is given in Figure 1 based on Christensen's (1982) survey between 1978 and 1979 and specimens deposited at the Western Australian Museum between 1959 and 1986. The main concentration of records is between the Blackwood and Kent rivers, a linear distance of about 180 km. There are only two records outside this area, both collected in 1976: from Canebreak Creek (30 km north of the Blackwood River) and near Lake Powell which is 15 km west of Albany or about 60 km east of the Kent River. This distribution pattern is closely associated with "non-forested areas of low open woodland, herbland, scrubland, and heaths" described by Christensen (1982). Bush fires frequently occur in this area during the dry season. This habitat forms a relatively narrow belt, approximately 20-40 km wide, which is sandwiched between coastal dune systems and karri *(Eucalyptus diversifolia)* forests.

Although *Lepidogalaxias* has a restricted range it is often locally abundant. The preferred habitat consists of slow flowing creeks, roadside drains, swamps, and still pools.

Aestivation

Lepidogalaxias is unusual among fishes for its ability to survive during drought periods. Aestivation or summer torpor is "a mechanism for surviving torrid ambient conditions" (Fishman et al. 1987). Pusey (1981) experimentally induced aestivation in three of 29 fishes by gradually (over 3-day period) removing the water in sand-filled troughs. He reported that aestivating fish assumed a U-shaped posture in a loose burrow and were able to metabolise their considerable fat reserves. He also noted that aestivating fish were characterised by copious secretion of mucus from epidermal goblet cells. It appears that not all individuals are capable of aestivating or at least not all fish survive this process. Most of Pusey's laboratory subjects were either found dead or disappeared (presumably they died and decomposed).

In this study strong circumstantial evidence was obtained for aestivation in the field. After the establishment of the 22 stations in early January 1986, 11 of the pools dried up within the next 3-4 weeks. On 21-22 February the area received 29 mm of unseasonal cyclonic rain and several of the stations once again contained water, including two (Stations 8 and 18) that had previously harboured fishes. These stations were sampled on 23 February. Seven *Lepidogalaxias*, 21-62 mm SL were obtained from Station 8 and nine individuals, 15-36 mm SL, from Station 18, which also had specimens of *Galaxiella nigrostriata*, 19-22 mm SL. Since there was no generalised flooding, and the ponds remained isolated the fishes must have emerged from the sand bottom following the rain. During May 1986, again following heavy rains, *Lepidogalaxias* was located in 14 study pools that were dry in April.

The evidence indicates that *Lepidogalaxias* must possess the ability to survive drought periods of up to 2-4 months duration in the substratum. As *Lepidogalaxias* lacks specialised accessory respiratory structures (Berra et al. 1989), it apparently does not breathe atmospheric oxygen, but either survives in damp sand if its gills and skin are kept moist, respires anaerobically, or seeks out subterranean waters. It is possible that the extensive burrow systems of the crayfish, *Cherax preissii*, are used as a conduit to a water refuge below the surface as suggested for *Galaxiella pusilla* in South Australia by Beck (1985). These crayfish burrows are a characteristic feature of the *Lepidogalaxias* habitat. Several were excavated without finding fish, but on 9 January 1986 a 14 mm SL specimen was found in moist sand in the bottom of the entrance (chimney) of a crayfish burrow. It was in good condition and active, not in a 'torpor' as described in the case of aestivating laboratory subjects by Pusey (1981).

Size and sex ratio

A total of 2,283 *Lepidogalaxias* specimens was measured ranging in SL from 12-67 mm. The size frequency of 1,801 fish captured from pools within the study area is indicated in Table 2. Most of these (1,100) were taken from Station 22 and were released after each monthly capture. Therefore the same individual may have been measured more than once in subsequent months. The majority of individuals were either juveniles under 25 mm SL (31.6%) or small adults in the 25-39 mm SL category (55.6%). Relatively few fish were 40-49 mm SL (9.4%) and only 3.2% and 0.2% of the total sample exceeded 50 mm and 60 mm SL respectively.

Adult females attain a larger size than males. The majority of fish 40 mm SL or longer were females (Table 2). Only five specimens exceeded 60 mm SL and all were females. The largest male measured was 53 mm SL in comparison to the largest female of 67 mm. The mean SL by month for females, males and juveniles is presented in Figure 4. Steady growth of juveniles took place from February to July, after which that size-class presumably entered the female or male data sets. The recruitment of newly spawned fish in the September sample and their subsequent increase in SL is readily visible in Figure 4. Females are clearly larger than males and mean size of both declined markedly in January. One way analysis of variance showed that there were significant size by sex differences (at the 0.05 significance level). One-sided t-tests of the differences between the mean sizes of males and females within each month showed a significant difference (at the 0.05 significance level) between sexes within months except for January where there were no significant differences. Females were larger than males except in May and July.

Table 2 Size frequency data of *Lepidogalaxias salamandroides* captured from study area from January 1986 —January 1987 (total sample = 1801)

Size range (mm SL)	No.	% of sample	no. ♀	no. ♂
12-24	570	31.6	—	—
25-39	1001	55.6	258	315
40-49	169	9.4	132	37
50-59	57	3.2	54	3
60-67	4	0.2	5	0

(note: no. of males and females not determined for all samples in the 25-39 mm group.)

Monthly sex ratios and the average size of juveniles, males and females are indicated in Table 3. On average there were fewer males than females (1:1.2 in the monthly Station 22 samples, excluding juveniles. The sex ratio within individual months is not significantly different from 1:1 (at the 0.05 significance level for Chi^2). However, there are some differences in numbers (normally slightly more females than males), and this difference is reflected in the overall number of fish examined (totalled over all months for both sexes). This total difference is significant (at the 0.05 significance level), with more females being caught overall than males. However, this slight difference in numbers may just reflect our inability to sex late developing males and may be of no biological significance.

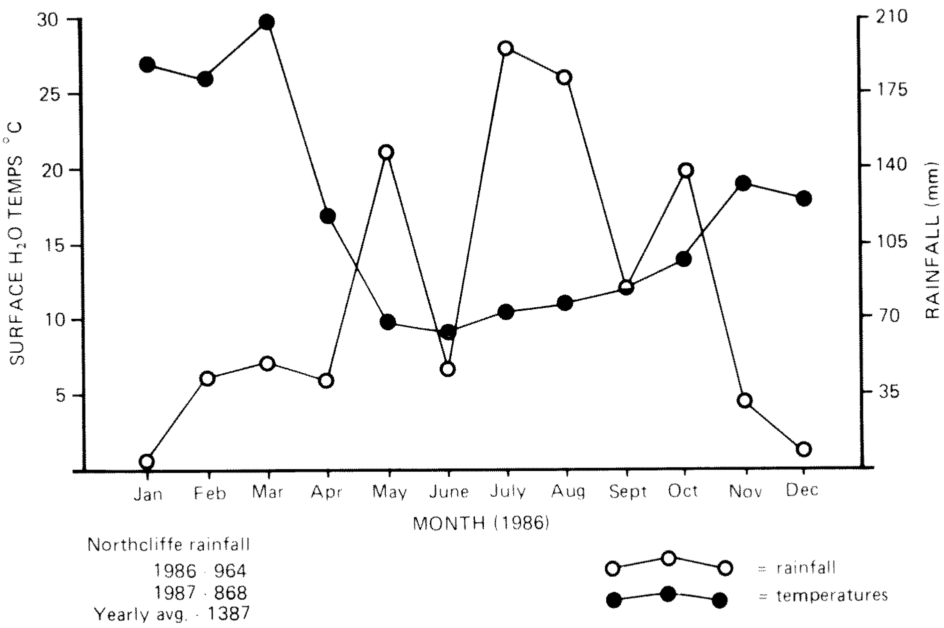

Figure 3. Average monthly water temperatures for study stations and Northcliffe rainfall. Temperatures and rainfall are plotted with solid circles and hollow circles respectively.

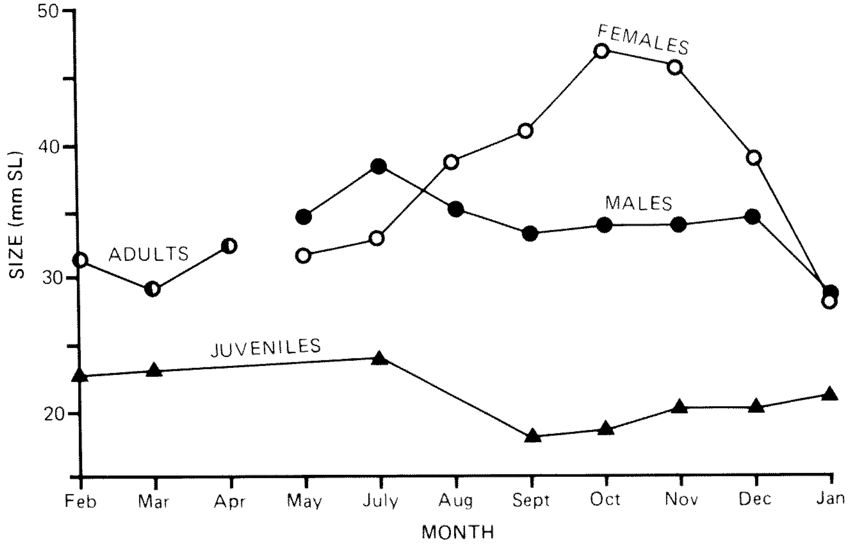

Figure 4. Mean standard lengths (mm) at each month for juveniles (25 mm SL), females, males, and unsexed adults from Station 22. N = 100 for each month.

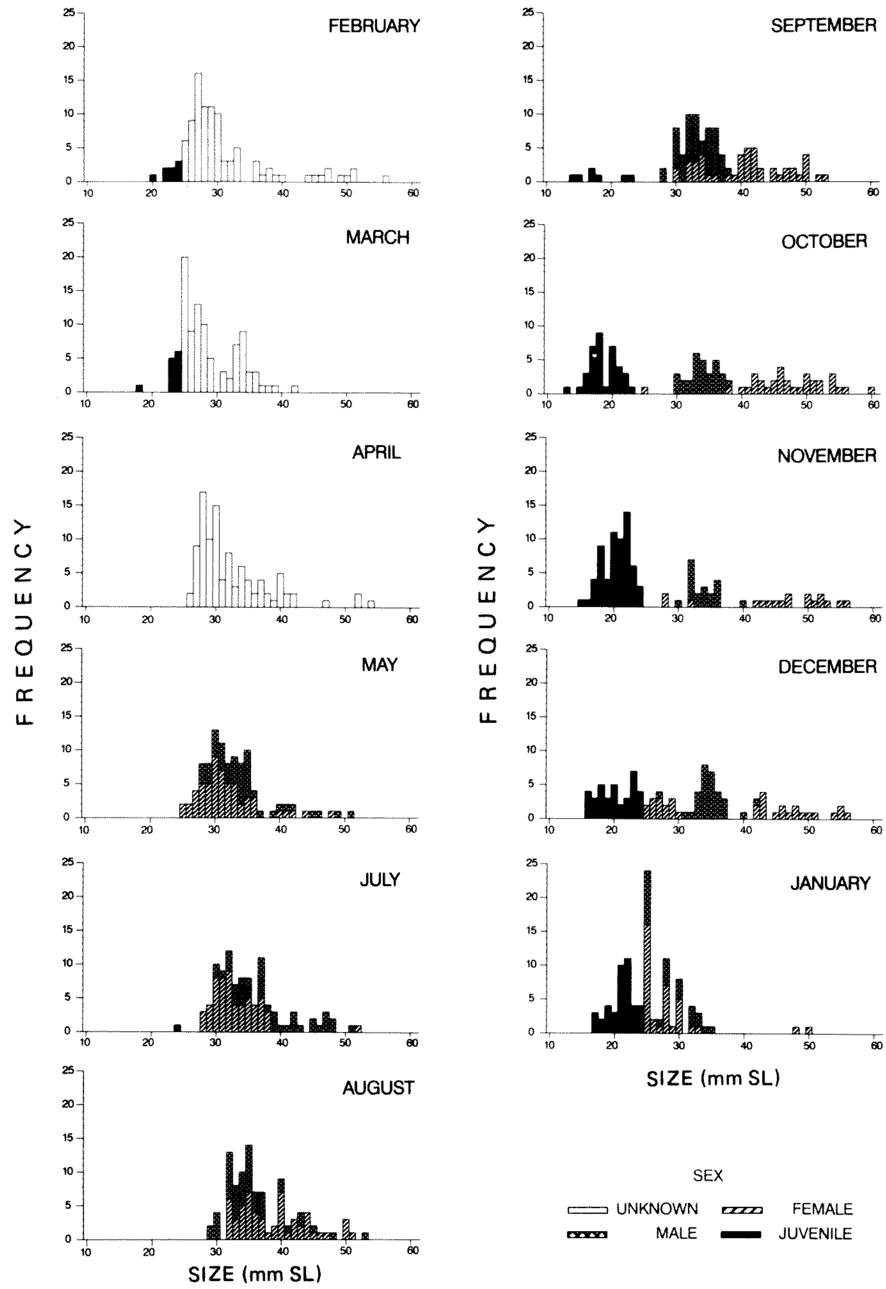

Figure 5. Length-frequency distribution of monthly samples from Station 22. Size is given in mm standard length (SL).

Population Structure and Growth Rate

Figure 5 shows the length-frequency plots by sex for 11 months. During February the bulk of the population was composed of juveniles and small adults from 20-40 mm SL with a geometric mean of 30 mm (Figure 5, Table 3). Some larger fish were present. The young fish continued to dominate the population in March and the geometric mean dropped to 28.2 mm which reflected the death or disappearance of larger fish. From April through August growth was apparent as the graphic presentation shifts to the right (Figure 5). The geometric mean size of females increased from 31.3 mm in May to 38.8 mm in August while males, which began in May larger (34.1), reached 35.1 mm in August (Table 3). From September to December, the older males grew very slowly, but the older females rapidly increased from 40.4 to 47.5 mm. Juveniles also grew quickly during that time.

In September and October a new generation of juveniles appeared and increased in SL through January. From October-January two distinct generations of females are present. This is most obvious in December (Figure 5).

Older generation females increased in geometric mean SL from 31.3 mm in May to 49.0 mm in January. The growth rate was about 2.2 mm/month (Table 3). Older males grew very little from May to December. New generation juveniles increased in geometric mean SL from 17.7 in September to 21.0 mm in January, a growth rate of 0.83 mm/month.

Table 3 Monthly Geometric Means for Standard Length (mm)

Month	Unknown	Female	Male	Juvenile
February	30.0 +/- 6(100)			
March	28.2 +/- 4(100)			
April	32.0 +/- 5(100)			
May		31.3 +/- 4(57)	34.1 +/- 5(44)	
June				
July		32.8 +/- 4(58)	38.1 +/- 6(41)	24.0 (1)
August		38.3 +/- 5(55)	35.1 +/- 5(45)	
September		40.4 +/- 6(46)	33.2 +/- 3(47)	17.7 +/- 3 (7)
October				
(new generation)		25.0 (1)		18.5 +/- 2(37)
(old generation		47.5 +/- 5(32)	33.9 +/- 2(30)	
November				
(new generation)		29.0 +/- 2 (3)		20.3 +/- 2(63)
(old generation)		48.7 +/- 4(15)	33.8 +/- 2(19)	
December				
(new generation)		27.0 +/- 2(14)		20.0 +/- 3(36)
old generation)		47.5 +/- 5(19)	34.6 +/- 3(31)	
January				
(new generation)		26.9 +/- 3(34)	28.5 +/- 3(23)	21.0 +/- 2(41)
(old generation)		49.0 +/- 1 (2)		

Mean +/- S. Deviation (No. of specimens)

It is not possible to determine from Figure 5 how long *L. salamandroides* lives. The very large fish may be rapidly growing two-year-olds or very slow growing older fish. We kept two 65 mm females alive for two years in an aquarium indicating that they are physiologically capable of reaching four years of age.

A similar picture emerged from the length-frequency distribution of 273 individuals collected in the January rotenone samples of Station 6 (122 fish) and Station 7 (151 fish) (Figure 6). The juveniles and small adults dominated the sample, two year-classes of females are apparent, and only a few large individuals were present. However, the largest *Lepidogalaxias* on record, a 67 mm SL female, was collected at this time. The rotenone samples indicate that the small pools can harbour at least 150 *Lepidogalaxias* in January. The two-hour seining effort at the large Station 22 yielded 543 fish in January 1986.

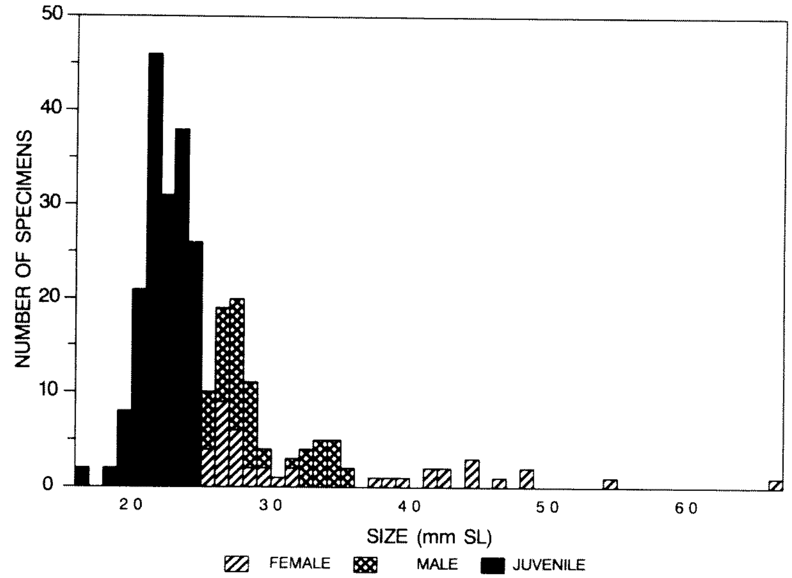

Figure 6. Pooled length-frequency distribution of *Lepidogalaxias salamandroides* collected by rotenone from Station 6 (N = 122) and Station 7 (N = 151) on 17 January 1986.

Diet

The stomach contents of 44 specimens, 26-60 mm SL, collected between January-March 1986 were examined. Nine of the stomachs were empty, but most were more than half full. The results of this analysis are presented in Table 4 as percentage volume of the major groups of food organisms. Percentages of each item found in individual fish (9 to 100%) were averaged to calculate the mean percent of diet volume for the 35 specimens containing food (Hobson 1974). The most common items were the larval stages of chironomid midges (Diptera), spring-tails

(Collembola), and hydrophilid beetles (Coleoptera), and a species of amphipod (Crustacea). Copepods and cladocerans were also common, but because of their minute size their contribution to the overall volume was relatively small. The same item was noted by Pusey (1981) in addition to arachnids, isopods, nematodes, and oligochaetes. Pusey found dipteran larvae were the predominant food item in summer and autumn, but were largely replaced by crustaceans during winter.

Table 4 Stomach contents of *Lepidogalaxias salamandroides*

	no. fish with item (n = 44)	mean % of diet volume
Diptera (larvae)	28	30.2
Amphipods	17	23.6
Coleoptera (larvae)	12	15.4
Collembola (larvae)	7	10.0
Unidentified fragments and sand grains	25	12.8
Copepoda	11	3.5
Tricoptera (larvae)	4	2.0
Cladocerans	6	1.5
Odonata (larvae)	1	1.0

Summary of Life Cycle and Conclusions

From the data provided in Figure 5 and Table 3 it appears that spawning takes place in August-September and that the juveniles become large enough to be collected by our technique in September-October. Juveniles increase in size slightly less than one mm/month from September to January, and adult females grow about 2.2 mm/month from May to January. They feed on aquatic insect larvae and crustaceans. It is likely that most *L. salamandroides* die by the second year, but some may survive as long as four years. The sex ratio is 1:1. It is highly likely that these fish survive the desiccation of their habitat by burrowing into the bottom sand during summer.

It is evident that *Lepidogalaxias salamandroides* is a "survivor" in every sense of the word. It is highly specialised with respect to its ability to survive in ephemeral waters. This habitat is largely devoid of other fishes except *Galaxiella* spp. This lack of predators may be a factor in the distribution of *Lepidogalaxias* in the temporary pools and its absence from permanent streams populated by larger fishes. The ability to withstand long periods of drought is an adaptation for surviving the harsh summer conditions of south-western Australia. Field research is continuing concentrating on burrowing activity. Reproductive, physiological, and embryological studies are also needed to fill gaps in our knowledge of this unusual fish.

Acknowledgements

Much of the fieldwork portion of this study was funded by a special grant to the Western Australian Museum for environmental studies in the South-West from the Western Australian Department of Conservation and the Environment. The second author was supported by an Ohio State University small research grant and a special research assignment in 1986 and a research challenge grant from the Department of Zoology of OSU for the 1988-89 continuation of this study. We are especially grateful to Dr. Ian Crawford for allowing us to use his holiday cottage at Northcliffe as our field headquarters. We thank Per Christensen of the Western Australian Department of Conservation and Land Management and the staff of the Manjimup office of this organisation for providing us with data from previous freshwater fish surveys in the south-western region. We are grateful to Jenny Edwards for preliminary help with the data analysis which was carried out at the Western Australian Regional Computing Centre by Terry Woodings and Sharon Coffey. The suggestions of P. Berry (WAM) and two reviewers proved very helpful. Special thanks are also due to Norrie Cross, Honorary Associate of WAM for providing assistance on several field trips and for conducting the December 1986 monthly sampling. Assistance on one or more field trips was also provided by Connie and Mark Allen, Rita Berra, Nick Haigh, Nick Lagos, and Brad Pusey. Greg Jackson prepared figures 3-5 and the map was drawn by Gary Howard. Frogs were identified by Laurie Smith of WAM. Identification of food items was assisted by WAM staff members Terry Houston (Emntomology) and Gary Morgan (Carcinology). Connie Allen typed the manuscript.

References

Allen, G. R. (1982). *A Field Guide to the Inland Fishes of Western Austraila.* (Western Australian Museum: Perth).

Beck, R. G. (1985). Field observations upon the dwarf galaxiid *Galaxiella pusilla* (Mack) (Pisces: Galaxiidae) in the south-east of South Australia. *South Australian Naturalist* **60:** 12-22.

Berra, T. M., D. M. Sever, and G. R. Allen. (1989). Gross and histological morphology of the swimbladder and lack of accessory respiratory structures in *Lepidogalaxias salamandroides,* an aestivating fish from Western Australia. *Copeia* 1989 (in press).

Christensen, P. (1982). The distribution of *Lepidogalaxias salamandroides* and other small freshwater fishes in the lower south-west of Western Australia. *J. Roy. Soc. West. Aus.,* **65**(4): 131-141.

Fishman, A. P., A. I. Pack, R. G. Delaney, and R. J. Galante. (1987) Estivation in *Protopterus.* p. 237-248 *in* The Biology and Evolution of Lungfishes. W. E. Bemis et al. (eds). Alan R. Liss, Inc.: New York.

Hobson, E. S. (1974). Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. *Fishery Bull.,* **72**(4): 915-1031.

McDowall, R. M. and B. J. Pusey. (1983). *Lepidogalaxias salamandroides* Mees — a redescription, with natural history notes. *Rec. West. Aust. Mus.,* **11**(1): 11-23.

Mees, G. D. (1961). Description of a new fish of the family Galaxiidae from Western Australia. *J. Roy. Soc. West. Aust.,* **44:** 33-38.

Pusey, B. J. (1981). The life history of the Shannon mud minnow *Lepidogalaxias salamandroides* (Mees) with special reference to aestivation. Unpub. Hons. Thesis, Zool. Dept. Univ. West. Aust.

Rosen, D. E. (1974). Phylogeny and zoogeography of salmoniform fishes and relationships of *Lepidogalaxias salamandroides. Bull. Am. Mus. Nat. Hist.,* **153**(2): 265-326.

Williams, R. R. G. (1987). The phylogenetic relationships of the salmoniform fishes based on the suspensorium and its muscles. Unpub. Ph.D. Thesis, Zool. Dept. Univ. Alberta, Edmonton.

Received 10 October 1988 Accepted 2 March 1989 Published 29 September 1989