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SPAWNING OF THE AUSTRALIAN LUNGFISH, *NEOCERATODUS FORSTERI* (KREFFT) IN THE BRISBANE RIVER AND IN ENOGGERA RESERVOIR, QUEENSLAND.

A. Kemp
Queensland Museum

ABSTRACT

The Australian lungfish, *Neoceratodus forsteri* (Krefft) breeds annually between mid-August and December. The onset of oviposition is not related to rainfall, temperature, pH or dissolved O_2 content of the water in which they live. Lungfish begin to spawn when daylength has been increasing for 6–11 weeks, provided that suitable weeds are growing, and the rate of flow of the water may also have an effect on the site chosen for spawning.

INTRODUCTION

Caldwell (1884) was the first to report finding eggs of the Australian lungfish, *Neoceratodus forsteri* (Krefft), in the Burnett River, 14 years after Krefft (1870) had described the adult fish from the Mary River. Semon, who studied the development of *N. forsteri* (1893), found eggs in shallow water amongst weeds in the Boyne River, a tributary of the Burnett (1899:96). Eggs are deposited among growing water weeds or on the sides and bottom of submerged logs (Illidge 1892). Plants important for egg laying in the Burnett River are *Hydrilla verticillata, Vallisneria spiralis* and *Nitella* sp. (Bancroft 1911). Spawn has also been found on the roots of the water hyacinth, *Eichornia crassipes,* in Enoggera Reservoir, Brisbane (Bleakly, per. comm., 1969), from "weeds" in a tributary of the Burnett River (Grigg 1965) and on the submerged roots of *Callistemon saligna* growing beside the Brisbane River (Kelly, per. comm., 1977). Spencer (1925) states that eggs are laid separately amongst vegetation, but not attached to it, and that they finally lie on the mud.

There is only one published report on the breeding behaviour of *N. forsteri* in the wild (Grigg 1965). The breeding season has been recorded as August-October in Enoggera Reservoir (Bleakly, cited by Grigg 1965), September in the Boyne River (Semon 1899), August-November in Enoggera Reservoir (Kemp 1977), September-October (Spencer 1926), November-December (Illidge 1893), August-October in the Burnett River (Bancroft 1911 and 1928) and August in a tributary of the Burnett River (Grigg 1965). Factors which influence spawning are not known.

This work was undertaken to determine the times and places of spawning of *N. forsteri* in a river and a lake environment in southeast Queensland, and to discover any possible environmental regulation of breeding. In this respect the Australian lungfish was compared with the African and South American species, *Protopterus annectens* (Owen), *Protopterus aethiopicus* Heckel and *Lepidosiren paradoxa* Fitzinger.

MATERIALS AND METHODS

Information on breeding, stages of eggs collected and weeds used for oviposition were recorded from Enoggera Reservoir from 1971–1973 and from the Brisbane River from 1978–1981. Rainfall data for these years was obtained from the Bureau of Meteorology in Brisbane, Queensland.

Information on hours of daylight was obtained from the records of the Department of Mapping and Surveying, Brisbane, Queensland.

Observations were made during the period July 1979 to November 1979 at two breeding sites in the Brisbane River: one was a bed of *Vallisneria spiralis* and the other, submerged roots of *Callistemon saligna* 1 km downstream. Temperature and dissolved oxygen were measured in the field between 11 am and 1 pm. Water samples were taken to measure pH in the laboratory. Eggs were collected from weeds or roots in the area from which the samples were taken. Plants were identified from Aston's (1973) description. Further observations on temperature and dissolved oxygen in relation to spawning were made during the period May 1980 to January 1981.

Eggs were kept in insulated containers and assessed for their stage of development in the laboratory, 1-2 hours after collection. The onset of oviposition was determined by subtracting the age of the oldest eggs found from the date of collections, e.g. minus 1 day if the oldest eggs were cleavage stages or minus 6 days if the oldest were neurulae of stage 18. Ages were based on times of development of eggs maintained in the laboratory at 18-22°C, temperatures comparable to those of the river at the time of collection (Kemp 1981).

RESULTS

Breeding Behaviour

i) Plants in the breeding areas and their potential as oviposition sites. A list of plants in the lake and river breeding areas is given in Table 1, with observations on the use made of the weeds for spawning. The weeds were present at all times except for *Eichornia crassipes, Hydrilla verticillata* and *Potamogeton javanicus,* all of which die off in winter.

Weeds used consistently for spawning are *E. crassipes* (in river and lake), *Vallisneria spiralis* and submerged roots of *Callistemon saligna* (river only). Fewer eggs were found on *H. verticillata, Potamogeton perfoliatus* or *Nitella* sp. Use of *Ceratophyllum* sp. or filamentous algae was incidental and occurred only when these weeds grew amongst *C. saligna* and *V. spiralis* (*Ceratophyllum*) or coated the *C. saligna* roots (algae).

TABLE 1: Utilisation of Weeds for Spawning in Enoggera Reservoir and in the Brisbane River.

Species of Weed	Lake	River
Eichornia crassipes	*	*
Hydrilla verticillata	?	*
Vallisneria spiralis	–	*
Callistemon saligna (submerged roots)	–	*
Nitella sp.	–	*
Potamogeton crispus	–	¢
Potamogeton perfoliatus	–	*
*Potamogeton javanicus***	¢	–
Ceratophyllum sp.***	¢	*
Nymphoides indica	¢	¢
Nymphaea capensis	¢	–
Nymphaea flava	¢	¢
Ludwigia peploides	–	¢
Brachiaria mutica	¢	–
Rumex bidens	¢	–
Sedge	–	¢
Filamentous algae***	–	*

* used for spawning
¢ not used
– weed has not been found
? weed too deep to sample
** breeding behaviour observed but no eggs found
*** growing with or on *C. saligna* roots or *V. spiralis* plants

ii) Oviposition in the lake. Eggs were always found attached to the roots or submerged floats of *E. crassipes.* Eggs have not been found on or among any other weeds in this locality, or lying free at the bottom of the lake, as measured by dredging samples or by diving. *H. verticillata,* used by fish in the Burnett River for spawning (Bancroft 1911 and 1928), also occurs in the lake but it was too deep to be easily sampled.

During the breeding season of *N. forsteri,* air breathing is frequent, and is accompanied by a distinct loud burp, made in the air with the lips clear of the water. During two periods of observation groups of fish appeared to be responding to each other. On the first occasion, one fish in the centre of a group 'sounded', then a fish to one side, then a fish to the other side, then the central fish, and finally one ahead of the first fish. On the second occasion one fish after another breathed air, in no particular order, along a weed bank about 20 m in length. The fish were spaced at 2-4 m intervals, and several minutes elapsed between each breath. During the period of observation (2 hours during the day), individual fish breathed at regular intervals of about 20 minutes. Pairs of fish also perform circling movements at the surface of the water close to weed banks.

Fish manoeuvre into the root mass of *E. crassipes* to spawn, and may lay eggs deep within the mass of roots as well as on the edges. Oviposition was observed once at 11 am in the lake. The female turns on her side when laying eggs and the male, entwined around her, fertilises the eggs as they emerge. Eggs less than 3 hours old (uncleaved, or in stage 1 or 2) were often found during daytime collecting trips.

Eggs laid at one time are found in a circumscribed area of the roots, for example all at the top. It is possible to distinguish individual clutches by their different ages, i.e. a set of late neurulae compared with a set of early cleavage stages. Eggs are laid over areas of 1-5 sq.m, on the roots and occasionally on partly submerged floats of the hyacinth, in varying positions from near the surface to a depth of one metre. They are attached quite firmly by the outer jelly layer which is sticky when first laid. Eggs were usually placed singly, or occasionally in pairs.

Fish performing frequent air breathing and circling movements have been observed in beds of *Potamogeton javanicus* in the lake, but eggs have not been found on this weed despite extensive searches. Adult lungfish have also been seen at night in para grass, *Brachiaria mutica,* which grows thickly in shallow water beside the shore, but again no eggs have been collected from this plant.

iii) Oviposition in the Brisbane River. Eggs are laid on the submerged roots of *Callistemon saligna,* with or without a covering of filamentous algae, in beds of *Vallisneria spiralis,* mixed stands of *V. spiralis* and *Hydrilla verticillata,* or on the upper parts of the alga *Nitella* sp. which also grows with *V. spiralis.* Eggs have also been found on fronds of *Ceratophyllum* sp. growing amongst *C. saligna* roots, and on *E. crassipes.*

Eggs were not found on sedge or on *Ludwigia peploides* which occur in shallow water near consistently used *V. spiralis* beds, nor on the *H. verticillata* growing in deep water nearby. Also fish did not appear to lay on *V. spiralis* growing in a substrate of fine black mud, but used weeds rooted in fine sand or gravel. In 1980 and 1981, logging operations upstream resulted in a deposit of silt throughout the *V. spiralis* bed, and although this was fine, it was not as fine as the mud and the fish continued to lay eggs.

Nymphoides indica, Nymphaea flava and isolated fronds of *Ceratophyllum* are also ignored by the fish, as is *Potamogeton crispus* which occurs in deeper or faster flowing water.

Eggs may be found close to the surface to a depth of 1.5 m. They occur on leaves or on the partly exposed upper roots of *V. spiralis,* sometimes partly buried in the substrate, and on any part of the *C. saligna* root mass, on or under the mat of filamentous algae if this is present. Sometimes the eggs are laid so high on the root mass that a drop in the water level after laying leaves the eggs exposed.

During 1980 *E. crassipes* was plentiful in the river and the fish used it for spawning. In one area they seemed to prefer it to *C. saligna* nearby laying eggs exclusively on the water hyacinth when it grew sufficiently dense (Fig. 1), and in another locality they used both. River fish often laid eggs in clusters of 4–14 eggs (i.e. close together but not touching) on *E. crassipes.*

In localities containing *V. spiralis* or *C. saligna,* different clutches of eggs could not usually be distinguished. Eggs of various ages appeared to be randomly distributed.

On one occasion only, in 1978, eggs were found lying free on the bottom of the river, in shallow, weed free areas amongst the *V. spiralis* plants. Many of these eggs were dead and all were exposed to sunlight and to higher temperatures than the eggs which were hidden in the *V. spiralis* leaves. The weed free areas did not look like nests and no adults were in attendance.

Other Observations

Both the lake and the river have a permanent inflow of water. Enoggera Reservoir is situated on a creek fed by springs in the D'Aiguilar Ranges to the west of Brisbane. Although the creek is reduced in times of drought, it is permanent. Water levels in the Brisbane River fluctuate because it supplies water for Brisbane, but the flow is continuous.

In both lake and in river,fish lay eggs in areas with a slow or moderate current of water, free of floating debris. Eggs are not found in still water, even if suitable weeds are available.

Fish do not guard the eggs in any of the spawning localities.

Suitable weeds for spawning are always present in the river. This was not always the case in the lake as *E. crassipes* dies off in winter. In 1973, as there was a mild winter and the weeds did not die off, so suitable weeds were present throughtout the year.

The timing of oviposition

Data on the duration of breeding by fish in the lake and in the river (calculated from the age of the oldest eggs found and the last date on which new laid eggs were collected) are shown in Figure 1. Changes in hours of daylight and the daily rainfall are included.

In the lake, breeding began in mid-September in 1971 and in early September in 1972. In 1973 oviposition began early in August, lasted for about one week and began again in early October (Fig. 1). In 1971 and 1972 breeding had been in progress for some time when the first eggs were collected, as a proportion of the eggs collected were in late stages of development (over 10 days old) in contrast to the first collection of 1973 when almost all the eggs found were at stage 11 (less than 2.5 days old) or younger. At the first part of the spawning season of 1973 progressed the high proportion of young eggs gave way to peaks of older embryos and finally to collections consisting entirely of larvae close to hatching. This progression is not always so obvious. Most collections from the lake show a proportion of older eggs, unlike collections from the river.

In the river, the breeding season started earlier and lasted longer, normally from mid to late August until November (Fig. 1). *V. spiralis* beds were used for spawning a little earlier than *C. saligna* roots in 1979 and at much the same time in 1980. The *V. spiralis* beds were discovered in the middle of the 1978 season, some time after breeding had begun. Oviposition is continuous in the *V. spiralis* beds throughout the breeding season, but not on the *C. saligna* roots where breaks may occur. In 1978 a small number of eggs appeared very late, in December, on *V. spiralis* plants (Fig. 1). In every collection from the river, even late in the season, a proportion of young eggs was present.

Leading Stimulus for Oviposition

The start of oviposition did not appear to be related to rainfall. In the lake during the 1971 and 1972, oviposition began after a dry winter, but before heavy rains. In 1973, spawning followed a heavy rainfall in the previous month, stopped after 2 dry months and started again during a month of moderate rainfall (Fig. 1).

On the river, rainfall was generally lower than on the lake, and oviposition began in mid or late August or early September in each year in both breeding areas (Fig. 1). In 1979, in the *V. spiralis* beds, there was a lag of two months between a peak of heavy rainfall and production of eggs. In 1980 heavy rain fell in May, very little in June, July or August and eggs were not found until the end of August (Fig. 1). In 1981, the start of spawning followed a dry month and came to an end before much rain fell.

In the *C. saligna* area, a peak of rain followed the start of oviposition in 1978, and preceded spawning by 3 and 4 months respectively in 1979 and 1980 (Fig. 1). This area was destroyed by logging operations before the start of the 1981 season.

Eggs less than 3 days old were found following rain within the preceding 3 days in 6 out of 15 collections that yielded new laid eggs in the lake. In the river 6 out of 24 and 3 out of 21 collections contained newly laid eggs in *C. saligna* and *V. spiralis* beds respectively. The rainfalls which did precede the finding of newly laid eggs were usually light, less than 25 mm. In both areas the heaviest rains occurred in January and February, when the fish do not spawn.

In every year, in both areas, *N. forsteri* begins to breed at a time of increasing daylength, in nine out of ten cases within 10 weeks after the shortest day and once in the lake after 11 weeks (Fig. 1).

Other conditions in the Brisbane River at the time of spawning.

The numbers of eggs found and the physical conditions at the time of collection on successive dates in two different localities in the Brisbane River in 1979 and 1980 are given in Fig. 2.

Temperatures are moderate initially and fairly steady but influenced by cold water from Somerset Dam higher up the river, released at irregular intervals in response to requirements in Brisbane. There was no marked rise until mid-October.

pH remains steady and slightly alkaline. Dissolved oxygen levels fluctuated, low at first and then higher, and were normally reasonably high during the day in the weed beds, probably because of photosynthesis by water plants. Levels of dissolved oxygen fell in November when water temperatures in the weed beds where the fish spawned were consistently over 24°C.

A large number of eggs were laid in the *V. spiralis* area in August 1979, at the same time as the level of dissolved oxygen rose, and fewer eggs were found in late September when the level of dissolved oxygen fell. There was a second rise in the number of eggs collected and in the level of dissolved oxygen before egg laying stopped in mid-November when levels of oxygen were low. A similar but less exact correspondence between number of eggs collected and levels of dissolved oxygen was found in the *C. saligna* area in 1979. Conversely, in 1980, oviposition began when levels of dissolved oxygen were falling in both areas, and reached a peak as the level of dissolved oxygen continued to fall.

DISCUSSION

Lungfish in the lake have been observed to spawn by day, and recently laid eggs are frequently found late in the morning in the river and the lake. This suggests that lungfish spawn during the day in these localities. This conflicts with the observation of Grigg (1965) who observed courtship behaviour in the evening and found eggs the following morning. Differences in timing are probably not important and more information may show that the time of oviposition is variable in both areas.

The significance of increased air breathing is also hard to assess. Normally this occurs rarely (Bancroft 1918 and Longman 1926). Possibly oxygen requirements are higher in the breeding season, or perhaps the sound made represents a "mating call" as Kesteven states (1944: 221). Johnels and Svensson (1955: 158) mention that "a

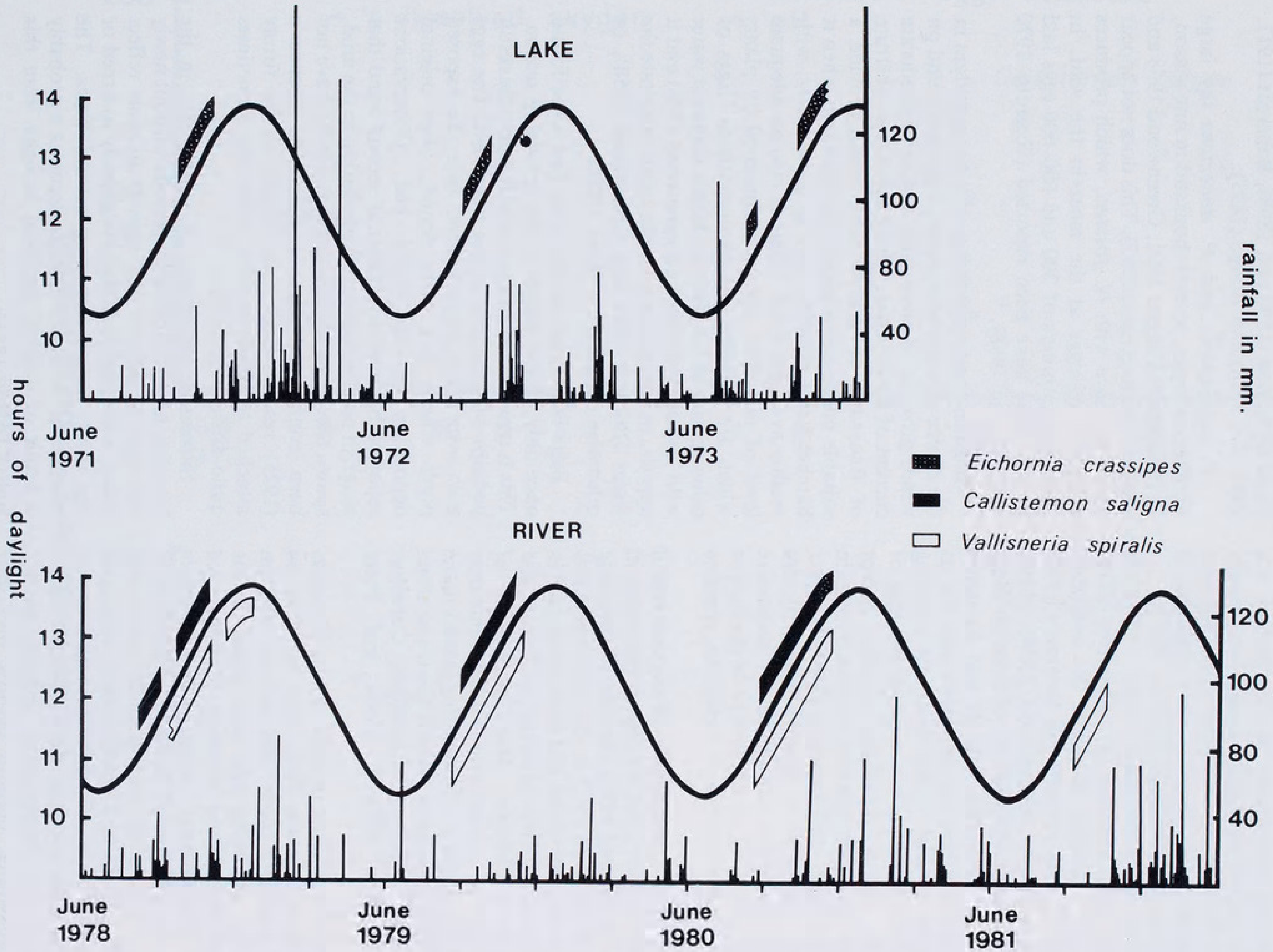

FIGURE 1. Hours of daylight, daily rainfall and duration of oviposition in Enoggera Reservoir (1971–73) and the Brisbane River (1978–1981). The first day of each third month is marked; rainfalls of less than 3 mm are not included; the start of oviposition is calculated by subtracting the age of the oldest eggs found from the date of collection, and the end from the last day on which new laid eggs were found.

substantial shrieking sound, which is very audible in the swamps'' can occasionally be heard when *Protopterus annectens* breathes air, but they do not associate this sound with breeding behaviour. *Lepidosiren paradoxa* is supposed to be able to make a cry like a cat (Natterer, cited by Kerr 1900). Circling movements at the surface are presumably part of courtship, as eggs are actually laid when the fish are entwined. This has also been observed when lungfish have spawned in captivity (Hegedus 1970 and Moreno 1968).

N. forsteri does not build a nest, unlike the South American lungfish, *L. paradoxa* (Kerr 1900) or the African lungfish, *P. annectens* (Budgett 1901 and Johnels and Svensson 1955) and *P. aethiopicus* (Greenwood 1958). Also, unlike the males of other species of lungfish (Kerr 1900, Budgett 1901 and Johnels and Svensson 1955), *N. forsteri* does not appear to care for its young. There is little similarity in the breeding behaviour of the Australian lungfish and that of African or South American species except perhaps the laying of separate clutches of eggs in one place (Johnels and Svensson 1955). Whether this suggests that male *N. forsteri* have territories for oviposition which are visited by successive females for spawning, as appears to be the case in *P. annectens,* or whether it is fortuitous, remains to be seen.

Suitable weeds are available all the year round in the Brisbane River, but they occur seasonally in the lake, and this may affect the time of spawning in the latter area. In 1973 in the lake weed was available during the winter and early spring and in this year spawning first occurred in August and again in early October. Also, availability of suitable weed for oviposition for a long time may determine the length of the breeding season in the river. Presence of suitable weed is known to affect the timing of spawning in goldfish, *Carassius auratus* Linnaeus (Stacey, Cook and Peter 1979a).

Lungfish are specific in their choice of weeds for oviposition. In the lake, eggs are laid on *Eichornia crassipes* roots, and perhaps also on *Potamogeton javanicus* and para grass. In the river, eggs were found attached to submerged roots of *Callistemon saligna* or *Eichornia crassipes,* to *Vallisneria spiralis, Potamogeton perfoliatus, Nitella* sp. and *Hydrilla verticillata* plants, occasionally to *Ceratophyllum* associated with *C. saligna* or *V. spiralis,* and also on filamentous algae covering the *C. saligna* roots. Some weeds, like *Potamogeton crispus,* are not used for spawning, perhaps because they only occur in fast flowing water. Weeds which do not form dense banks, e.g. *Nymphaea capensis* and *N. flava, Nymphoides indica, Ludwigia peploides* and *Rumex bidens,* which all have submerged stems, are likewise not used for egg laying. Some of the results reported here are in agreement with those of Semon (1893 and 1899), Bancroft (1911, 1918 and 1928) and Illidge (1893).

P. aethiopicus and *P. annectens* lay large numbers of eggs, several thousand in one season, in their nests (Budgett 1901, Greenwood 1958 and Johnels and Svensson 1955). This does not appear to be the case with *N. forsteri,* which produces hundreds of eggs at the most in the wild. In captivity, numbers of 200 and 500–600 eggs laid at one time have been reported (Hegedus 1970 and Moreno 1968).

Substrate and current may also be important in the choice of a spawning area. Eggs are found on weeds growing in areas with a slow or moderate current of fresh water, where there is a substrate of fine sand or gravel. Such areas provide a suitable micro-environment for the larva when it hatches i.e. a place to hide in dense cover, with readily available food. There is also an adequate level of dissolved oxygen maintained by plants which are carrying out photosynthesis. Eggs of other species of lungfish are laid in stagnant water with low oxygen tension (Greenwood 1958) and it appears to be necessary for the adult to agitate the water (Budgett 1901 and Greenwood 1958), or otherwise oxygenate it (Kerr 1900).

Eggs laid loose on the river bed were found once only, at the height of the spawning season. This is regarded as an abnormal feature, the result perhaps of crowding in the weed bed. The eggs may even have been washed into the exposed pools where they were found, after original deposition in the weed bed. Observations reported by Macleay (1884) at second hand that lungfish pair, scoop out an identation in the mud, spawn there and remain together nearby have not been confirmed. Also, contrary to Spencer's (1925) results, eggs were found to be firmly attached to weeds in most cases and sometimes quite difficult to remove.

Successive collections of young eggs in the breeding areas followed by periods without newly laid eggs or without any eggs at all must reflect either individual fish becoming ready to breed or the same female spawning several times. The number of old eggs in lake collections is probably a result of delayed hatching in eggs from this source (Kemp 1981).

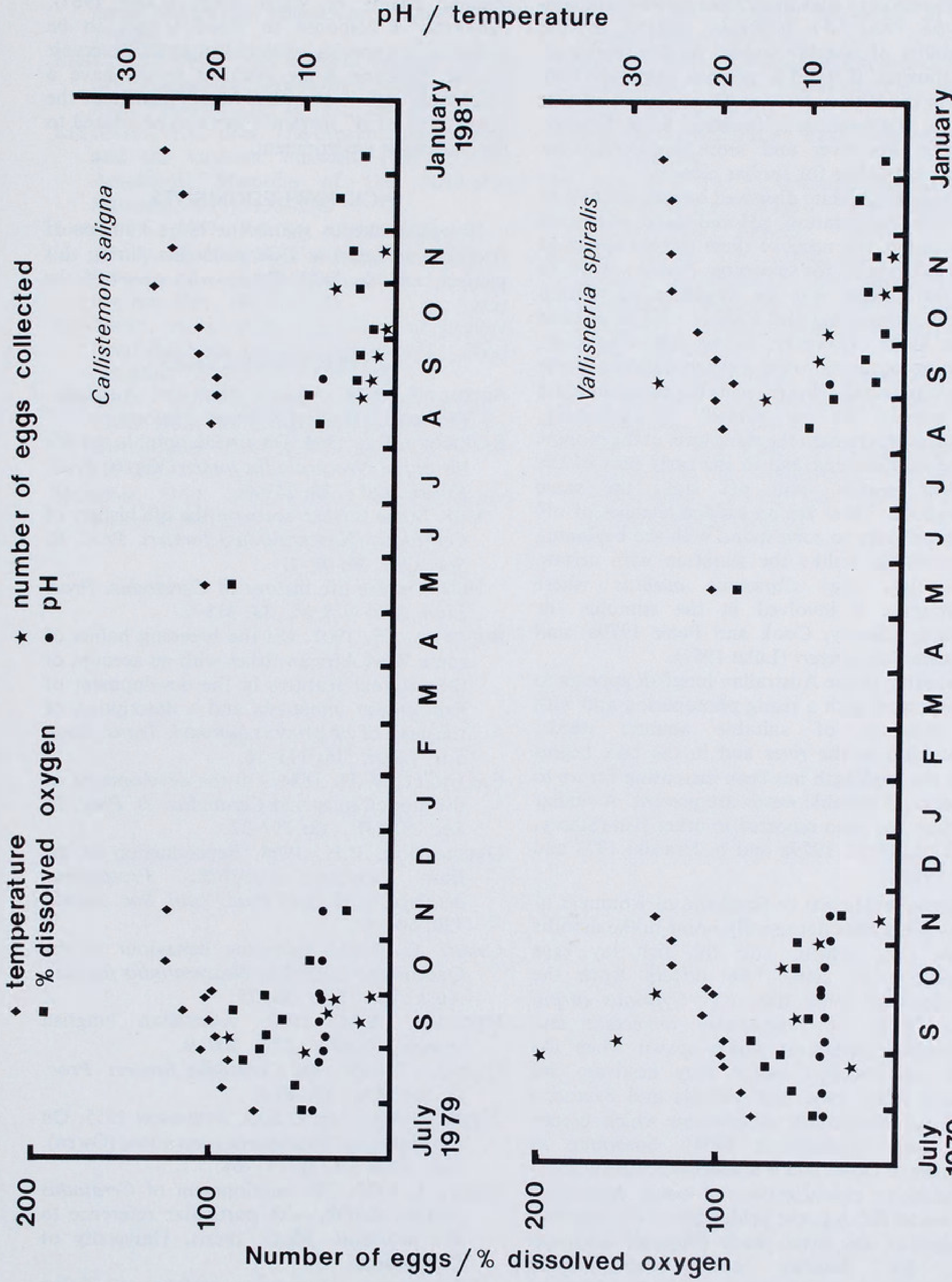

FIGURE 2. Physical conditions and number of eggs collected in 1979 and 1980 in two areas of the Brisbane River.

Differences in spawning times between the lake and the river are probably related to the availability of suitable weeds. As the season of 1973 showed, if weed is present spawning may occur in the lake as early as August, as it does in the river. Differences in breeding times between the lake, the river and more northerly river systems may arise for similar reasons.

Attempts to relate dissolved oxygen content of the water, temperature, pH and water level were inconclusive, but none of these factors appeared to act as a trigger for spawning. In one season, in the river, there was an apparent correlation between oviposition and a raised oxygen content in the water. However, in the following year, spawning occurred while oxygen content in the water was falling. Water levels fluctuated but did not appear to be related to spawning. Temperatures remain the same level in the months preceding spawning and in the early part of the breeding season, and pH stays the same throughout. There are no sudden changes of pH or temperature to correspond with the beginning of spawning, unlike the situation with certain other fish, e.g. *Carassius auratus* where temperature is involved in the stimulus for spawning (Stacey, Cook and Peter 1979a) and *Carassius klungingeri* (Lake 1967).

Breeding in the Australian lungfish appears to be associated with a rising photoperiod and with the presence of suitable aquatic weeds. Oviposition in the river and in the lake begins when the daylength has been increasing for up to 11 weeks, if suitable weeds are present. A similar situation has been reported in other fish (Stacey, Cook and Peter 1979a and b, Urasaki 1973 and Pike 1973).

Rainfall sufficient to flood the environment of the lungfish does not usually occur in the months before they spawn, and the fish lay eggs irrespective of rain. This differs from the behaviour of other fish, e.g. *Cyprinus carpio* (Pike 1973), or *Protopterus annectens* and *Lepidosiren paradoxa* which spawn when the dried out swamps where they aestivate are flooded (Kerr 1900 and Johnels and Svensson 1955) or *Protopterus aethiopicus* which breeds after rain (Greenwood 1958). Spawning in response to flood and a minimum temperature is an adaptive characteristic of some Australian freshwater fish e.g. the golden perch *Plectroplites ambiguous,* the silver perch *Bidyanus bidyanus* and the Murray cod *Maccullochella macquariensis,* all of which live in the Murray-Darling River system which often dries out to become chains of water holes (Lake 1967). However, a response to flood is not to be expected in a species living in Enoggera Reservoir or the Brisbane River both of which have a permanent inflow of water. Most features of the oviposition of *N. forsteri* appear to be related to the particular environment.

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