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FRESHWATER BIOLOGICAL ASSOCIATION

TEESDALE UNIT

Report to: Department of the Environment,
Northumbrian Water Authority,
The Natural Environment Research Council.

Date: 14 July 1981.

Title: Survival of Intragravel Stages of Brown
Trout (Salmo trutta L.) in Teesdale.

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SUMMARY

1. Mean survival of eggs in planted boxes ranged between 27-85% to eyeing and 16-71% to hatching.
2. Mean estimates of survival from eggs to swim-up fry in alevin traps ranged from 0.3 - 11.9%.
3. A number of intragravel water oxygen concentrations were shown to be lower than published critical levels for good egg survival.
4. Gravel samples from redd sites were analysed for percentage fines and percentage organics. No correlation was found between gravel composition and survival of eggs.
5. Evidence of overcutting of redds was found in some Teesdale streams.
6. Eggs and fry were shown to be vulnerable to downstream displacement by high water velocities.
7. No evidence was found to show that in situ freezing of eggs occurred.

INTRODUCTION

This report brings together information collected in Teesdale concerning, I The survival rates of intragravel stages of brown trout and, II The factors influencing survival.

The streams on which this information was collected are shown in Table 1 and they are described in further detail in Ottaway et al. (in press). Although all the becks contained brown trout spawning areas, some were utilised by more spawning trout than others. The best spawning sites as judged by this criterion were Thorsgill and Great Egglehope becks where the research effort was therefore concentrated. There were two different spawning areas in Egglehope, namely Great Egglehope beck itself and Great Egglehope spring fed tributary (Esft), data from these two areas are analysed separately in most parts of the text.

Table 1. A summary of the activities carried out on the different streams. x signifies that the activity took place

Site	Grid ref. of areas studied	Redd counting	Egg box burial	Alevin trapping	Quantitative electrofishing	Water temp. recording	Intragravel water sampling	Gravel sampling
Great Eggeshope	NY 984288/ 978299	x	x	x	x	x	x	x
Eaft	NY 978298/ 979298	x	x	x	x	x	x	x
Thorsgill	NZ 062153/ 047152	x	x	x	x	x	x	x
Carl Beck	NY 948232/ 943228		x		x	x		
R. Lune	NY 948231/ 951235		x					

I. THE SURVIVAL RATES OF INTRAGRAVEL STAGES OF BROWN TROUT

Planted egg boxes were used to estimate survival of eggs to eyeing and alevin traps to estimate survival to swim-up.

Survival estimates using egg boxes

Ripe female and male fish caught by electrofishing in the field were stripped for eggs and sperm. Fertilisation of the eggs was carried out according to the "dry" method (Bagenal & Braum, 1978). After water hardening, the eggs were counted into lots of 50, each lot being interbedded with gravel in a modified Harris egg box (Harris, 1973) (Fig. 1). In 1979, all the brown trout redds observed in the study sites were marked and measured as previously described (Ottaway *et al.*, in press). Two egg boxes, secured to and marked by a metal stake, were buried in the pot of each redd. (Fig. 1). Egg boxes were also buried in areas of stream that were not utilised for spawning, these locations were termed "false redds". A sample of 5 boxes was dug up 24 h after planting to check that the eggs had been properly fertilised. Mean egg mortality in the boxes was $2.0 \pm 1.3\%$ S.E.

Water temperature data were used to estimate the time of 50% eyeing and hatching of the eggs (Crisp, 1980 unpubl. report). The boxes were checked at weekly intervals around the predicted dates. One box was removed when the eggs were judged to be eyed and hatched respectively and the contents examined for survival of the embryos. The dead eggs could not always be counted with certainty since they rapidly decomposed, percentage survival was therefore estimated by expressing the number of eyed or hatched eggs as a percentage of those buried.

Survival estimates using alevin traps

Alevin traps modified in size from those described by Phillips & Koski (1969) were installed over a small number of suitable redds after eyeing (Fig. 2). Suitable redds were designated as those sufficiently isolated to prevent disturbance of other redds or the stream bank at installation, and in which egg boxes had been previously buried so that the times of eyeing and hatching were known. The traps were checked one to three times a week after egg hatching and any alevins present in the cod end of the trap were removed and counted. In order to test that all the emerging alevins were caught and that they did not escape laterally, one of the alevin traps was enclosed within a large outer trap. Both traps were checked for emerging fry.

An approximation of the percentage survival to swim-up was obtained by using the initial redd dimensions to estimate the size of female cutting each redd (data recalculated from Ottaway et al., in press) and by then applying a length/fecundity relationship (Appendix 1) to estimate the number of eggs the redd contained. The percentage survival was calculated by expressing the total number emerged as a percentage of the number of eggs in the redd. Other applications of alevin trap data are briefly described in Appendix 2.

Results

Survival of eggs to eyeing. The mean survival to eyeing ranged from 27-85%, the highest values being obtained in Esft and the lowest in Thorsgill Beck (Table 2). There was no difference in egg survival in real as against false redds except for Thorsgill where survival in false redds was significantly lower (Student's t-test, $P < 0.05$).

Table 2. Estimated mean percentage survival of eggs to eyeing as derived from planted egg boxes 1979/80.
 Number in parentheses represents number of values meaned.

Real/False redds	Site	No. boxes washed out	% survival to eyeing in remaining boxes \pm S.E.	Total % survival to eyeing assuming 0% survival for washed-out eggs \pm S.E.
Real	Esft	0	84.9 \pm 8.8 (9)	84.9 \pm 8.8 (9)
	Great Egglehope	2	54.9 \pm 11.2 (9)	44.9 \pm 11.3 (11)
	Thorsgill	1	57.3 \pm 7.3 (16)	53.9 \pm 7.6 (17)
	Carl	1	65.0 (2)	43.3 \pm 24.3 (3)
False	Esft	0	70.5 \pm 8.2 (4)	70.5 \pm 8.2 (4)
	Great Egglehope	0	63.3 \pm 16.8 (3)	63.3 \pm 16.8 (3)
	Thorsgill	1	26.9 \pm 11.2 (9)	24.2 \pm 10.4 (10)
	Carl	0	40.9 \pm 12.8 (7)	40.9 \pm 12.8 (7)

Survival of eggs to hatching. Mean values ranged from 16-71% and were significantly higher in Esft than any other site (Student's t-test $P < 0.05$) (Table 3). Although there were significant differences between real and false redds in survival to eyeing in Thorsgill Beck, no such difference could be demonstrated in survival to hatching.

Survival to swim-up. The number of alevins caught was very variable (Table 4) the total catch per trap ranging from 0-512. In the one redd doubly trapped, one alevin emerged in the outer trap as compared to 23 in the inner trap. The outer trap was slightly damaged in a spate and it is possible that the one alevin swam in from outside rather than emerged into the trap. This result is therefore a little inconclusive but it does suggest that most of the emerging alevins were contained within the inner trap.

Estimates of percentage survival from eggs to swim-up fry were generally very low (Table 5). Survival rates in Esft were consistently higher than at any other site.

Discussion

Survival rates estimated from egg boxes are more likely to have been over- than under-estimated since the boxes were firmly staked in the gravel and this may have prevented a certain amount of washout. Within those boxes remaining in the gravel, survival of properly fertilised eggs should, according to Harris (1973), have been similar to that of eggs buried loose in the gravel. Fertilisation loss was shown in this study to be in the region of 2%.

Table 3. Estimated mean percentage survival of eggs to hatching as derived from planted egg "boxes."
 Numbers in parentheses represent number of values meaned.

Real/False redds	Site	No. boxes washed out	% survival to hatching in remaining boxes \pm S.E.	Total % survival to hatching assuming 0% survival for washed out boxes \pm S.E.
Real	Esft	0	71.3 \pm 5.6 (9)	71.3 \pm 5.6 (9)
	Great Egglehope	3	35.5 \pm 11.3 (8)	28.8 \pm 9.5 (11)
	Thorsgill	1	15.9 \pm 3.3 (16)	14.9 \pm 3.2 (17)
	Carl	1	18.0 \pm 15.1 (3)	13.5 \pm 11.6 (4)
False	Esft	1	51.0 \pm 10.2 (4)	40.8 \pm 12.9 (5)
	Great Egglehope	0	33.3 \pm 12.7 (3)	33.3 \pm 12.7 (3)
	Thorsgill	1	26.9 \pm 11.2 (9)	24.2 \pm 10.4 (10)
	Carl	0	23.7 \pm 9.7 (7)	23.7 \pm 9.7 (7)

Table 4. Summary of alevin trap data 1979-80. E represents Egglesthope
T represents Thorsgill.

	1979		1980		1981
	E	T	E	T	E
Number of traps installed	12	10	14	6	19
Number of traps vandalised	2	0	0	1	00
Number of traps damaged by spates	0	2	0	0	0
Remaining number of traps	10	8	14	5*	19
Number of traps with a catch of:-					
0 alevins	4	6 ^I	3	4	7
1-5 alevins	4	0	2	0	4
6-10 alevins	1	1	2	0	1
10 alevins	1	1	7 ^I	1	7

^I three of these traps were subsequently stranded after installation

^I one trap was temporarily part-stranded.

* all traps were stranded for approximately 4 weeks.

Table 5. Estimated mean percentage survival from eggs to **swim-up** fry as derived from alevin trap data.

Spawning season	Site	Range of % survival	Mean % \pm S.E.	n
1978/79	Esft	0 - 20.9	3.8 \pm 3.4	6
	Great Egglehope	0 - 00.8	0.2 \pm 0.2	4
	Thorsgill	0 - 2.8	0.4 \pm 0.4	8
1979/80	Esft	0 - 34.3	9.6 \pm 5.9	6
	Great Egglehope	0 - 14.6	4.6 \pm 1.9	8
	Thorsgill	0 - 1.6	0.3 \pm 0.3	5
1980/81	Esft	0 - 90.8	11.9 \pm 7.6	12
	Great Egglehope	0 - 28.3	8.2 \pm 4.7	7

The results (Tables 2 & 3) indicate values of approximately 50% survival to eyeing and 30% to hatching in Teesdale streams. These values are generally much lower than others reported in the literature (Hobbs, 1948 Harris, 1970). There was some variation between sites, survival at Esft being particularly good and survival at Thorsgill rather low. Apart from eggs to eyeing in Thorsgill, no difference was seen in survival of eggs planted in real or false redds. This result supports a previous suggestion (Ottaway *et al.*, in press) that in Teesdale, redds are dug wherever there is gravel fine enough to be moved rather than in particularly specialised sites.

The estimates of survival to swim-up using the alevin traps could be criticised for several reasons:

1. The method used to compute the number of eggs in the redd relies on several estimated values, the redd dimensions were used to estimate the female size digging the redd and a fork length/fecundity relationship was used to estimate the number of eggs a female of this size produces.
2. The way in which the survival rate was computed pre-supposes that each female cuts only one redd (the term "redd" here being taken to mean the structure in the gravel containing all her eggs in several egg pockets). This fact is commonly implied in the literature (Jones & Ball, 1954) but if it were untrue it would cause the survival rates to be under-estimated.

3. The redds over which the traps were installed, were assumed to be real redds rather than the results of the trial digging that trout have been observed to occasionally undertake. Care was taken to minimise this source of error.

4. The trap may not have captured all the emerging alevins, some may have escaped laterally, although such escapement was thought to be small.

5. Silt collected on the surface of the gravel within the alevin trap and this may have hindered emergence or reduced intragravel flow. Phillips & Koski (1969) also noticed the tendency for alevin trap to silt-up but did not investigate how this affected survival.

The values for survival to swim-up (Table 5) may thus be underestimated, but, even allowing for considerable error, they are much lower than other values reported in the literature (Hobbs, 1948; Allen, 1951; Le Cren, 1961; Harris, 1970).

II. FACTORS INFLUENCING SURVIVAL OF YOUNG STAGES OF BROWN TROUT.

Factors thought to influence survival of young salmonids include HIGH WATER FLOWS, which can cause washout of eggs and young fry (Needham & Jones, 1959; Coble, 1961, 1961; Elliott, 1976); LOW WATER FLOWS, which associated with gravel siltation and, in extreme cases, stranding of redds can reduce the intragravel oxygen supply to eggs resulting in their death by asphyxiation (Shelton, 1955; McNeil & Ahnell, 1964} McNeil, 1966} Hall & Lantz, 1969); SHORTAGE OF SPAWNING SPACE, which can result in loss of eggs through overcutting of redds (Hobbs, 1948; McNeil, 1966);

PREDATORS, leading to loss of both eggs and fry (McNeil, 1969)5 LOW WATER TEMPERATURES, which can cause death of eggs in the gravel (Peterson et al.,1977; Reiser & Wesche, 1979); and SIZE OF BED MATERIAL which can influence the entrapment of alevins within the gravel (Hausle & Coble, 1976; Platts et al.,1979).

Information is presented here relating to some of these factors in brown trout redds in Teesdale. Other information has been discussed elsewhere and the results are summarised.

Intragravel oxygen

Standpipes were driven into the upstream end of the tails of selected redds (Fig. 1) enabling the removal of small water samples from 15 cm below the gravel surface. The standpipes were of two types (Fig. 3). Type 1 had to be installed and removed for each sampling occasion otherwise the standpipes were damaged or lost by washout in spates. Type 2 could be left in the stream bed indefinitely but was costly to produce and therefore only available in small numbers. Approximately once a month during the egg incubation period 10 ml water samples were removed from the stand-pipes. Their oxygen concentration was determined using a micro-Winkler technique - scaled down from the method described in Mackereth et al. 1978).

The values of oxygen concentration obtained are shown in Appendix 3. Lethal oxygen concentrations for brown trout eggs are not known. Davis (1975 - Table 8) suggest that the following concentration represent oxygen response thresholds for salmonid fish in general i.e. levels below which effects due to oxygen deprivation are seen:

spawning - eyeing	1.14 mg l ⁻¹
eyed eggs	5.93 mg l ⁻¹
hatching - swim-up	8.09 mg l ⁻¹

Turnpenny & Williams (1980) found 50% mortality between eyeing and hatching of brown trout embryos at 6.5 mg l^{-1} . What is clear from the values in Appendix 3 is that the measured oxygen concentrations in many of the redds fell below these critical levels during incubation. No relationship was however found between percentage survival of eggs and the oxygen concentration of the intragravel water (Fig. 4). No information on intragravel seepage velocity was obtained so that the rate of oxygen supply to the eggs could not be calculated.

Percentage fines in bed material

When the alevin traps were taken up in the summer of 1980, gravel samples were taken from immediately adjacent areas of stream bed using short lengths of 20 cm diameter plastic piping. The pipes were pushed approximately 25 cm into the stream bed and all the loose fines and gravel from inside the pipe removed. The average sample size was 8 kg (dry weight). The samples were air dried and then sieved to determine percentage composition by weight of fine fractions less than 2 mm diameter. In addition, fractions smaller than 0.5 mm diameter were ashed in a muffle furnace for 1.5 hr at 500°C to determine their organic content. The organic analysis was carried out because the organic content of bed material might affect the amount of oxygen available to salmonid embryos.

The results are summarised in Tables 6 & 7. The mean percentage by weight of fines and the mean percentage by weight of organics was generally greater in Esft than Great Egglehope or Thorsgill - a not unexpected result since the bed of Esft consists largely of tailings from a disused lead mine. The proportions of fines and of organics in the fine fractions were very similar between Great Egglehope and Thorsgill. No correlation was found between survival of eggs (to eyeing,

Table 6. Mean percentage by weight of fines in gravel samples taken from different sites. n = number of samples

Site	n	Percentage by weight x mm diameter \pm S.E.					
		2 mm	1 mm	0.5 mm	0.25 mm	0.125 mm	0.063 mm
Esft	11	23.8 \pm 4.3	17.6 \pm 3.7	11.3 \pm 2.8	5.6 \pm 1.9	1.4 \pm 0.6	0.3 \pm 0.1
Great Egglehope	11	12.2 \pm 2.0	6.8 \pm 1.6	2.8 \pm 0.7	1.1 \pm 0.3	0.4 \pm 0.12	0.1 \pm 0.04
Thorsgill	10	13.7 \pm 3.3	10.1 \pm 2.9	6.8 \pm 2.4	3.6 \pm 1.4	0.8 \pm 0.3	0.2 \pm 0.1

Table 7. Mean percentage by weight of organics in total gravel samples. n = number of samples.

Site	n	Mean percentage by weight \bar{x} mm \pm S.E.			
		0.5 mm	0.25 mm	0.125 mm	0.063 mm
Esft	11	0.39 \pm 0.09	0.17 \pm 0.05	0.06 \pm 0.01	0.02 \pm 0.005
Great Egglehope	9	0.12 \pm 0.04	0.05 \pm 0.02	0.02 \pm 0.01	0.01 \pm 0.00
Thorsgill	9	0.19 \pm 0.09	0.09 \pm 0.04	0.04 \pm 0.02	0.02 \pm 0.00

hatching or swim-up) and percentage organics or percentage fines (any size class) in individual redds.

Shortage of spawning space

An attempt was made in 1978/79 to mark all the redds cut in the study sites. Some overcutting of redds was observed chiefly in Esft (Table 8).

High water flows and washout

- i) Eggs Washout of eggs is discussed in a separate report. Disruption of stream bed was shown to occur to the level of the egg pockets in some Teesdale streams. A minimum figure of 12% egg loss through washout was suggested.
- ii) Swim-up fry Results of experiments in Grassholme channels show that swim-up brown trout fry are vulnerable to displacement by high water velocities (Ottaway & Clarke, in press).

Low water temperatures

Stream and intragravel water temperatures were measured, over the course of a year, on a brown trout spawning riffle in Great Egglehope Beck (unpubl. data). Lethal temperatures for brown trout eggs are not known but thought to be c. 0°C (Alabaster & Lloyd, 1980). Intragravel water temperatures never fell below 0.5°C. In situ freezing of trout eggs is not thought to occur in this beck.

Table 8. Number of redds overcut in the 1978/79 spawning season

Site	Number of redds marked	Number overcut	%
Esft	49	4	8.2
Great Egglehope	90	1	1.1
Thorsgill	45	0	0.0

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APPENDIX 1.

Table 1. Length/fecundity data of brown trout sampled from study sites

$$f = 0.30 l^{2.21}, \quad r^2 = 0.69, \quad r = 0.83^*$$

Fork length l (cm)	Fecundity f
22.0	192
24.3	377
26.8	491
27.8	835
27.9	376
35.5	591
42.1	1169

APPENDIX 2.

The use of alevin traps

Alevin traps designed after Phillips & Koski (1969) were installed over redds in Teesdale streams in 1978-1980. They were used to collect three different types of information:

1. To estimate survival of eggs to emergence

(See Table 5 of report). As a method of estimating survival the alevin traps were not very successful because of:

- (i) The difficulty of knowing exactly how many eggs were originally buried in the trapped area.
- (ii) possible alevin lateral escapement
- (iii) possible siltation of the gravel - hindering emergence.

A better procedure in the field may have been to install traps over false redds, i.e. over known numbers of eggs stripped from trout and buried in the stream gravels.

2. To collect temperature data on time to 50% swim-up

Trout collected in the cod-ends of the alevin traps were mainly swim-up fry i.e. the yolk sac had almost disappeared and the fish were feeding externally. From temperature records of thermographs installed in the streams, the mean water temperature to 50% emergence (= swim-up) was calculated. A relationship between temperature and time to 50% swim-up was established but the range of temperatures over which the equation applied was rather small (Table 1).

APPENDIX 2. TABLE 1. Time and temperature to 50% swim-up
from alevin trap data.

Redd No.	Time(D) (days)	Mean water temperature(T) (°C)
34	186	4.0
42	189	4.2
21	177	4.2
101	204	4.3
19	177	4.3
36	166	4.5
24	151	4.9
9	168	5.1
31	151	5.3
27	172	5.8

$$\log_{10} D = 3.83 - 0.62 T + 0.06 T^2$$

$$r^2 = 0.61 \quad r = 0.78^{**}$$

3. To collect information on the general pattern of emergence of young trout.

For alevin traps in which the total catch was 50 fry the frequency patterns of emergence were plotted (see figures). The total emergence period was in some cases very long e.g. redds 36, 44, 9, 24 and in some cases very short e.g. redds 42, 27. The long emergence period in some instances may have been due to the inadvertent trapping of more than one redd since there were examples of percentage frequency plots with bimodal patterns (e.g. redds 24, 9). The long emergence period could also have been due to some fry remaining in the body of the trap for some time before moving into the cod-end. Size at emergence was generally 24-26 mm (see figures), and a gradual increase in size of alevins was seen over the emergence period in most traps.

No correlation could be found between mean condition factor of alevins at emergence (w/l^3) and percentage fines in the gravel (percentage by weight 2 mm or percentage by weight 0.063 mm) or mean gravel size (data given in table). Neither could a correlation be established between length of emergence period and these same gravel parameters (data given in Table 2).

APPENDIX 2

TABLE 2. Information on redds where total catch 50 fry. Esft rep. Egglestone spring fed trickle. Esft₁ = upper course. Esft₂ = lower course. E(m) = Great Egglestone Beck - main stream. CF rep. condition factor.

Year	Redd No.	Site	Length of emergence period(days)		Mean CF at emergence x 10 ⁻⁶	Mean grain size (mm)	% fines (by weight)	
			total period	10-90% emergence			% 2 mm	% 0.063 mm
1978	101	Esft ₂	64	43	6.30	26.7	-	-
1979	31	Esft ₁	59	30	6.53	9.5	43.53	0.70
	36	Esft ₂	88	42	6.41	19.0	19.08	0.22
	42	Em	32	7	6.95	35.5	13.91	0.06
	34	Em	35	32	6.27	54.8	9.31	0.10
1980	27	Esft ₁	28	11	6.49	16.3	7.31	1.32
	9	Esft ₂	73	49	6.57	29.7	6.40	0.12
	24	Esft ₂	69	32	5.62	34.6	5.96	0.08
	19	Em	54	19	7.57	35.1	12.01	0.07
	21	Em	38	21	6.01	44.5	4.68	0.20

APPENDIX 3.

Table showing dissolved oxygen content of intragravel water sampled from redds during the 1979/80 spawning season.

TABLE 1. Esft = Great Egglestone spring fed trickle. Em = Great Egglestone Beck. T = Thorsgill Beck.

Redd No.	Site	Sampling date (day, month, year)					Mean O ₂ conc. mg l ⁻¹ ± S.E.(n)	
		4.2.79	19.12.79	28.1.80	21.2.80	16.4.80		
31	Esft	9.9	9.0	6.8	7.9	7.6	8.2 ± 0.5 (5)	
84		7.9	9.5	6.8	8.9		8.3 ± 0.6 (4)	
68		11.8	8.8	10.8	8.9	9.5	10.0 ± 0.6 (5)	REAL
11		11.4	9.0	11.0	7.3	8.5	9.4 ± 0.8 (5)	REDDS
40		10.1	10.7	3.4	3.8	7.2	7.1 ± 1.7 (5)	
36					10.1		10.3 (1)	
37	Em	9.2	4.0	8.9	2.7	1.7	5.3 ± 1.6 (5)	
18		8.5	8.5	5.8	5.0	11.0	7.8 ± 1.1 (5)	
42		10.5	7.4	5.6	4.2	7.2	7.2 ± 1.1 (5)	
50					0.5		0.5 (1)	
32					7.0		7.0 (1)	
13					2.1		2.1 (1)	
146	Esft	2.7	1.7	2.4	2.0	3.5	2.5 ± 0.3 (5)	
140		8.6					8.6 (1)	FALSE
122		7.1	4.6	2.7	5.3	5.8	5.1 ± 0.7 (5)	REDDS
144	Em	9.8	14.1	8.6	5.1	7.3	9.0 ± 1.5 (5)	
148			6.4	1.4	2.6	10.3	5.2 ± 2.0 (4)	

APPENDIX 3.

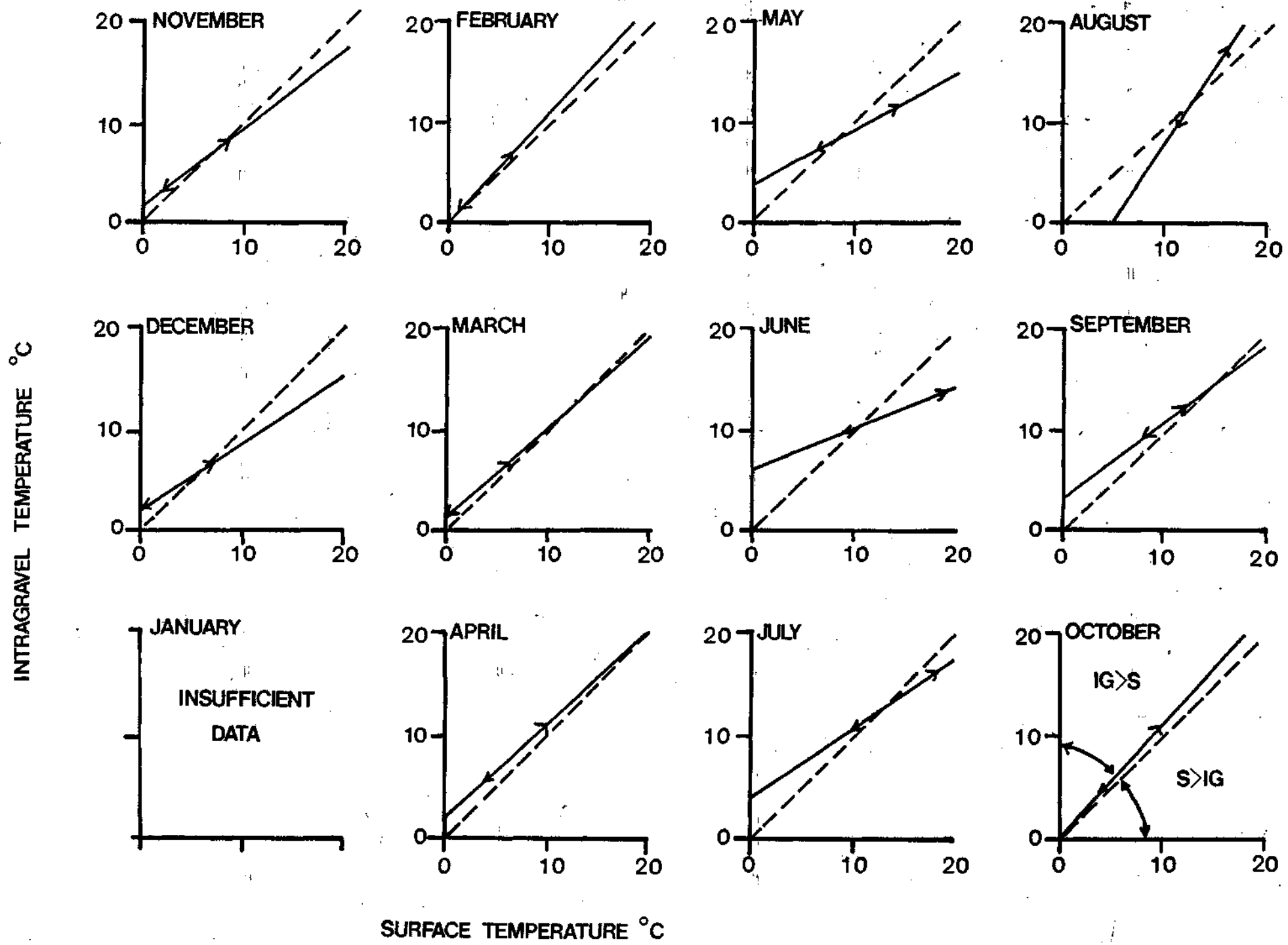
TABLE 1. Continued.

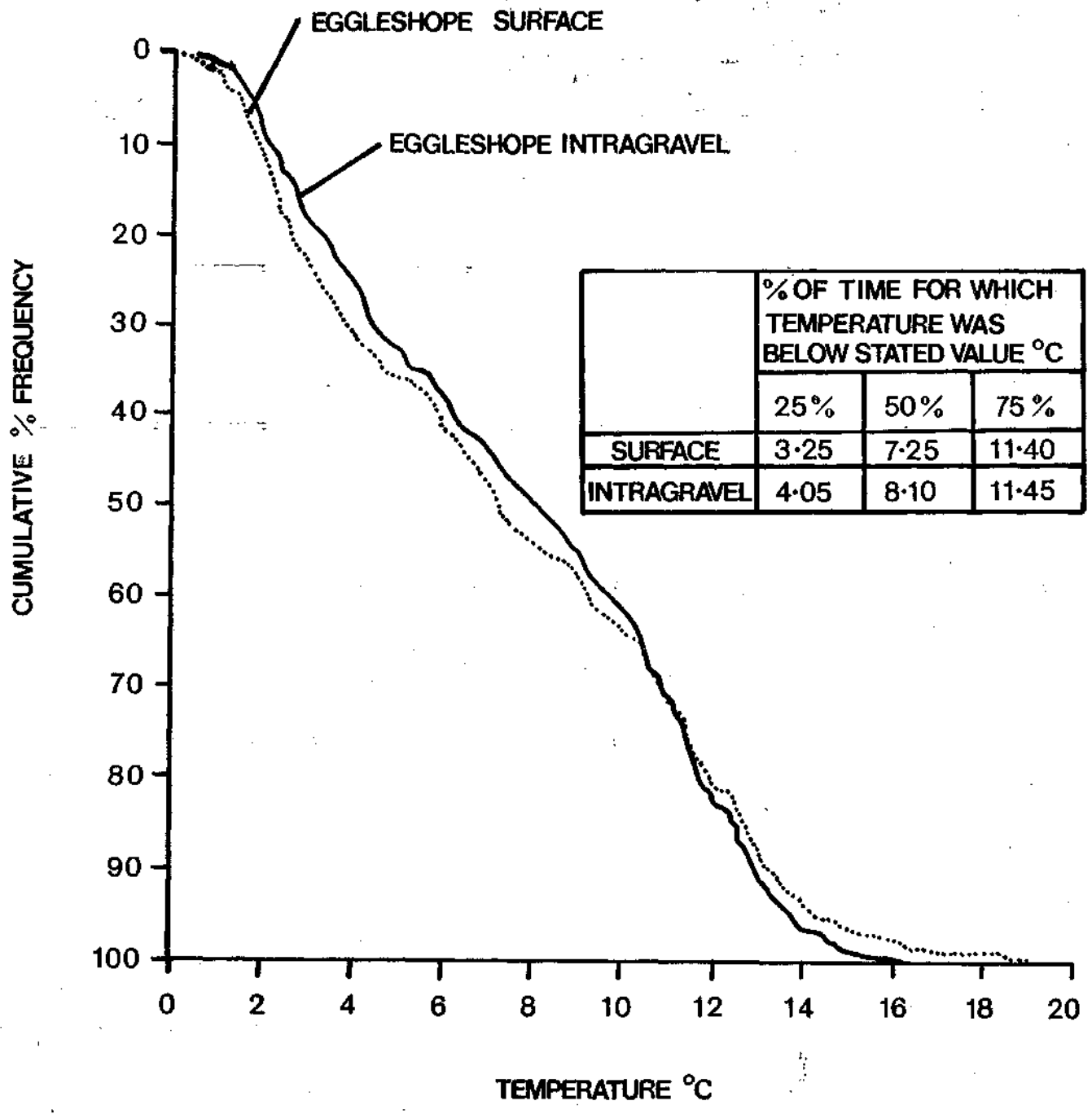
Redd No.	Site	Sampling date (day, month, year)					Mean O ₂ conc. mg l ⁻¹ ± S.E.	
		4.2.79	19.12.79	28.1.80	21.2.80	16.4.80		
54	T	3.9	10.8		0.9	1.2	4.2 ± 2.3 (4)	
86		7.8	10.8				9.3 (2)	
35		6.1	2.3	0.5	2.8	1.3	2.6 ± 1.0 (5)	REAL
61		7.2	11.2	10.9	11.9		10.3 ± 1.1 (4)	REDDS
145		3.1	7.3	2.9	1.4	3.9	3.7 ± 1.0 (5)	
39		7.0	7.4	9.9	2.2	1.9	5.7 ± 1.6 (5)	
38		0.0	10.8	1.8	6.8	2.8	4.4 ± 1.9 (5)	
80		6.7						
12				3.0	1.4		2.2 (2)	
58				3.2	1.8		2.5 (2)	
48					1.7		1.7 (1)	
105	T		8.4	1.5	1.4	4.2	3.9 ± 1.6 (4)	
109			9.1	7.5	5.5		7.4 (3)	FALSE
111						8.9	8.9 (1)	REDDS
104						4.9	4.9 (1)	
126						7.2	7.2 (1)	

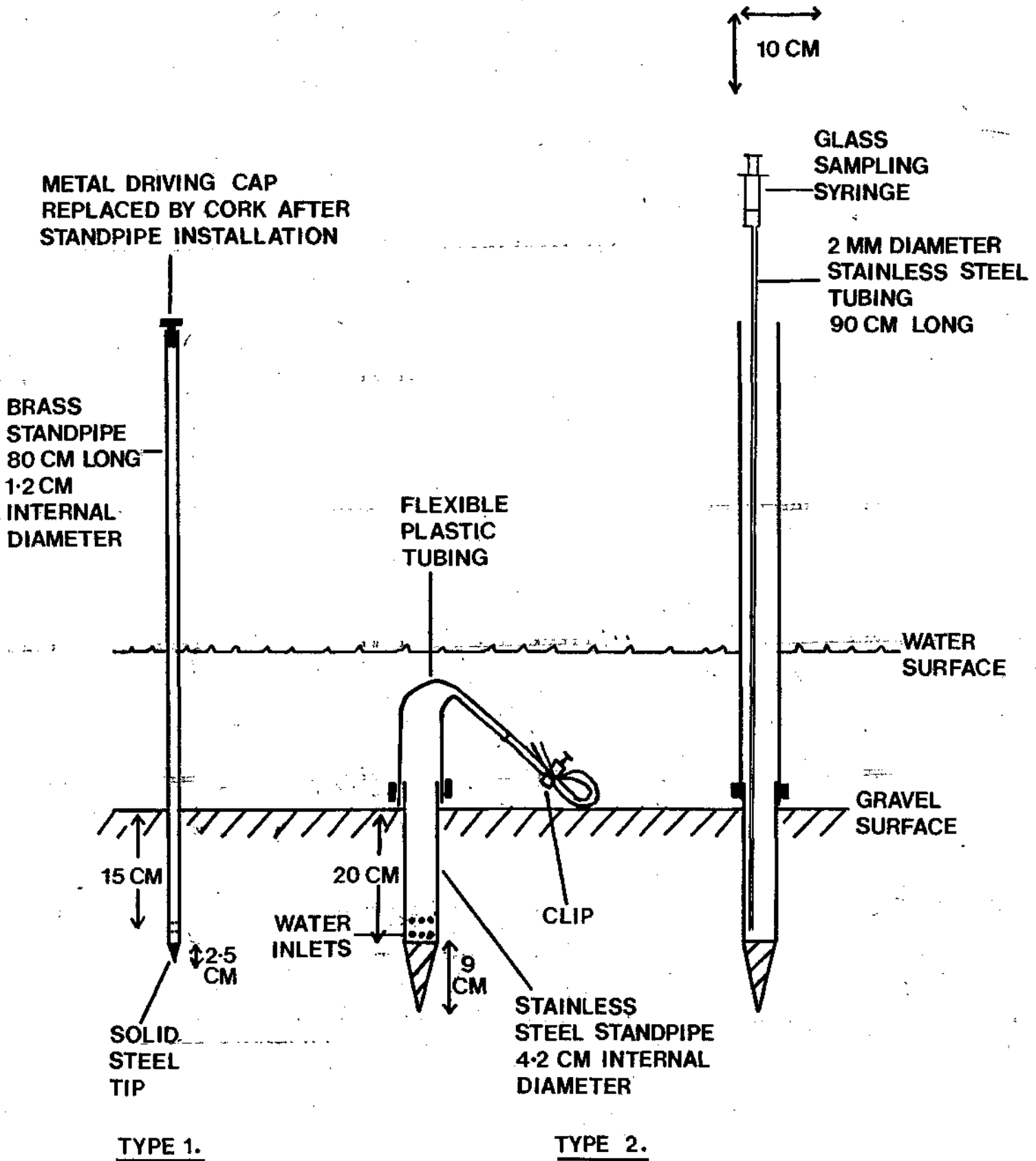
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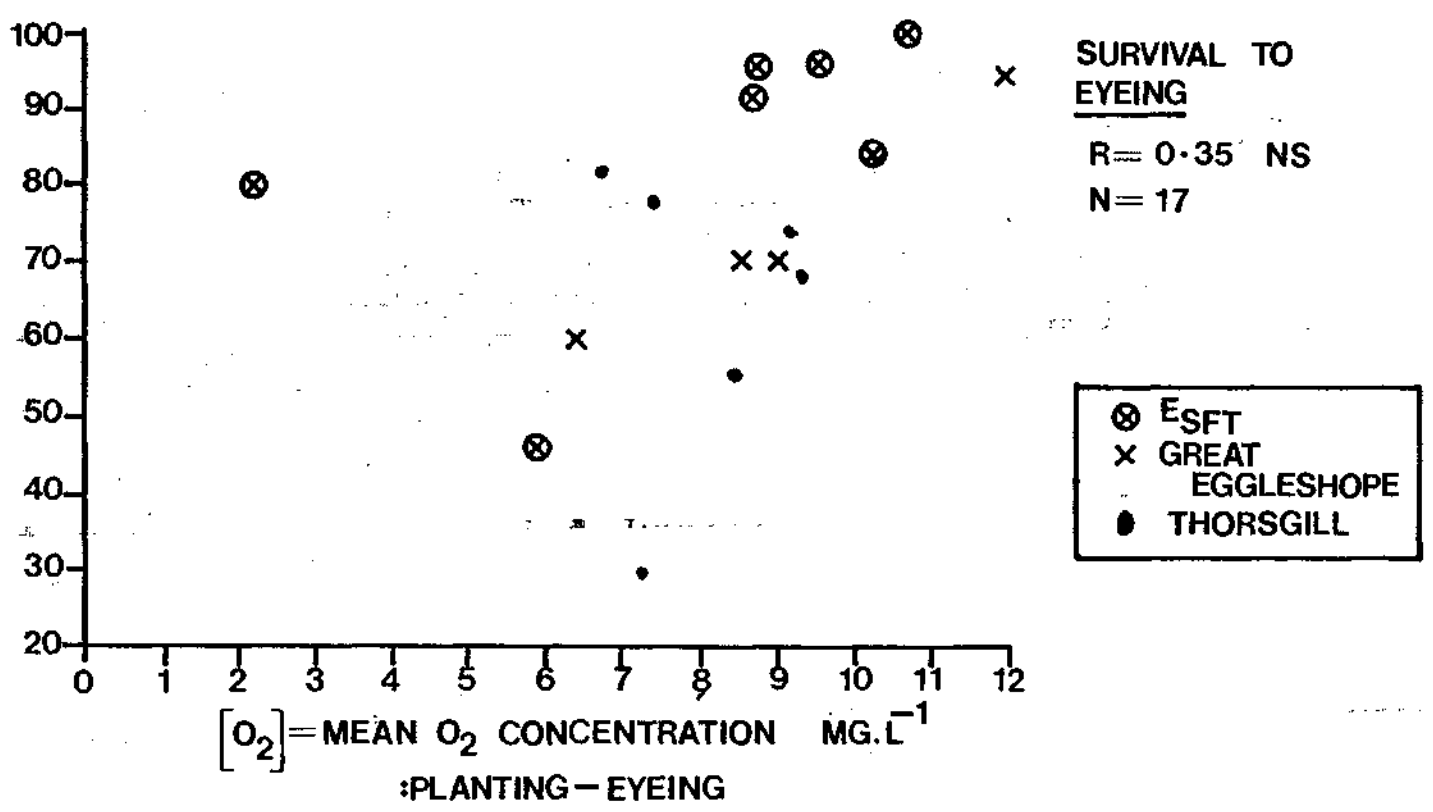
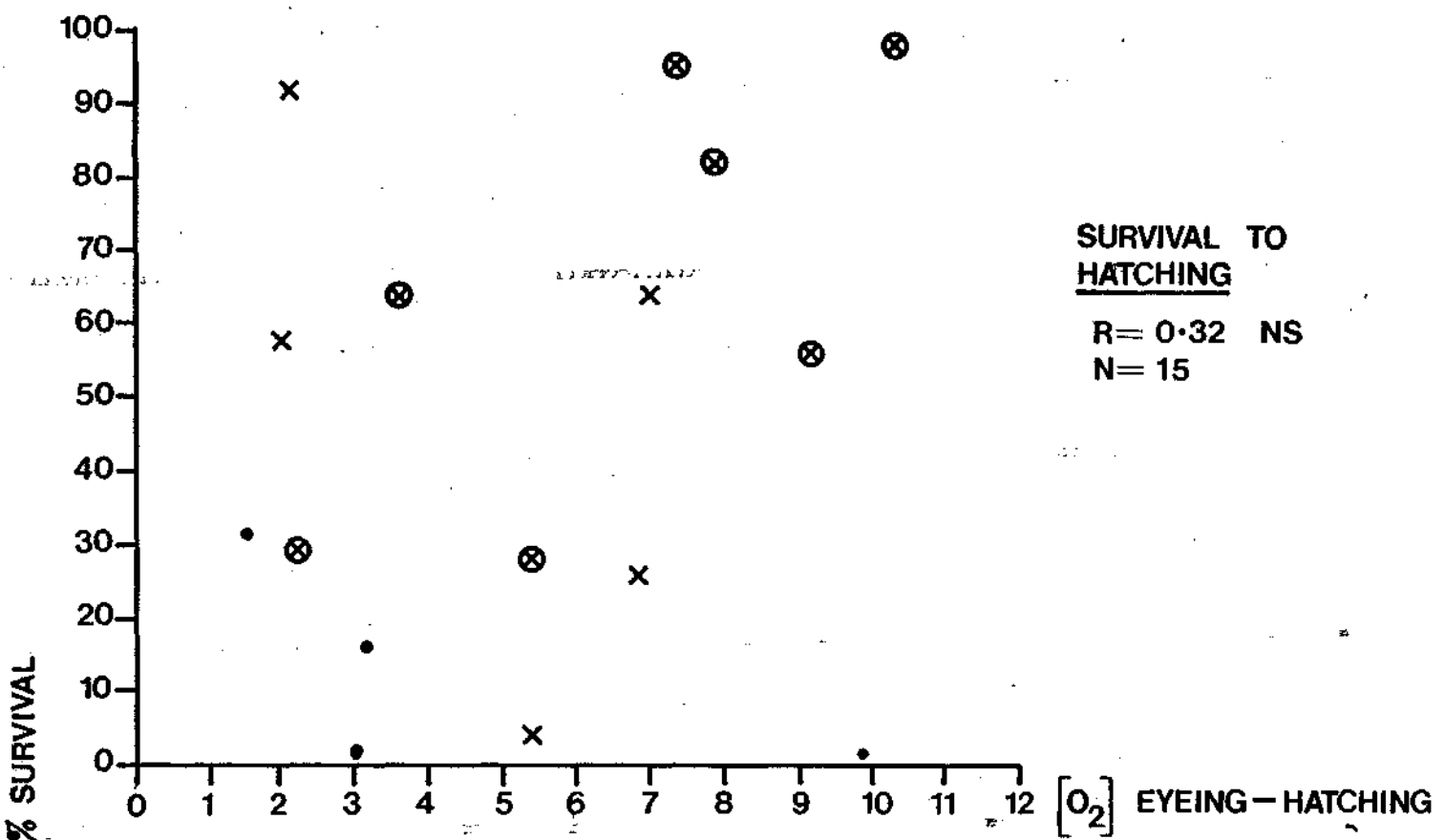
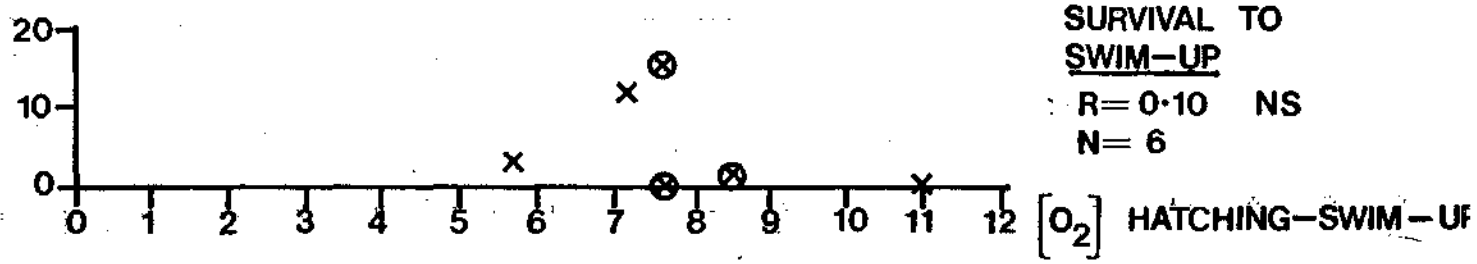
hatched

Fig 1









⊗ ESFT
 × GREAT
 ● THORSGILL

