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The Past and Present
Distribution of Marron,
Cherax tenuimanus (Smith),
in
Western Australia

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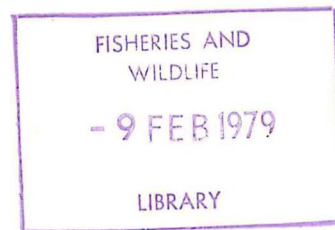
N. M. MORRISSY

1978



WESTERN AUSTRALIAN
MARINE RESEARCH LABORATORIES
DEPARTMENT OF FISHERIES AND WILDLIFE
PERTH, WESTERN AUSTRALIA

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DEPARTMENT OF FISHERIES AND WILDLIFE, PERTH,
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THE PAST AND PRESENT DISTRIBUTION OF MARRON, *Cherax tenuimanus* (Smith), IN WESTERN AUSTRALIA N. M. Morrissy, Western Australian Marine Research Laboratories P.O. Box 20, North Beach, Western Australia, 6020.

ABSTRACT

The past and present distributions of a native south-western Australian freshwater crayfish, marron, are described. Transplantings by man have extended the riverine distribution of marron north along the west coast and east along the south coast from the pristine locations in the extreme south-west rivers. Marron have also been established in farm dams over a greater range, to the north and east and to the inland, than in rivers. The development of agriculture on the upper catchments of the four major rivers, with their reversed sequence of valley form, has led to a retreat of marron stocks down these rivers because of oxygen depletion produced by summer eutrophication. Besides control of overfishing, maintenance of the important amateur fishery for marron also depends upon conservation of the remaining still favourable coastal riverine habitats which are threatened by increasing development.

I INTRODUCTION

The social importance of the large amateur marron fishery, and the extent of its public fishing waters, in south-western Australia has been described by Morrissy (1978) using research logbook data. About half of the annual amateur catch of marron is currently provided by a few large public water supply dams in the Darling Ranges between Perth and Bunbury, there being no natural lakes in the coastal hills of the south-west; a few shallow coastal dune "lakes" or lagoons on the south coast provide minor sport while the large saline lakes in the arid interior are too inhospitable for marron with one or two minor exceptions nearer to the coast. Traditionally marron fishing, or marronning, is associated with the rivers of the south-west; numerous clues have suggested that the distribution of marron has changed both within and between rivers over the short history of European settlement.

The past and present extent of the distribution of marron in the south-west, and the changes, both positive and negative brought about by man, are described. Although the reported decline of marron stocks due to "overfishing" has long been an issue of public and, hence, Departmental concern, the importance of the hitherto neglected subject of the occurrence of unfavourable changes in the quality of the environment of marron in the native rivers is revealed.

II THE ORIGINAL DISTRIBUTION OF MARRON?

The early literature has not recorded any information of use for delimiting the original distribution of marron. Saville-Kent (1897) failed to record marron in a book devoted to the oddities and extremes of the Australian fauna. Helms (1900) commented that: "The extreme south-western very humid portions, which scientifically are scarcely known, are likely to harbour some unknown species, as there the natural conditions are favourable for these animals." Fraser (1903) in notes on the Natural History of Western Australia did not mention marron. Both early explorers, for example Grey (1841) and Bunbury (1930), and documenters of the food of aboriginals, for example Meagher (1974), failed to mention marron although other freshwater crayfish associated with coastal swamps (koonacs or gilgies) are recorded. However, Evans (undated) in a popular account of pioneering in the Pemberton district mentioned that the Warren tribe supplemented their diet with marron. The name "marron" is of aboriginal derivation (Morrissy 1978). The scientific naming of the species by Smith in 1912 occurred much later than that of the other more widespread types of native crayfish, the koonac and gilgie (Haswell 1882). These clues suggest that the native distribution of marron was

more isolated, and restricted, than at present from centres of settlement such as Perth and Albany. However, it is also puzzling to note that marron are not recorded in accounts of early settlement, for example on the Upper Blackwood River and tributaries (Schorer, 1968, Bignell 1971), where, unless the original distribution was extremely restricted to only one to two of the other most isolated, south coast rivers, they must be assumed to have been native inhabitants.

Smith (1912) gave the type locality of *Cherax tenuimanus* as the Margaret River (at the centre of the present coastal distribution). McCulloch (1914) obtained most specimens from the Harvey River (thought to be the most northerly and closest native river to Perth), with a few specimens also from the Margaret River, Balingup Brook (a tributary of the Blackwood River) and the Warren River; he was also informed of its occurrence from Kojonup (a wheatbelt town near the upper reaches of a major tributary of the Blackwood River). Shipway (1951) noted that the W.A. Museum had specimens or records of marron from the Harvey and Collie Rivers, south of Perth, to the Hay, King and Kalgan Rivers near Albany and from Corrolup Brook (upper Blackwood River), Correcalup River and Gordon River (upper Frankland River); introductions (on dates unknown) to the Murray, Serpentine, Canning and Swan Rivers near Perth were mentioned.

Riek (1967) considered that marron inhabited "... the deeper water of all the freshwater streams from the Perth area to the Kalgan River near Albany." His distribution map showed an inland boundary uniformly following the coastline about 50, or so, km inland.

Riek discounted Shipway's (1951) suggestion that the present distribution of *Cherax* species had been influenced by introductions carried out by man although, as an indication of this general human practice, Shipway had recorded the growing practice of establishing marron in inland ("wheatbelt") farm dams. Riek conceded the possibility of a former more limited riverine range for marron, with introduction to some coastal streams, such as the Kalgan River (near Albany) which seemed somewhat isolated from the main centre of present distribution. However, he seemed to think that even this possibility was unlikely since the present distribution embraced most of the species' seemingly preferred type of habitat in the permanent freshwater streams of the south-west, though he noted, wrongly, that marron were absent from the Moore River just north of Perth.

Evidence, presented in the following section (II A, B), has accumulated to show that the riverine distribution of marron was very much more restricted formerly; European man has extended the distribution by introductions, i.e. transplantings, to more northerly and

easterly streams. On the other hand there is also evidence that marron formerly flourished much farther inland in the longer native rivers and that there is a continuing decline in stocks in the middle reaches of these rivers mainly because of organic pollution from agricultural catchments (Sections III A-E).

A. Transplantings

Departmental Fisheries Inspector, D. Gordon, after reporting his identification of a "good sized" male marron captured in the Chapman River just north of Geraldton in 1969, discovered that employees of the Geraldton Tourist Bureau, D. Reiger and C. Burns, had stocked 100 small marron, purchased from the Pemberton Hatchery, in the Chapman River in May 1964; no recoveries had been made up to that date from a similar stocking of the Greenough River farther south (Departmental File 50/44, December 12 and 19, 1969).

According to Mr. C. J. Wedge, an honorary Fauna Warden of Gingin, marron were introduced into the Moore River on the Edwards property by Mr. Ted Burne, a proprietor of the Midland Hotel, about 30 years ago (1947): Mr. Wedge said that there were no marron present before the introduction but many large ones have been taken since (H. B. Shugg, Departmental Fauna Officer, March 7, 1967, pers. comm.).

The annual report of the Fisheries Department for the year 1933 noted that: "Marron (freshwater crayfish) transferred from their natural habitat to a stream near Yanchep (possibly Loch McNess) during the previous year have, it is stated, been seen". This transfer was carried out in 1932 by the Fisheries Department at the request of the State Gardens Board.

A Mr. A. Smith related (December 2, 1969, pers. comm.) "... how the marron got into the Serpentine River ...".

He and his wife caught thirty marron, "... all with spawn...", about 28 or 29 years ago (1940) in Wellington Dam and transported them by utility (car) in an old tub with wet bags, releasing them in the river about 100 yards on the right hand side of the (south-west highway) bridge behind "Turner's old house".

Departmental Technical Officer, J. S. Simpson, while investigating the marron stocks in the North Dandalup River received the information that "... the first stocking was made in 1954 and the public have apparently only recently learned that there are marron in these waters." (Departmental file 50/44, November 20, 1959).

Mr. C. W. Brown, Hon. Sec. Murray-Dwellingup Trout Acclimatization Society later also recorded that "... marron were not native to our waters"; but were planted in the Murray and North and South Dandalup Rivers (Departmental File 194/46, October 31, 1961).

The minute book records of the early Acclimatization Committee of Western Australia contain only one reference to marron for the period 1896-1932; in 1913 the meeting "resolved to procure some marron to be placed in the Murray and Canning Rivers" (Acclimatization Committee 1913).

Technical Officer, J. S. Simpson, reported that, in general, "... marron are not indigenous to the waters of the Canning, Serpentine and Murray Rivers, having been introduced some fifteen years ago (about 1940)." (Departmental File 11/29, June 24, 1954).

A President of the Murray Trout Society, Dwellingup, Mr. H. Birmingham, related that "... The Murray River does not naturally carry marron. In the spring

of 1938 some of the local fishermen caught two or three dozen marron in the Collie which ... they released in the Murray ...". (*West Australian*, October 12, 1954). "In the Murray, Serpentine, North and South Dandalup and the Canning Rivers, where marron have been planted, the population is steadily increasing, despite the fact that these waters have been stocked with trout for a number of years." (Departmental File, 11/29, 1960).

Fishing Inspector, L. J. Smith of Mandurah, related that "... Marron were first brought to Denmark 25 years ago (1914) and put in what they call Staker's Pool some 8 miles up the river from Denmark township." "The top end of the Denmark, Bow, and Kent Rivers are full of marron ...". (Departmental File 50/44, February 23, 1939).

Morrissy (1970a) in relating the history of Murray Cod introduced to Lake Grassmere, west of Albany, from information in a Departmental File and other sources, recorded that marron were not indigenous to the Albany area and had been introduced to Marbellup Creek, supplying the lake, in the late 1940's or early 1950's.

Mr. E. A. Maxton of Kalgan River, near Albany, informed the Chief Inspector of Fisheries in 1939 that "... we put about 20 marron in this river about 8 years ago, before that I don't think there were any in the river. Last year was the first time we caught any. Not too many know that they are about at present." (Departmental File 50/44, August 11, 1939).

Inspector Goodlad of Albany reporting in 1939, stated, "There are places just outside Albany where marron have been put in by private persons ... Angove Creek for instance." (Departmental File 50/44, February 24, 1939).

The author was told in 1967 that marron had been introduced to Moates Lagoon, east of Albany, 35 years ago (about 1940) (Departmental File 133/60. Fisheries Research. *Marron*. Research and Investigations). Inspector Ostle of Albany reported in 1970 that marron had been established in Shark Lake, Doombup and Stockyard Creeks, and White Lake near Esperance after numerous unofficial introductions he carried out in the late 1960's (Departmental File 11/29, August 6, 1970).

Marron have also been introduced to the King Creek and to the Waychinicup River, east of Albany, with success; both are very short coastal streams. From these documented accounts and also from summer observations by the author of habitat conditions in all south-west streams, it is possible to deduce that the eastern coastal limit to the native riverine distribution of marron was the Kent River, while the Harvey River was the most northerly native river (Fig. 1).

B. Deteriorating inland riverine conditions.

Turning to the extent of the inland native distribution of marron, it is apparent from the above conclusions that the native river of greatest interest, i.e. extending farthest inland, is the major Blackwood-Arthur River system which virtually bisects the south-west, extending through the centre of the marron distribution, past or present.

Associated with the agricultural development of the upper reaches of the river over the past 50 years or so there has been a gradual decline in fishable stocks and, farthest upstream, disappearance of stocks. A great deal of first hand anecdotal information has and still can be, obtained to confirm this change. Moreover,

within the past few years research surveys have shown perhaps the last stages of the retreat downstream of marron stocks, from the upstream part of the system where there is extensive agricultural development (see Section III D).

Very near the headwaters of the Beaufort River, a major tributary of the Blackwood-Arthur River system, there is a long beautiful water-hole-type pool called Marron Pool (on the Carlecatup River just east of Kojonup); a similar pool nearby, is called Cobbler Pool (native freshwater cobbler, *Tandanus bostocki*).

Farther downstream Cherry Tree Pool provided marron fishing until quite recently for a boys' camp.

On the Arthur River at Formation Pool, a long deep pool just above the Beaufort River Branch near Duranillin, Mr. Murray Anderson related to the author (28 November 1973) that he used to catch lots of marron in the old days, for example "1½ dozen up to 1½ lbs" but they then got scarcer until it was no longer worth fishing. In the last few years he did not think any were left until there was a flood in March 1973, when a few big ones came out of the water after "muck" from the pastures was washed in by the runoff.

Officer B. Wright of the Agriculture Protection Board reported in 1961, "I have noticed a large number of marron in the Arthur River, near Moodiarrup. Some good catches of perch were reported during the hot weather, and plenty of cobbler can be caught while the river is running." (Departmental File 50/44, March 27, 1961).

Mrs. Hurley, living adjacent to the large extremely long pool on the Arthur River near Moodiarrup, stated in 1973 that they used to catch lots of marron 18 years ago or more, while the local Fauna Warden, P. Shinzig, thought that the marron fishing had been "going downhill for years."

Of course, claims of a decline in fishing have been associated with the marron fishery for many years in all parts of the fishery. However, the fishing history associated with the upper Blackwood system differs in three aspects from elsewhere. Firstly, fewer and fewer large marron were caught, but not more and more undersized as in the lower reaches of the rivers, indicating a breeding failure; secondly, the popularity of the river for fishing declined; and, thirdly, there have not been recorded any complaints that the decline was due to overfishing. Instead the decline has been associated usually with the obviously increasing salinity of inland rivers following clearing and agricultural development.

While the increasing agricultural use of inland catchments has led to a decline in worthwhile stocks of marron for fishing in the more inland, native, riverine habitats, it has provided a new and more extensive, man-made, habitat suitable for marron, the small private stock dam on farms (Morrissy 1970c, 1974a).

The inland farm dams have been stocked with marron over an extensive area of the greater south-west by farmers transplanting marron captured from wild situations nearer the coast, by interchange between dams, and the Pemberton Fish Hatchery has provided a useful and growing service of selling marron for farm dams since the mid 1960's (Appendix—Sales of marron from the Pemberton Fish hatchery). The only element missing in fishing for marron in farm dams is that of the "bush entertainment" provided in the aesthetically more pleasing picnic atmosphere of riverine surroundings.

III FACTORS INFLUENCING THE INLAND DISTRIBUTION OF MARRON

A. Salinity resistance of marron

Experiments were carried out during the spring of 1976 to estimate the salinity resistance of marron in laboratory tanks at the Pemberton Fish Hatchery. Previous attempts at estimating the salinity resistance of marron indicated that marron should be tested over a range of from full seawater to half seawater and that times to death at the lower salinities were greatly protracted.

As facilities for using an open water supply system, providing constant salinities for long periods, were not available, the closed water supply system necessary created certain problems. Feeding could not be carried out because of inevitable pollution problems, generating possible causes of death other than salinity, and hence, each individual in a tested sample had to be isolated to prevent cannibalism with prolonged starvation.

Six 1+ year-old pond bred (1974–75 year class) marron, mean O.C.L. 2.83 cm, range 2.22–3.57 cm, were held in a partitioned Nylex mesh basket in a laboratory tank, 52.5 x 34.4 cm, for each test at a selected salinity. Strong continuous aeration was provided in each tank. Water temperature varied from 11.0°C to 19.5°C with a mean of 14.8°C during the tests.

Most of the tests were started on 15 September, 1976 using five tanks (Table 1). In all these tests the mesh basket holding the marron was only about half submerged, allowing a marron to climb out of the water as would occur in nature.

Later the test in "full seawater" was repeated, starting on 29 September using a holding basket cut down so as to be fully submerged. Perhaps surprisingly, the mean resistance time, or geometric mean time to death, was longer (53 hours) in this test than where the marron could crawl out of the water (35 hours) (Table 1).

A "freshwater" control tank of six marron showed only one death, over the 85 days (2 040 hours) of the majority of the tests, when a marron escaped into an adjoining compartment and was eaten (30 October). Three marron ecdysed under the control conditions.

The intermediate salinities were made up by mixing seawater (conductivity $K_{20} = 46\ 180\ \text{S cm}^{-1}$, 34.51°/oo) with Lefroy Brook, Pemberton, freshwater ($K_{20} = 333$, 0.213°/oo) to a volume of 20 litres.

Marron were classed as dead when found lying on the side or back. After frequent examination for deaths during the first few days of the tests, subsequently the tanks were usually examined three times during the working day.

After 85 days (or 2 040 hours) all the surviving marron were very active. At "5/8ths seawater" (21.4°/oo or 21 400 mg/l, salinity) the mean resistance time was 40 days, two marron were still alive and one ecdysis had occurred. At "½ seawater" (17.4°/oo or 17 400 mg/l, salinity) one death of a marron recently ecdysed had occurred, after 73 days, and there had been two other ecdyses.

The incipient level of lethal salinities for marron, therefore, appears to be in the vicinity of 17°/oo or 17 000 mg/l of total salts. Salinities of that magnitude, or greater, are only attained in the very headwaters of the inland rivers during summer (except, in the case of large shallow lakes progressively concentrated by evaporation through years of less than above average rainfall, where lethal temperatures are also to be expected; for example, Lake Towerrining adjacent to the middle

TABLE 1—RESULTS OF EXPERIMENTS ON THE SALINITY RESISTANCE OF MARRON (TERMINATED ON DECEMBER 9, 1976)

Experiment	Conductivity K_{20} (salinity)	Deaths						Ecdyses
		1st	2nd	3rd	4th	5th	6th	
Control "freshwater" started 17 September at 1630 hours	333 (0.213°/oo) (one due to cannibalism)	6 October 23 October 19 November
"Full seawater" started 29 September at 0900 hours*	46 180 (34.5°/oo)	30 Sept. 31 hours	30 Sept. 36 hours	30 Sept. 36 hrs	1 Oct. 47 hrs	4 Oct. 96 hrs	5 Oct. 120 hrs	
"Full seawater" started 15 September at 0930 hours	46 180 (34.5°/oo)	16 Sept. 31 hrs	16 Sept. 31 hrs	16 Sept. 31 hrs	16 Sept. 35 hrs	16 Sept. 35 hrs	17 Sept. 47 hrs	
"7/8 seawater" 15 September	41 617 (30.5°/oo)	16 Sept. 29 hrs	17 Sept. 47 hrs	17 Sept. 47 hrs	17 Sept. 50 hrs	18 Sept. 72 hrs	21 Sept. 144 hrs	
"3/4 seawater" 15 September	35 358 (25.5°/oo)	24 Sept. 217 hrs	5 Oct. 480 hrs	14 Oct. 699 hrs	16 Oct. 745 hrs	26 Oct. 992 hrs	31 Oct. 1 144 hrs	
"5/8 seawater" 15 September	30 221 (21.4°/oo)	30 Sept. 360 hrs	26 Oct. 992 hrs	5 Nov. 1 257 hrs	3 Dec. 1 911 hrs			19 October
"1/2 seawater" 15 September	25 085 (17.4°/oo)	26 Nov. 1 743 hrs (after ecdysis)						– November 11 November

* Using a fully submerged holding basket, see text.

reaches of the Blackwood (Arthur) River where a salinity of 13 760 mg/l was recorded during February 1973 after mass mortality). In one of the very few places on the upper Blackwood River (—Beaufort River) where marron have still been encountered, young-of-the-year marron were found in the deep shaded Cherry Tree Pool at a salinity of 7 500 mg/l during February 1973.

Although the salinity tests were only performed on larger juveniles it is possible that the embryos (fertilized ova) and larval young of marron attached to the spawning mother or some other stage in spawning, perhaps during the external fertilization, are less tolerant to salinity. However, the salinities of the major rivers in the upper reaches are at a minimum in the spring-time, when spawning occurs, because of the flushing effect of the winter rains and low evaporation.

B. The unusual pattern of water salinity which has developed over the south-west

Since human settlement and development of the south-west of Western Australia commenced in the early 19th century, there has been a history of increasing salinization of inland water supplies and surface soil (Wood 1924). For example, a military outpost was established on a permanent spring at Kojonup on the overland route between Perth and Albany in 1837; by 1848 the spring had become brackish (Bignell 1971). By 1974 Malcolm and Stoneman (1976) estimated that 1.17% (167 294 hectares) of all land cleared and used for crops of pasture in the State had become unusable saltland. The effect of this local salinization of soils and water sources has been an increasing salinity of the major rivers arising on the inland agricultural areas; for example, the salinity of the Blackwood River has increased approximately 300% at Bridgetown over the

first half of the 20th Century (Peck pers. comm. August 25, 1972). The distribution of salinization over the south-west, increasing in intensity inland, has produced a marked reversed longitudinal salinity profile for the major rivers of the south-west which has been documented by Morrissy (1974c) for the predominant Blackwood River system.

The causes of the phenomenon are:—

- The reversed sequence of valley forms (Bettenay and Mulcahy 1972), with the sluggish headwaters in mature valley forms and, farther inland, old valley forms of ancient river systems, on the Old Plateau of the inland south-west where the flat terrain has allowed extensive agricultural development (the "Wheatbelt"); the lower reaches of the rivers are the young valley forms deeply dissecting the scarp, or edge of the Plateau and largely preserved as State Forest;
- the higher evaporation rates inland during the summer dry season, contributing particularly to the high salinities of large shallow lakes on the headwaters (Climatic Surveys undated, 1962, 1965);
- the saltfall from rain (Hingston 1958) which with decreasing rainfall inland (Climatic Surveys undated, 1962, 1965) has resulted in an increasing accumulation of cyclic salt (sea salt from rain) in the ground water towards the inland; and
- the extensive clearing of deep-rooted salt-tolerant native eucalypts farther inland for agricultural development resulting in the salt-laden permanent water-table rising to the surface and contributing to stream flows (Peck and Hurlle 1973).

Additional data, to those already presented for the Blackwood System (Morrissy 1974c), are shown in Fig. 2 for the smaller Murray River system, sampled during the spring-time when the river was flowing at all points sampled. The salinity (measured as conductivity, K_{20}) of the main stream progressively decreased moving down-stream, due to the influence of tributaries of low salinity in the forested, higher rainfall catchments on the heavily dissected plateau bordering the Darling Scarp. Where the river flowed from south to north, before turning west just south of Dwellingup, it can be clearly seen that the (perennial) tributary streams entering from the western catchments were less saline than those entering from the east where the rainfall is less. There was also a dramatic difference between two southern tributaries, Match Brook in State Forest ($K_{20} = 372$) and the brook (DM81) on cleared farming land ($K_{20} = 2180$) just to the east of the State Forests. A description of the general pattern of salinity of the inland waters of the south-west can be derived from conductivity data obtained during the "summer" dry season from localities sampled between Perth and Albany. The entire data (212 readings) were partitioned into two groups for analyses:—

- (i) readings ($n = 76$) for the four major rivers containing marron (the Murray, Blackwood, Warren and Frankland Rivers), which extend to the agricultural hinterland and show markedly higher salinities upstream; and
- (ii) readings ($n = 136$) for shorter coastal rivers rising largely in State Forest near the coast, tributaries of the long rivers in group (i), dams, springs, swamps and ponds.

Morrissy (1974c) related the salinity readings of the Blackwood River system to distance upstream from the estuary for the purpose of showing the atypical reversed salinity trend; he suggested that the variation in salinity between localities could be related to rainfall, run-off (or catchment area), and the percentage of cleared land.

Trotman (1974) used multiple regression analysis to relate stream salinity to these parameters in the Manjimup area; the highest per cent (55.8%) of the variation in stream salinity which could be accounted for by regression, was found by using the 30% of the catchments sampled which had areas of less than 500 ha, the significant catchment factors being rainfall (R), cleared area (C), $R \times C/A$ (catchment area = A), C/A , and R^2 .

However, an examination of the present data and the relevant literature suggested that the quadratic model used by Trotman (1974) for relating salinity (S) to rainfall (R) i.e., $S = a + bR + cR^2$, should be replaced by the model, $S = a.R^b$. Since river discharge (Q) is related to rainfall, the latter model is analogous to the model usually employed to relate salinity or concentration of salts (C) to discharge (Q), $C = aQ^b$. Hall (1970, 1971) has provided the theoretical derivation of this and other models.

The catchment factors influencing the atypical salinities of south-western rivers are all correlated with rainfall to some extent; viz. surface runoff and ground discharge, the extent of saltfall from rain accumulated in the soil and groundwater, the extent of clearing for agriculture, the gradient of drainage lines, and evaporation.

Annual rainfall, at a site where conductivity was measured, was estimated by visual interpolation between isohyets shown for five inch increments of rainfall in

the current series of Commonwealth Bureau of Meteorology Climatic Surveys for the various Regions covering the sampled area of the south-west.

Regression analyses were performed on the linear transformation of the model equation, with rainfall in millimetres. The back transformed equations were (Fig. 3, a and b);

(i) for major rivers,

$$K_{20} = 0.1170 \times 10^{11} \cdot R^{-2.1325}$$

(ii) for coastal (short) rivers, tributaries, etc.,

$$K_{20} = 0.3497 \times 10^{15} \cdot R^{-3.9019}$$

Although the regression correlations were highly significant ($P \leq 0.001$), the variations in untransformed K_{20} values accounted for by rainfall, were barely satisfactory; (i) 56% and (ii) 39%. A major part of the remaining variability would be due to the catchment factors included by Trotman (1974) in his regression analyses of data from very small catchments. Trotman found that the heterogeneity of large catchments confounded correlation analysis. However, since many of the factors are related to rainfall the local diverse influences are averaged in K_{20} values for major rivers and accounted for by rainfall, allowing a more precise description in the present case by rainfall alone.

Although the calculated equations are not satisfactory for predicting individual values of K_{20} , particularly for a localized water, the pattern of mean K_{20} variation over the south-west is well-described as shown by the 95% confidence limits for the mean (Fig. 3, a and b).

Therefore, it is possible from these relationships to map salinity isopleths for the south-west using the greater documented detail of rainfall distribution, and examine the relationship to the distribution of marron. However, while the south-western rainfall generally increased towards the coasts, on the Perth plain rainfall decreases from foci of high intensity, on the scarp, towards the coast. Also the basic inland causes of saline stream and ground water, reviewed earlier and applied in the analytical model, may not be applied in coastal areas where waters can be influenced by coastal limestone, irrigation, and urban development. While all of the data utilized were chosen so as to avoid these problems, the relationship between salinity and the distribution of marron is best confined to examining inland isohyets corresponding to certain relevant salinities, as shown in Table 2.

The present day upstream limits of the distribution of marron in the four major south-western rivers (Section III E, summary), are far downstream of the incipient lethal salinity level but upstream of the upper limit to "freshwater". The latter occurs after the rivers have passed downstream into State Forests where the rejuvenated drainages of higher rainfall areas maintain perennial tributaries of low salinity; note the correspondence between the rainfall location for coastal rivers, tributaries, etc. at 500 mg/l and for major rivers at 3 000 mg/l in Table 2.

C. Organic pollution

Research work aimed at discovering the cause of the variable success of marron in farm dams, at Boscabel on the upper catchment of the Blackwood River System, first discounted the obvious suggestion of unfavourable salinity levels (Morrissy, 1974a). Later research established that overloading of the dams with organic debris from the paddocks washed in by unseasonal summer floods, caused oxygen deficiencies as the debris rapidly decomposed; if outright mass mortality of the marron

did not occur, a subsequent failure to breed successfully was apparent, a situation which has subsequently been simulated by overfeeding of brood-stock marron in Pemberton ponds at the commencement of the breeding season.

When an investigation of the inland distribution and abundance of marron in the upper Blackwood River System was undertaken after the Boscabel dam study was completed, a similar situation was rapidly recognised as existing in the river pools.

In early 1974, Dr. G. W. Kendrick, Department of Palaeontology, Western Australian Museum, in a reply to the Chairman of the Estuarine and Marine Advisory Committee concerning environmental and faunal changes in the Avon River, also indicated the not so obvious influence of organic pollution (G. W. Kendrick pers. comm. via. B. K. Bowen).

"... I have obtained evidence that the greatest damage to the Avon's mollusc fauna was sustained from about 1930 to 1950, apparently as a consequence of greatly increased water salinity, following the clearing of the drainage basin for agriculture."

"In my estimation, another potent factor that seems to have become intensified in its effects over recent decades, is the pollution of the Avon pools from animal waste. This seems to be a hazard mainly of the late summer and autumn, when the fauna is already under great stress from high salt concentrations. Heavy rain at such times may wash large quantities of manure into the pools, leading to eutrophication and mass mortality of aquatic life."

"Other rivers in the south-west of the State are showing symptoms of the same trouble."

The salinity of the Avon-Swan reaches a level of 2 000 mg/l on the Darling Scarp (E. P. Hodgkin, pers. comm.) but upstream is much more saline than the major marron rivers to the south; although reports have been recorded of isolated occurrences of marron in the Swan at Guildford, only introductions to "fresh" hills tributaries have been successful. Although no salinity tolerance tests have been made on the Avon species of molluscs, Kendrick (1976) considered that salinity, rising above the level of tolerance, was responsible for their catastrophic demise; the relatively restricted osmoregulatory ability of molluscs, at the cellular level, would place this native aquatic fauna at more risk than the inland freshwater crayfish; for example, *Cherax plebejus* (koonac) still thrives in the saline head waters of the Blackwood River system (see later) and also, where introduced, in very "fresh" farm dams in the same area.

The agency which brings about catastrophic organic pollution and hence, eutrophication of the inland rivers and farm dams is the summer thunderstorm.

Although, for example, the summer rainfall over the great southern region of the wheatbelt is only 76 to 127 mm in the form of normal showers, over a period of a few years there is likely to be an extremely heavy downpour, due to the passing of a tropical depression, which produces 50 mm or more of rainfall over a very short period (Climatic Survey undated). Usually these downpours are sporadic, even on a single farm, but more rarely they can be general and cause appreciable input to rivers (Section III E).

A letter on Departmental File (50/44, Vol. 2) graphically illustrates the phenomenon: "Due to the cyclone "Ingrid" in February many dam waters were contaminated due to the washing in of large quantities of sheep

manure and debris from paddocks. In a number of cases marron were found dopey and sick." (P. A. Brett, Department of Agriculture Stock Inspector, April 29, 1970.)

The normal soaking rains of the winter wet season do not usually overload farm dams with organic debris from the paddocks (but can do so with sheep manure); by winter such debris, in pasture or crop paddocks, is at a minimum due to summer grazing, decomposition is slower in the water due to lower temperatures, and when organic inputs are heavier, the higher runoff fills the dams giving a dilution, by overflow, of at least the dissolved organic matter. In contrast, the high intensity of the summer thunderstorm produces, literally, a sheet of runoff carrying the, at that season, more abundant debris into the dams, or rivers, where the higher temperatures cause rapid decomposition, a drastic fall in oxygen levels, and there is no following runoff giving overflow and dilution.

In farm dams, at least, this pollution is not transient and affected dams remain unfavourable for marron unless the thick deposits of highly organic sediment are removed.

It has long been recognized that the clearing of land for agriculture in south-western Australia is followed by the development of saline soils and streams, giving a loss of productive land and a fall in quality of water supply for domestic, stock and other purposes.

Less recognized has been the more insidious potential for greatly increased organic input to inland waters following clearing of land and cultivation of cereal crops or stock pastures, particularly from the large jump in wheat and wool production after 1945 (Bartlett 1973).

Hynes (1972) in a major review of the ecology of running waters considered the neglected subject of the insidious long term effects of agricultural development on the distribution and abundance of freshwater species.

Williams (1954) recorded the much more restricted present day distribution of a freshwater crayfish in mid-western U.S.A., than in former times, due to the siltation of streams following agricultural development.

D. Investigation of the distribution and abundance of marron along the four major river systems

Blackwood River

Five river pools were sampled, using drop nets, on the Arthur River and Beaufort River upper tributaries during the spring of 1973. A long, deep pool on a tributary of the Beaufort River just north-east of Kojonup was of the most interest because of its name, Marron Pool.

No marron were captured during this survey, although there was some sighting or evidence of a few individuals.

The former abundance of marron in these waters was related by local inhabitants (see earlier). One person, M. Anderson, owning a property near Duranillin on the Arthur River, related that the heavy summer input of organic debris in March 1973 appeared to kill the few remaining large marron in Formation Pool which was also sampled.

Measurements of oxygen concentration in Marron Pool showed a steep drop in level from 200 to 250 cm depth, which was correlated with temperature stratification (Fig. 4). Marron Pool, like many other Australian inland river pools is of the water-hole type, i.e. the pool does not dry out and changes little in area and depth when flow ceases. Because of the steep banks, oxygen measurements in the bottom water layer fell rapidly below 70% saturation at 1½–2 metres from shoreline.

TABLE 2—ANNUAL RAINFALL CORRESPONDING TO VARIOUS SALINITY LEVELS DERIVED FROM CONDUCTIVITY—RAINFALL REGRESSION EQUATIONS FOR THE SUMMER DRY SEASON

Salinity mg/l		K ₂₀	Annual Rainfall mm (inches)	
			Major Rivers	Coastal Rivers, tributaries, etc.
500	Upper limit for domestic drinking water	810* (....)	960 (38)
1 000	1 610* (....)	800 (31)
2 000	3 230*	1 180 (46)	670 (26)
3 000	Upper limit for "freshwater" (Bayly and Williams 1973)	4 840*	980 (39)	610 (24)
17 000	Incipient lethal level for marron	25 000†	450 (18)	390 (15)

* Salinity (mg/l) = 0.62 K₂₀; this conversion factor was the mean value determined by Morrissy (1974c) for the Blackwood River System.
 † Test Value.

Thus, the available area of pool bottom favourable for marron consisted of, mainly, steeply sloping bank. Marron do not burrow to any extent and escape predation from birds such as cormorants, by taking refuge during the daylight hours under sunken logs, etc., in deep water; thus there was little habitat favourable for marron. In addition, a smaller inland species of crayfish, *Cherax plebejus* (koonac or perrin), is abundant in the ephemeral streams and river pools of the area. Normally, it survives the summer drying up of the smaller creeks by living in capped burrows reaching down to the water table. In the river pools it burrows into the banks. The koonac has remained an abundant species because its preferred refuge habitat unlike that of the marron, is not affected by the summer oxygen deficiencies in deeper water.

By April 1974, the decline of marron stocks down the Blackwood system had been traced, by questioning local farmers on the river, to Winneup just east of Bridgetown. At Mandalup, a farmer who "used to catch a lot" said that he was catching about 50% of the dozen or so marron seen at night while scoop netting over baits; very few undersized were seen.

At Winneup Ford, just upstream of Winneup Bridge, good catches of 20–30 legal-sized marron per night had been made up until 1970. This farmer, owning five kilometres of river frontage, had caught ten marron on a recent trip in 1974 and the next farmer upstream, only two marron on a recent trip.

Drop net sampling of Clark's Pool at Winneup Ford and the pool below Winneup Bridge, still fairly heavily fished in the 1973/74 season by parties from Bridgetown, suggested that downstream from the bridge and upstream from Bridgetown, environmental conditions for marron became more favourable (Fig. 5). Measurements of oxygen concentration supported this view (Fig. 6). At Clark's Pool, core samples of the bottom sediments taken along a transect across the pool gave values of % organic matter of 12.9%, 13.5%, 10.5% and 7.8% while below the bridge values of 2.7%, 3.0%, 6.0% and 11.1% were obtained.

Further sampling of pools at Bridgetown, near Nannup and at Sue's Bridge (close to the upstream limit of summer tidal water) during October 1974, gave higher catch-rates with representation of juveniles (Fig. 5).

However, the comparison of these catches with comparable data from the lower Warren River indicated that even in the most favourable environment remaining in the lower Blackwood River system, the stocks showed a reduced survival, or production, of juveniles.

While the cause of declines in marron stocks in farm dams to a few large adults (or even no adults), with no evidence of successful breeding, is oxygen deficiency in the bottom water due to too high an input of organic matter, other factors may contribute to the homologous situation in the Blackwood River.

None of the people living on the upper Blackwood River system blamed overfishing for the decline of marron stocks; this opinion would be difficult to support in view of the size of the river pools, which increase in size upstream from Bridgetown and to which there is no public access over many kilometres.

The possible influence of successful introductions of exotic fish, the predatory redfin perch, *Perca fluviatilis*, and the aggressive mosquito fish, *Gambusia affinis*, is discussed in a later section (III E).

Although salinity tests have indicated that larger marron can survive the prevailing salinities in the Blackwood River system, as some still do, perhaps fertilization of the ova or survival of the brief early larval stages could be influenced by salinity. However, a salinity exceeding the level recorded at Sue's Bridge on the Blackwood in October 1974, was recorded in the same month in a pool on the Murray River just south of Dwellingup where the catch rate and length frequency distribution were similar to those of the Warren River (Morrissy 1974b). Mating of marron occurs in September and the embryos, and later the larval young, are carried by the female from October until December or January (Morrissy 1970b, 1976b).

While one consequence of pool bottom sediments overloaded with organic matter is oxygen deficiency in the deeper water, another more obvious eutrophic development, also found in farm dams, is that the release of phosphate from the anaerobic sediments during summer stagnation of the pools encourages strong algal blooms. On April 17, 1974, Inspector Harman of the Department investigated a report of fish deaths at Trigwell Bridge between Boyup Brook and Moodiarup on the Blackwood-Arthur River. In a pool two kilometres in length he found 157 dead Redfin perch and 4 dead large marron. The pool was not flowing and no evidence of spillage of a pollutant was found but an unusual green "substance", "unlike any weed or algae I had seen before", was observed. The latter was identified as *Anabaena circinalis* by Mr. E. Aplin of the Department of Agriculture. This blue-green algae releases toxins when the blooms die off towards the end of summer, a common experience in sewage polluted lakes near Perth, e.g. Lake Monger.

A more insidious effect of strong algal blooms is their removal of oxygen from the upper layers of the water mass overnight, due to respiration, which prevents replenishment of oxygen in the deeper water when the overnight equilibration of surface and deeper water temperatures allows mixing by early morning (Morrissy 1974a, and see below for an example in the Murray River).

Frankland River

The major headwater tributary of the Frankland, the Gordon River, was found to have a history of disappearing marron stocks. Farmers of long residence, K. Marshall and R. W. Denney, related on 21 February, 1977, that Slab Hut Gully Brook, flowing south-west across the Albany Highway north of Kojonup to join the Gordon River, had fishable stocks of marron up to 20 years ago while Tom South Pool on the Gordon River just north-east of the highway (Fig. 7) ceased to contain marron stocks at an earlier date. Only a tortoise and mosquito fish were seen in this pool. Slab Hut Gully Brook still contained very small numbers of marron up until eight years ago, but redfin perch had disappeared three years before over a two year period where previously they had provided excellent fishing, and then the Brook "went more salty" and dead koonacs were found. Marron were still present in the Gordon River in this vicinity just west of the highway up until 1958 although no perch were present. R. W. Denney was adamant that the causes of these declines in fish stocks was not overfishing. There were some indications from these discussions that marron stocks may have been initially affected by high salinity (certainly the salinity at Tom South Pool east of the highway now exceeds the incipient lethal level). Remnants of former stocks seem to persist where pool salinity was influenced strongly by a local, fresher than usual, spring. The very destructive role played by cattle in breaking down pool banks and denuding pool side vegetation, including bank-holding reeds, was frequently noted in travelling down the Gordon River valley.

Farther down, on the Frankland River near Tambullup Pool, present day salinities were below the lethal range, salt patches were not so evident in the gullies, and the large pools were better preserved. R. Wharburton related that both marron and perch "disappeared" at the same time about fifteen years ago, after a heavy March flood when the river was polluted ("smelled"). Cobblers and minnows, and perhaps a very few marron, were still present.

Still farther south with bad salt flats again evident in more undulating country, R. H. Brown near Round Pool observed that "lots of people from Mt. Barker used to come out (marronning) but no longer". Mr. Brown had seen the perch disappear ten years ago—dead ones were found floating—but some few marron were still left. Two years ago summer rainfall had run into his farm dams causing them to go "black and bubbly".

Recent marronning activity was discovered for the first time on this survey where the Frankland River enters State Forest south of the Muir Highway. However, only much farther south near Mt. Frankland where the valley form was markedly "younger", was the river found to be flowing.

On this, February 1977, survey sampling showed de-oxygenated conditions in both the marronning pool just below Muir Highway and a pool near Trollop Hill upstream on the Gordon River (Figs. 8 and 9). Both

pools had steep banks. Bottom sediment transects across the pools gave readings for % organic material of 24.6, 5.1, 1.9, 1.7 and 7.7 for the Frankland River and 15.0, 18.1, 15.9, 16.8, and 15.5 for the Gordon River at these localities. The sizes of marron carapaces found discarded at campfires agreed with those of marron sampled from the Muir Highway Pool. In comparison with a research sample taken just above Circular Pool on the lower Frankland River (Fig. 10), the Muir Highway Pool showed much fewer juveniles and evidence of heavy over-fishing. In addition, only drop nets set close to the bank, or on a spot where there was a rocky bottom in the middle (see % organic values above), caught marron.

Warren River

The major tributary of the Warren River, the Tone River, rises just south of Kojonup where a tributary called Murrin Brook may have been named using a phonetic spelling of the aboriginal word for marron (Morrissy 1978).

A Shire road plant foreman, V. Burchell, of long standing in the district, related that both marron and perch disappeared thirty years ago or more from Billinmorbarrup Pool (Hillier Road), and also from the nearby Towerlup Brook flowing into the Gordon. While marron also ceased to be caught slightly later at the Tone Bridge farther south, some still existed until the 1969–70 drought at Mullidup Crossing still farther downstream (Fig. 7).

During the continuation of the survey in a south-westerly direction downstream on the Tone River, patches of forest country were encountered at Marterup Pool, itself surrounded by natural scrub. Just upstream Mrs. L. B. Conner said that there were no marron present now although she had caught them there as a child about 1920–30. The last time she knew "any amount of marronning was done was the 1940–50's". Some locals had tried two weeks prior to our questioning on 23 February, 1977, but had only captured a tortoise.

M. Muir, of the long established south-western family, at Mordalup, upstream, said that the "last large catches" were made fifteen years ago in his pools; these wide (30 m), long pools were dark and muddy and the banks were bare from cattle grazing.

Farther south at Meribup Bridge, on the Muir Highway, in State forest, water was flowing into a clear deep pool but there was no evidence of recent marronning. Farther downstream the Tone River runs westerly and after being joined by the more saline Perup River, flowing south through a cleared valley, forms the Warren River. The Boonwiup Pool sampled on the lower Perup River had a very strong algal bloom.

Farther west the Warren River also receives the much fresher Wilgarup River and then turns southward into the higher rainfall areas of State jarrah and karri forest; a small flow was apparent and the long deep murky water-hole-type pools of the mature valley had changed to smaller, clear V-shaped pools sometimes with base-rock bars. Near Big Hill Brook, adequate catches of brood stock had been obtained by Pemberton Hatchery staff in the recent past, with juveniles strongly represented in catches.

Therefore, the stretch of the Warren River farther upstream, between the Wilgarup and Tone River confluences, appeared to be where conditions had changed from favourable to unfavourable for marron.

R. A. Cutting, a rock lobster fisherman before establishing a farm at Kin Kin just below the Wilgarup River, 28 years ago, said that when he settled alongside the Warren River there he "could not handle the marron on six baits". By 1971 salinity had increased from about 1 500 mg/l to 5 000 mg/l. In 1970 he caught 200 large perch and "each had marron in their guts". He considered that the enormous Tribulation Pool on his property had definitely not been fished heavily but large marron were becoming fewer and fewer; 1972 was the last year when one could obtain a "decent feed". Perch and some trout were still present and mosquito fish were "wiping the minnows out".

At Chulingup Pool farther upstream in State Forest there was evidence of recent marronning from campfires and marks on trees used to indicate drop net positions and the small catch, although containing juveniles, showed evidence of overfishing in comparison with catches from the lower Warren River (Fig. 10).

De-oxygenated conditions occurred in the bottom water (Fig. 11), a strong algal bloom was present, and a transect of the bottom sediments gave % organic values of 21.4, 31.9, 5.6 (on small stones), 8.9 (stony), and 21.5.

Murray River

The survey of the Murray River system, where marron were introduced (see Section II A), was commenced on 17 March, 1977 by examining the upper tributaries crossing the Albany Highway in a westerly direction. A conspicuous feature of all pools examined was the presence of numerous mosquito fish.

At Bannister on the Highway (Fig. 12) the Bannister River was flowing through small, cattle damaged pools containing aquatic plants (*Chara*, *Potamogeton*), an unusual occurrence in south-western streams, and minnows (*Galaxias occidentalis*). Just downstream from the highway, the water in similar pools was much more saline, and no minnows were present, indicating that the flow at the highway was due to a local, fresher than usual, spring. A similar local influence of a spring was found at Crossman, on the highway farther south, where the major Hotham River was quite fresh compared with localities on the same river farther upstream or downstream. The original location of stopping places on these now unused springs at Bannister and Crossman (and Kojonup) for the inland route between Perth and Albany still has validity. The pool at Crossman contained a small school of redfin perch and the banks were scored with gilgie holes.

At the Hardie property near Dwarderdine Gully upstream from Crossman, marron were introduced ten years ago to several large pools in an area where there were said to be "a lot of fresh springs". However, an inflow during the 1969-70 summer "killed off" the marron, after which there had been no good winter flows to flush the river, and while perch and cobbler remained, there were perhaps only a few marron.

The Crossman River running northward to join the Hotham River below Crossman was very saline with salt-affected gullies much in evidence.

In contrast to the Hotham River, the Williams River farther south presented a very degraded appearance with no flow, strong algal blooms, and banks damaged by cattle and sheep. At Marling Gully between Quindanning and Williams (Fig. 12) the temporary local influence of fresh springs on the salinity of the river was noted.

Just below the junction of the Hotham and Williams River evidence of heavy marronning, in the form of baits, strings and traps, was found in the deep, clear pools on the second to last property before State Forest was encountered. The new owner, J. Davis, said he was prohibiting the entry of marronners, allowed by the previous owner, and P. Wilmot of Quindanning related later that some large catches had been made in these pools during the previous season.

Farther downstream only small stagnant pools, lined by paper barks, were seen in the State Forest until the Murray River swung northward, the pools lengthened and deepened, while flow was received from perennial tributaries from the west.

Following the Hotham River upstream from its junction with the Williams River, large deep pools with steep banks were encountered close to the road. There were many paper bark trees, as occurred downstream on the Murray River, and reed pockets in gullies indicated fresh springs.

Farther upstream to the north, a large flowing brook with deep reed-lined pools entered the Hotham River near Marradong from the prominent easterly catchment of forested Mt. Saddleback. The favourable influence of this brook on the main river for some distance downstream, until after Davis' property on the Murray River, was apparent. For example by contrast to Camballing Crossing upstream where a deep, stagnant, pool showed a strong algal bloom (and cattle damaged banks).

At Boddington and above the confluence with the Bannister River, at Ranford, local people mentioned that marron occurred but there was no evidence of the heavy fishing expected with such close proximity to towns. P. Wilmot of Boddington referred to his fishing for large marron during the daytime and inferred that where stocks of marron still existed they were heavily overfished; large redfin perch were plentiful but many were killed by past summer floods. Reference was made to a property between Boddington and Camballing Crossing, which has been owned by the Farmer family since early settlement of the district, where access to marronners had been recently restricted due to "overfishing". The pool below an historic stony crossing, where a small flow was evident, was sampled. At this point, the Hotham River valley narrowed and the Farmers related that the valley had undergone extensive flooding as a result of the widespread summer downpours in 1956. The long but narrow (15 m) pool with steep banks was said to contain cobbler, perch and marron, but the native minnows had been replaced by the ubiquitous mosquito fish.

The post sunset sampling for marron yielded nearly all legal-sized individuals from drop nets set close to the banks (Fig. 10). R. Farmer had observed smaller sizes of marron in the shallower, smaller pools nearby.

The sampling of bottom sediments across the pool gave readings of 28.4, 23.1, 16.4, 9.8 and 7.8 (stones, and an eroding bank).

The narrow pool was well shaded by paperbark trees so that the sampling of the temperature-oxygen profile at 09 00 hours gave a clear example of the combined effects of overnight equilibration of the water mass followed by mixing of the water column (maximum air temperature the previous day 31°C, overnight minimum air temperature 11°C—18 March, 1977) and surface oxygen

depletion caused by the overnight respiration of the strong algal bloom, adding to oxygen depletion over the sediments (Fig. 13).

Summary

The close relationship between the approximate upstream limit to existing fishable marron stocks and the upstream limits to young valley form, flow in summer, and State Forest are shown in Fig. 14, superimposed on salinity-rainfall profiles, for these four major rivers.

E. Discussion of factors limiting the present inland distribution of marron in rivers

The exploratory surveys, outlined above, were originally innocently conceived for the purposes of, (a), de-limiting the natural inland distribution of marron so as to describe the extent of the amateur fishery, and, (b), for academic interest, to establish the natural environmental components limiting the inland riverine distribution of marron. Instead the surveys have revealed a widespread decline in the inland extent of marron stocks along all four of the major rivers, the causes of which appear to be wholly induced by man and without any foreseeable remedy.

The management problem associated with the still apparently "healthy" marron stocks in the more coastal reaches of these rivers, has historically, always been seen as one of preventing "over-fishing". The above revelation presents an, at least, equally serious potential management problem on these stocks if future environmental disruption occurs farther downstream, or if the effects of the present inland disruption intensify and extend farther downstream. There are indications from the characteristics of the marron stocks that this problem is already occurring in the Blackwood River, as discussed earlier.

Factors associated with the decline of the inland marron stocks

Salinity

There is no positive evidence that high salinities *per se* were responsible alone for the documented decline in inland stocks of marron. Lethal salinities are now present in headwater pools during summer where marron once existed, for example on the Gordon River. Since the decline of stocks extends much farther downstream than the apparent limit of lethal salinity, the continuing survival of small numbers of marron inland would indicate another cause of mortality less pervasive than salinity. However, future research should establish the, possibly lower, salinity tolerances associated with spawning in the early spring, although inland river salinity is lowest at that season. In addition, the temporary passage of "slugs" of highly saline water from the far inland, particularly with the first general winter runoffs and summer runoffs should be examined. The summer flood event may impose the highest salinity stress on the lower reaches of the long rivers, since the diluting effect of the fresh coastal tributaries would then be a minimum.

A summer phenomenon of the most saline rivers, first observed on the Avon River (Dr. E. P. Hodgkin, pers. comm.) and more recently on the Murray River during the severe drought of early 1977, is the formation of a halocline in the pools (Fig. 15). In the most popular marronning stretch of the Murray River south of Dwellingup (Fig. 2) summer flow becomes totally dependent upon small very fresh tributaries from the west. A layer of very fresh, very clear water had

developed over an extensive bottom layer of saline de-oxygenated water in the pool sampled. The seasonal development of the halocline and its effect on the distribution of marron requires investigation. A similar phenomenon has developed in Wellington Dam (J. Imberger, pers. comm.; CSIRO 1975).

Eutrophication

The present surveys along the inland stretches of the major south-western rivers have revealed the classical symptoms (Wood 1975) of an insidious and widespread long term eutrophication of these surface waters:—A deteriorating native fishery for marron (and that for the exotic redfin perch could also be included), the proliferation of an extremely hardy exotic pest fish (*Gambusia affinis*), summer algal blooms including a toxic species, and conditions of gross oxygen depletion associated with the highly organic bottom sediments and the overnight respiration of algal blooms. This inland phenomenon is so general that apparently nowhere can the original natural state of these waters be appraised to provide a base level for measuring the extent of the deterioration directly. However, the full range of conditions has been described, and the eutrophic change observed, for inland man-made waters, i.e. farm dams (Morrissey 1974a, unpublished farm dam data). Also the retrospective documentation of the increasing salinity of the major rivers, e.g. the Blackwood River at Bridgetown, caused, too, by the increasing extent of agricultural development, may be a measure of the development of eutrophic conditions. A highly significant positive linear correlation existed between a rough spectrophotometric measure of dissolved organic matter (Mackereth 1963) and conductivity for samples taken from the Blackwood and Murray Rivers during the spring of 1974 when the rivers were still flowing strongly in the inland (Fig. 16).

The destruction of the delicate hydrologic balance of inland catchments by clearing of the native bush has been accompanied by a buildup in soil fertility, from the very low pristine levels to the high levels necessary for sustained farming, by importation of phosphate (fertilizer) and the use of legume nitrogen (clover) Mulcahy 1973).

Besides the resulting greatly enhanced input to rivers of nutrients and organic matter, from agricultural fertilizers, stock wastes and pasture and crop debris, other factors contribute to the development of a state of summer eutrophication each year.

The major factor in this region is the summer dry season, of the Mediterranean type climate, when the discharge of streams decreases dramatically, usually to negligible or zero flow farther inland.

The lack of flow through the long deep trench-type pools, typical of the inland U-shaped mature valley form, and temperature stratification, allows the development of low oxygen levels in the bottom water (≥ 2 m depth) over the highly organic sediments during summer, as described for farm dams (Morrissey 1974a). By contrast farther downstream in the higher rainfall areas of most rejuvenated drainage, stagnation is prevented by the summer flows through the smaller pools, of more heterogeneous profile and depth, in the V-shaped young valleys. Moreover, the more protracted annual flows of higher discharges through this type of pool inhibit the accumulation of fine highly organic sediments. An excellent example of these two contrasting types of pool was sampled for two years on the lower Warren River (Morrissey 1970b, 1974b). The flow through a corner

pool, of about 0.1 ha area, passes through the deep eroding corner of the pool where the local marron population shelters (the number of 1+ and older marron was estimated at about 1 500 individuals during the period 1969–70). The rest of the pool shallows out unevenly over sand lightly covered in detritus. Running back from a corner of the pool is a long deep backwater through which a flow passes down into the river pool during only the severest winter flooding when the river farther upstream “breaks” its banks. Subsequent drop net sampling has shown that marron only occurred in the backwater close to the banks and not in the deeper water in contrast to their occurrence in the river pool; the deep backwater provided conditions favouring the deposit of fine organic matter and hence oxygen depletion over the sediments similar to inland pools (Fig. 17).

The grossest and most obvious eutrophic pollution of the inland pools, which produces dramatic mass mortalities of marron and fish, is due to the contributing factors of cyclonic summer downpours and the summer condition of the agricultural catchments. The heaviest daily rainfalls recorded annually occur during summer in the lower rainfall inland areas (Fig. 18a). At this season the lack of growing plant cover on the sunbaked ground contributes to an extremely heavy runoff of warm water carrying the crop debris of the previous season or stock-fragmented pasture debris, and, of course, stock wastes, into watercourses (and farm dams). The runoff is of short duration so that there is a rapid decrease in river flow and return to stagnant conditions. The incidence of such summer downpours in the past 25 years can often be related to observed mass mortalities of marron (Fig. 18b).

Exotic Fish

Gambusia affinis (top-minnow, killi-fish or mosquito fish—gambusino (Cuban) = worthless).

These small fish have become the most widely distributed and possibly the most abundant freshwater fish in the south-west of the State (Anon 1966, Griffiths 1972).

Their ability to tolerate extremes of salinity, temperature, turbidity and stagnancy, their seeming disfavour as a food for large predatory fish such as trout and perch, their aggressiveness which leads to the elimination of native minnows and the young or even older members of larger fish species, and their ineffectiveness in controlling mosquitoes because of avoidance of aquatic cover, harbouring larvae, makes the fish a most unfortunate introduction (Myers 1963, Anon 1966, Dees undated, Griffiths 1972). In addition, Hurlbert *et al* (1972) discovered experimentally that the fish promotes extraordinary development of phytoplankton (algal) populations by intensive predation on populations of zooplankton.

Because of the behaviour of young-of-the-year marron in dwelling in dense bottom cover and the protection afforded crayfish by the exoskeleton or shell, predation by *Gambusia* on marron is unlikely to be significant. A test conducted at the Pemberton Fish Hatchery with the two species at high densities (115/m²) showed no significant mortality in either species, over a period of three weeks, both in the presence and absence of refuge cover for the young-of-the-year marron.

Perca fluviatilis (Redfin perch)

A number of large exotic freshwater food and sport fish, both overseas and eastern Australian, were introduced to Western Australia by a State Acclimatization Committee (1896–1932) at the turn of the century. By 1918, redfin perch were recognized as a widespread, successful introduction (Kingsmill 1918).

Weatherley (1963a) has estimated that the incipient lethal temperature of redfin perch is 29–32°C, i.e. very similar to marron (Morrissy 1976a) and about 5–6°C higher than the introduced trout (Morrissy 1973). Weatherley (1963b), reviewing the zoogeography of redfin perch, noted that the fish prefers slow, mature and often turbid streams of a silted eutrophic nature, provided there is no marked oxygen depletion, and is unable to persist in the rapid mountainous streams or oligotrophic lakes, preferred by trout. The observed distribution of perch in south-western Australia corresponds closely to

TABLE 3—OCCURRENCE OF VARIOUS FOOD ITEMS IN THE STOMACHS OF REDFIN PERCH NETTED FROM WELLINGTON DAM

	JANUARY (9.i.75, 16.i.75, 22.i.76)		APRIL-MAY (23.iv.75, 6.v.75, 7.v.75)		AUGUST-SEPTEMBER (13.xiii.75, 23.ix.75, 23.xiii.76, 24.xiii.76)	
	% of fish containing (1)	% of total number of food items (2)	(1)	(2)	(1)	(2)
Empty	37.6	39.5	11.8
Marron	7.1	8.2	21.0	17.3	17.6	3.9
Gilgies	12.9	16.4	6.2	5.1	0.0	0.0
Perch	27.1	34.2	2.5	2.0	0.0	0.0
Frogs	0.0	0.0	1.2	1.0	0.0	0.0
Shrimp	0.0	0.0	16.0	16.3	17.6	32.5
Odonata nymphs	9.4	32.9	25.9	30.6	47.1	23.4
Trichopteran larvae	1.2	1.4	7.4	20.4	2.9	9.1
Chironomid larvae	7.1	6.8	2.5	2.0	0.0	0.0
Dytiscid beetles	0.0	0.0	3.7	3.1	23.5	5.2
Corixids	0.0	0.0	1.2	1.0	0.0	0.0
Daphnids	0.0	0.0	0.0	0.0	11.8	(numerous)
Ostracods	0.0	0.0	0.0	0.0	5.9	(numerous)
Terrestrials	0.0	0.0	1.2	1.0	17.6	26.0
No. of fish samples	85	81	17
No. of food items	73	98	97

Weatherley's description of preferred habitat. Unlike trout in the south-west (Morrissy 1972, 1973) perch naturally sustain high densities, particularly farther inland in the major rivers, and here, as elsewhere in the world, often their high reproductive success leads to the formation of dense, stunted populations.

The occurrence of marron, and other food items, in the diet of redfin perch has been studied in Wellington Dam where, except for some farm dams, the lowest natural densities of marron have been encountered (Morrissy 1974b). The very low density of marron was attributed to heavy predation by the abundant perch in this dam, which lacks the refuge cover of natural debris for young-of-the-year marron found in rivers.

Samples of perch were obtained from Wellington Dam by fishing a 50 m length monofilament gill net (mesh size 6.25 cm) during the afternoon up to sunset. Perch display dawn and dusk peaks of activity similar to marron (Craig 1977). The range of sizes of perch captured was 15–35 cm fork length with a mean size of 21.5 cm.

The stomach contents of the perch showed a strong seasonal pattern (Table 3). The size of gilgies and marron ingested was approximately 2 cm—O.C.L. In January the marron present were the smallest of the 1+ year-old age group, while by April-May they were the largest of the fast-growing 0+ year-old age group.

Therefore, while no quantitative estimates of the extent of predation by perch on marron in Wellington Dam has been made, the evidence that marron were an important component of the fishes' diet, seasonally, supports the hypothesis that the low density of marron is due to heavy perch predation on the young marron where refuge cover for the latter is sparse.

Although with the much more abundant cover evident in inland rivers perch are unlikely to exert such a heavy predatory influence on recruitment, they, and the mosquito fish, may have contributed to the decline of marron stocks.

Other predators

Other known predators on marron are tortoises, cormorants, water rats, herons, egrets, and kookaburras; except for the last named, these are all animals which are endemic to Western Australia.

IV FACTORS LIMITING THE ORIGINAL DISTRIBUTION OF MARRON IN RIVERS

Evidence presented in the previous sections revealed that prior to the interference of European man, the riverine distribution of marron was more limited coastally, northward along the west coast and eastward along the south coast, and less limited inland than at present. The marron was apparently confined to the south-west landmass between longitudes 115° and 117°30'E and latitudes 33° and 35°S (Fig. 1). All these waters lie to the west of the Meckering line in the region of rejuvenated riverine development (Mulcahy and Bettenay 1971). An hypothesis for this containment, in view of the more coastally widespread riverine success, albeit short term, of marron at present, should involve the dispersive powers of marron and limiting long term climatic factors.

Dispersal

The dispersive powers of freshwater crayfish are extremely poor. Crayfish eggs remain attached to the female until hatching and cannot be transported by adventitious means; unlike marine crustacea, the young

do not hatch into larvae which have the opportunity and morphological adaptations for dispersal. When they do hatch as larvae, these metamorphose into crawling juveniles while still attached to the mother. These juveniles could not be transported by water birds or, by their own slow forward walk, move large distances because they are very subject to desiccation, having no waxes in their integument.

The most probable means of dispersal are by river capture or by adults walking short distances between water bodies in an area of ill-defined drainage between two catchments, particularly in a season of extreme flooding. In comparison to the gilgie and koonac types of other south-western freshwater crayfish, the marron is, by virtue of its adaptation to the environment of the larger permanent stretches of rivers (Morrissy 1972), least likely to have opportunities for such dispersal. The gilgie and, particularly, the koonac types are adapted to the seasonal impermanency of the swamps, tributaries and headwater streams associated with the boundaries of the river catchments, where opportunities for dispersal to an adjacent system are likely to be highest.

Since there is no collaborative evidence that marron were introduced to the Harvey River by European man, the common estuarine system shared by the Harvey, Murray and Serpentine Rivers, and the fairly high salinity tolerance of marron indicate a poor dispersive ability.

An examination of the distribution of rivers in the south-west reveals several avenues of possible past dispersal of marron between river systems (Fig. 1). Firstly, the three major, native marron river systems, the Frankland-Gordon, the Warren-Tone, and particularly, the Blackwood-Arthur-Beaufort, all have closely adjacent headwaters in the vicinity of Kojonup, containing large permanent water hole-type pools formerly occupied by marron before agricultural development. Interestingly, as Fig. 1 illustrates, originally there was very little penetration of marron into the plateau north of the Blackwood system which, from the evidence of submarine canyons (von der Borch 1968), has, like the Avon-Swan and the Frankland, been a feature of the south-west for a very long period of geological time. These headwaters are just west of the Meckering line where flat, sluggish, ill-defined, ancient, drainage systems are rejuvenated increasingly in the downstream direction to mature and, then, young valley forms (Mulcahy and Bettenay 1971).

Secondly, an examination of Fig. 1 suggests several examples of river capture, for example between the Kent and Gordon Rivers on the south coast, and between the Collie South Branch and the Blackwood River.

Thirdly, the extensive coastal system of lakes and swamps, particularly those backed up behind the unstable coastal dunes, provides an avenue for dispersal. For example marron populations are present in the larger permanent freshwater "lakes", which form a diffuse pattern often subject to extensive winter flooding, on the south coast. This avenue of dispersal may have been the major route for recolonization of the short coastal streams after interglacial periods when the sea drowned most of the coastal valleys.

Climate

There is good present day evidence that the long term availability of permanent deep water also limited the original distribution of marron. Not only have marron

been successful in the short term, since man's advent, when introduced to more northerly and easterly rivers, but where man has established perennial farm dam water supplies for stock purposes they have been successfully introduced into much drier and hotter areas as far north as Northampton, as far east as Esperance, and inland to the Lake Grace area (Morrissy 1974a).

North of the Collie or Harvey Rivers on the west coast there is a higher rainfall but also a higher evaporation rate in comparison to east of the Kent River where there is a lower evaporation rate but a lower rainfall (Fig. 19). (Climatic Surveys undated, 1962, 1965). Therefore, on the west coast loss of deep water pools and stream flow is infrequent, occurring in the long term only in the rare years of extreme drought. On the south coast, lack of deep water pools and summer flow tend to be more of a continual limitation due to the lower average rainfall. This part of the hypothesis is supported by the favourable summer appearance of pools in rivers such as the Canning, Serpentine, Dandalup (before damming) and Murray on the west coast, contrasting with the pools of rivers on the south coast, in travelling westward from Albany until the Kent River is crossed.

Given the relative year to year constancy of evaporation (correlated with summer air temperature), the limiting climatic factor for marron may be, therefore, the long term frequency of extreme drought. The occurrence of the last such drought and the poor ability of marron to colonize an adjacent river system may have been the reason for their absence in rivers north of the Collie (Harvey) and east of the Kent. Such a drought would also cause the retreat of stocks down each river system but recolonization upstream could be expected to be rather more rapid. All the original marron waters having head waters far inland, where the combination of rainfall and evaporation is more unfavourable, also extend through the most favourable combination of factors near the coast (Fig. 19). Ameliorating the climatic effects inland is the presence of large pools in the mature valley forms which are not dependent on flow for depth of water as occurs nearer the coast.

V CONCLUSIONS RELATING TO THE EXTENT OF MARRON WATERS AVAILABLE FOR AMATEUR FISHING

A major component of the total annual catch of marron in recent years has come from a few large, man-made, public water supply dams in the Darling Ranges which are open to public fishing. These waters, and private farm dams together with transplantings to more northerly and easterly rivers have to a degree compensated for the loss of marron habitat, over the past twenty years or so, in rivers by dam building and, inland, by environmental deterioration.

The extensive loss of marron habitat due to environmental deterioration in the upper reaches of the major rivers appears to be irreversible with continuing agricultural use of the watersheds. However, this problem seems likely to extend to the lower reaches of these rivers and to the shorter coastal rivers which provide approximately half of the total annual catch of marron at present. These river ecosystems have evolved under conditions of very low input of decomposable (non-woody) organic matter and dissolved nutrients from the infertile forested watersheds of the south-west (Halls-worth 1977). Increased input to rivers of forest debris, loss of stored nutrients from forest litter and increased

importation of inorganic nutrients, as farm fertilizers, pose the considerable threat of increasing eutrophication to the remaining river fishery. Increased water extraction for irrigation, use of pesticides, and erosion, leading to turbidity and siltation, are also obvious consequences of the increasing multiple land use in the south-west (forestry, mining and irrigation farming).

Preservation of at least one of the most nearly pristine of the (short) river systems remaining in the south-west and its catchment has been proposed as vitally necessary in providing a control or bench mark for scientific understanding of changing conditions, in many fields, in other south-west catchments undergoing multi-development (W.A. Environmental Protection Authority 1975). The justification for this preservation could include the obvious future need for environmental monitoring of the marron fishery in rivers.

The marron is the most important aquatic species in south-western rivers because of the large biomass (Warren River 600 kg/ha, Morrissy 1974b) sustained by detritivorous consumption based upon allochthonous organic input. The sensitivity of marron stocks to the depleted oxygen conditions accompanying eutrophication suggests that the marron could be a valuable "indicator species" for monitoring this unfavourable by-product of development.

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VIII APPENDIX—SALES OF MARRON FROM THE PEMBERTON FISH HATCHERY

In 1947 an inquiry originated from Dwellingup as to whether Pemberton could supply marron for stocking purposes (Departmental File, 50/44, January 3, 1947). The supplying of marron from the Pemberton Hatchery for stocking private waters, particularly inland farm dams, commenced in the mid 1960's. It has been noted elsewhere (Morrissy 1978) that sale of marron for consumption was widespread in the inland wheatbelt towns distant from marron streams. Shipway (1951) suggested that: “The habits and life history of the marron are such that it appears eminently suitable for stocking farm ponds and dams, and there are possibilities of its furnishing a valuable addition to the fare of country people in areas where fresh sea foods are unavailable.” Prior to 1972 the Pemberton Fish Hatchery was administered by the Pemberton Hatchery Board with representation from the then, Department of Fisheries and Fauna; the majority of annual running funds and funds for capital improvements were provided by the State Government. In 1972 the Department of Fisheries and Wildlife assumed full responsibility for staffing, day to day running and administration of the Hatchery and, henceforth, there was a very significant increase in the annual sale of marron, viz:—

Year	Number of Marron Sold
1967/68	6 500 (\$10/50 marron)
1968/69	8 865 (\$10/50 marron)
1969/70	4 100 (\$10/50 marron)
1970/71	4 352 (\$10/50 marron)
1971/72	2 965 (\$10/50 marron)
1972/73*	9 650 (\$10/50 marron)
1973/74	11 700 (\$10/50 marron)
1974/75	15 900 (\$10/50 marron)
1975/76	17 765 (\$15/50 marron)
1976/77	22 000 (\$15/50 marron)

* Department assumed control of Hatchery, January 1, 1972.

Although for consignment purposes the marron sold are small, a batch of 50 is sufficient to establish a stock in the typical “2 000 cubic yard” farm dam of the inland (Morrissy 1970c).

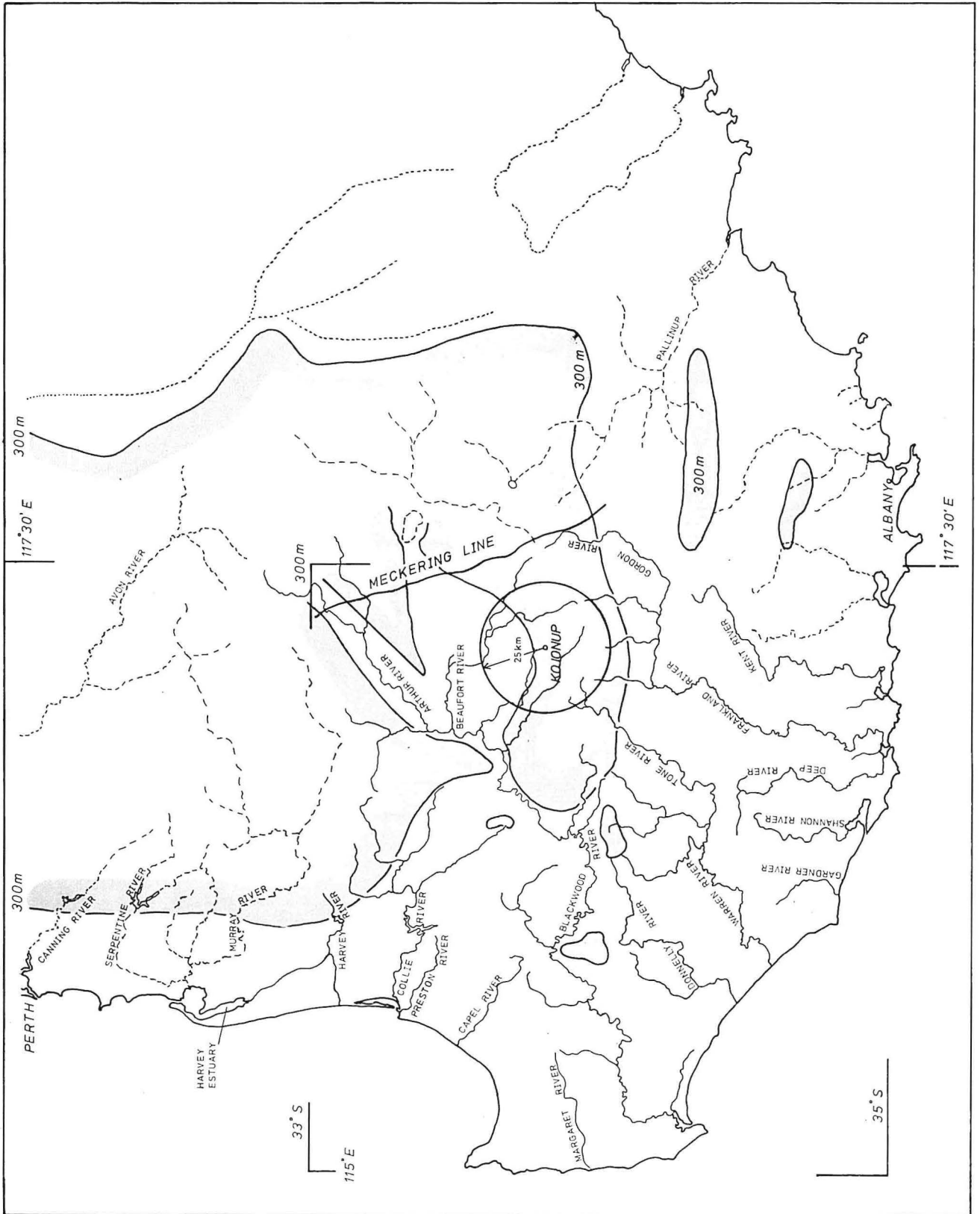


Figure 1—Probable extent of the original distribution of marron in south-western rivers (mapped as continuous Water courses).

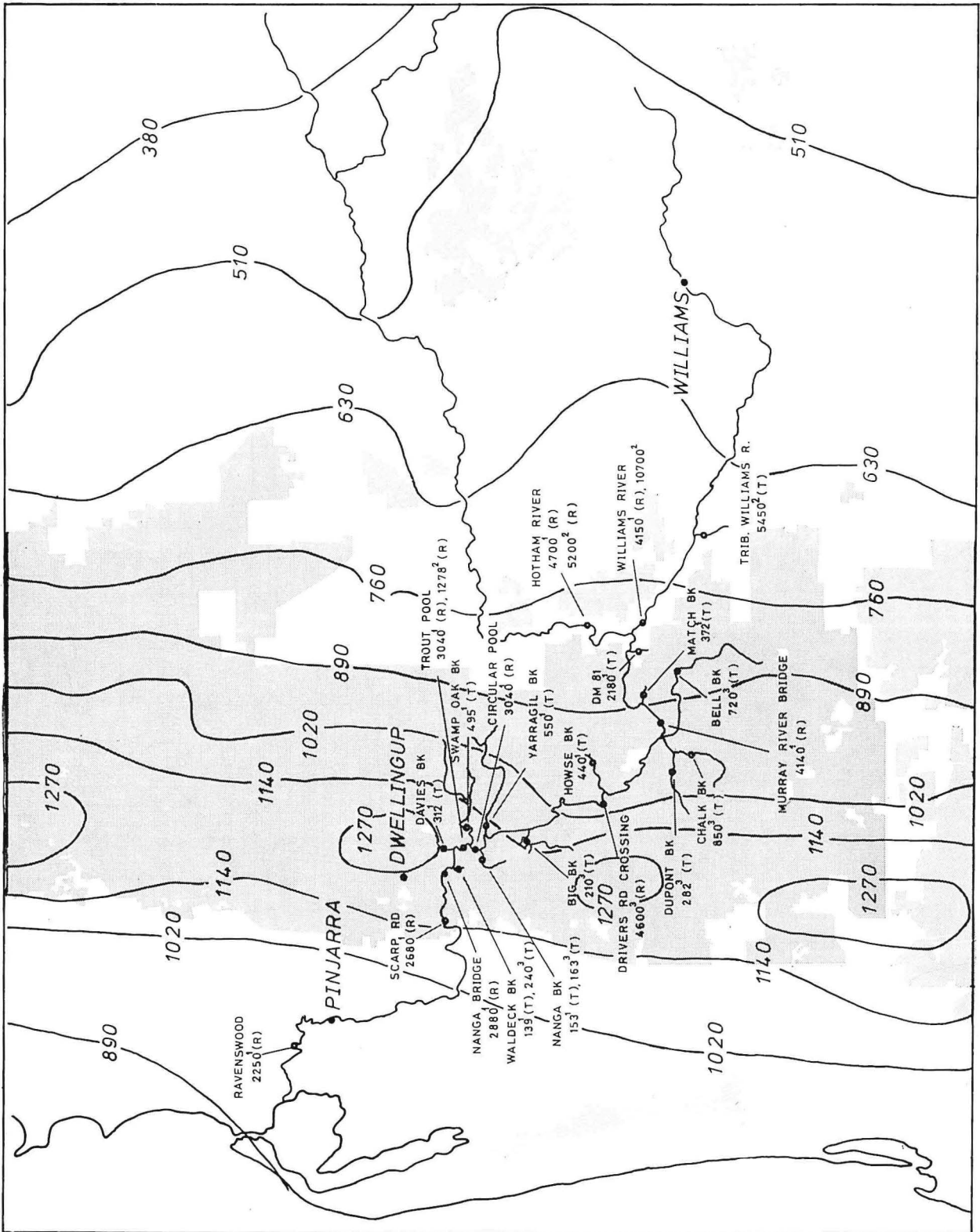


Figure 2—Conductivity data showing the reversed longitudinal salinity profile of the Murray River in relation to isohyets mm and State Forest (shaded). Superscripts on conductivity values $S\text{ cm}^{-1}$ (20°C) indicate sampling date; 1, 5 September, 1973, 2, 2 February, 1973, 3, 13–16 November, 1973.

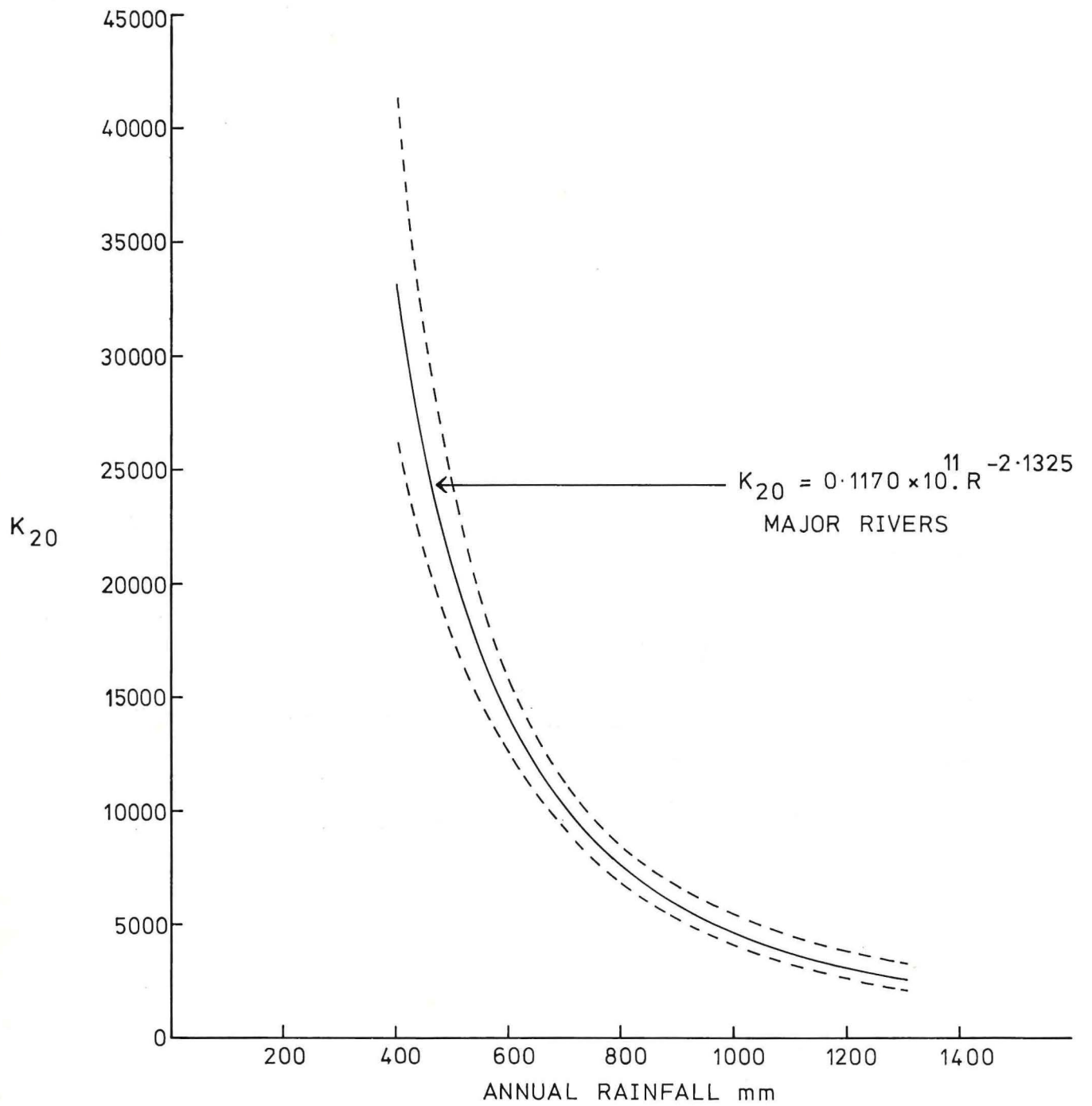


Figure 3—The relationship between salinity, as conductivity (K_{20} , $S\ cm^{-1}$) and annual rainfall mm for (a) major rivers and (b) short coastal rivers, tributaries, etc. Also shown are the 95% confidence limits for mean conductivity.

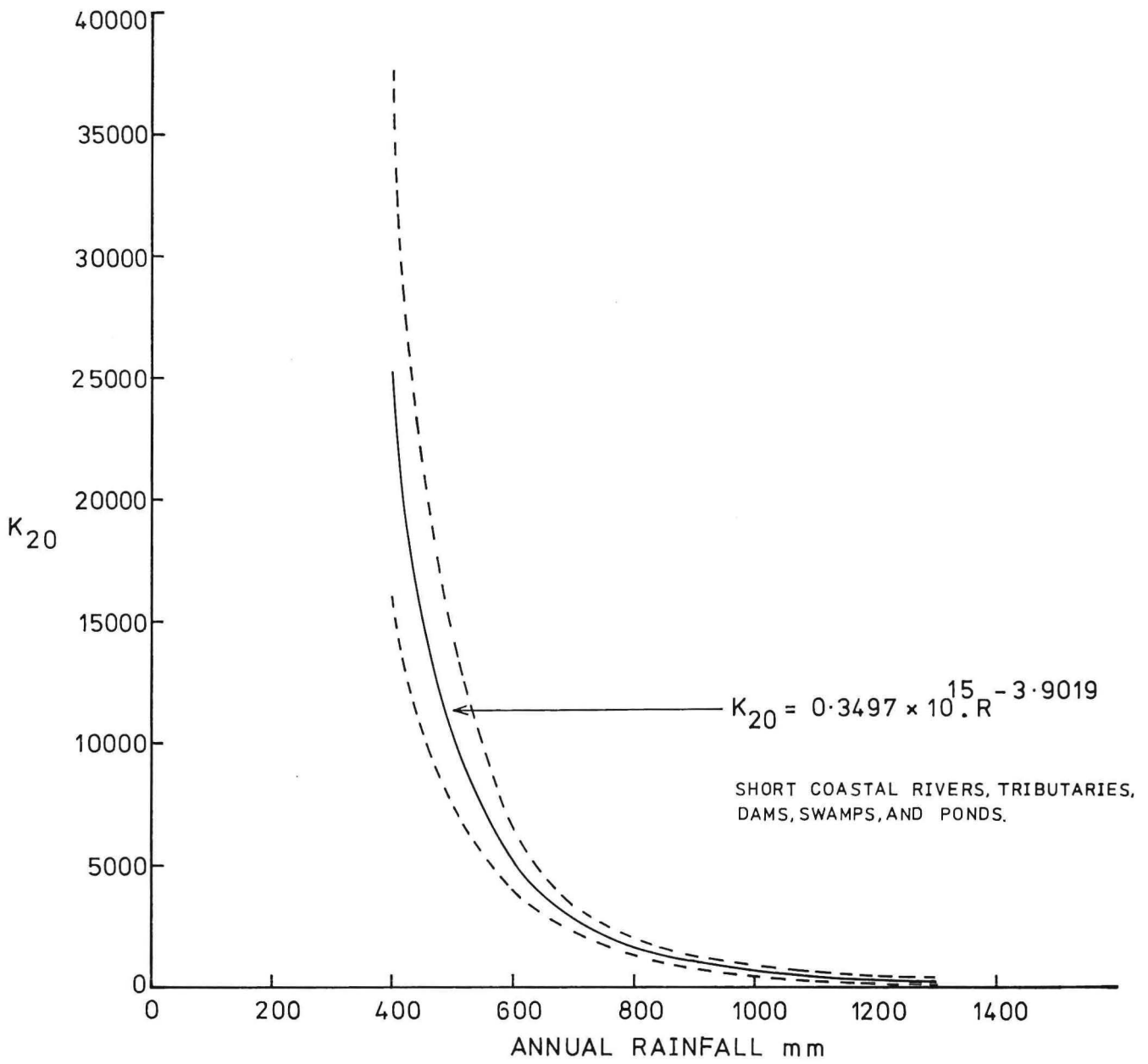


Figure 3 (b)—See page 21.

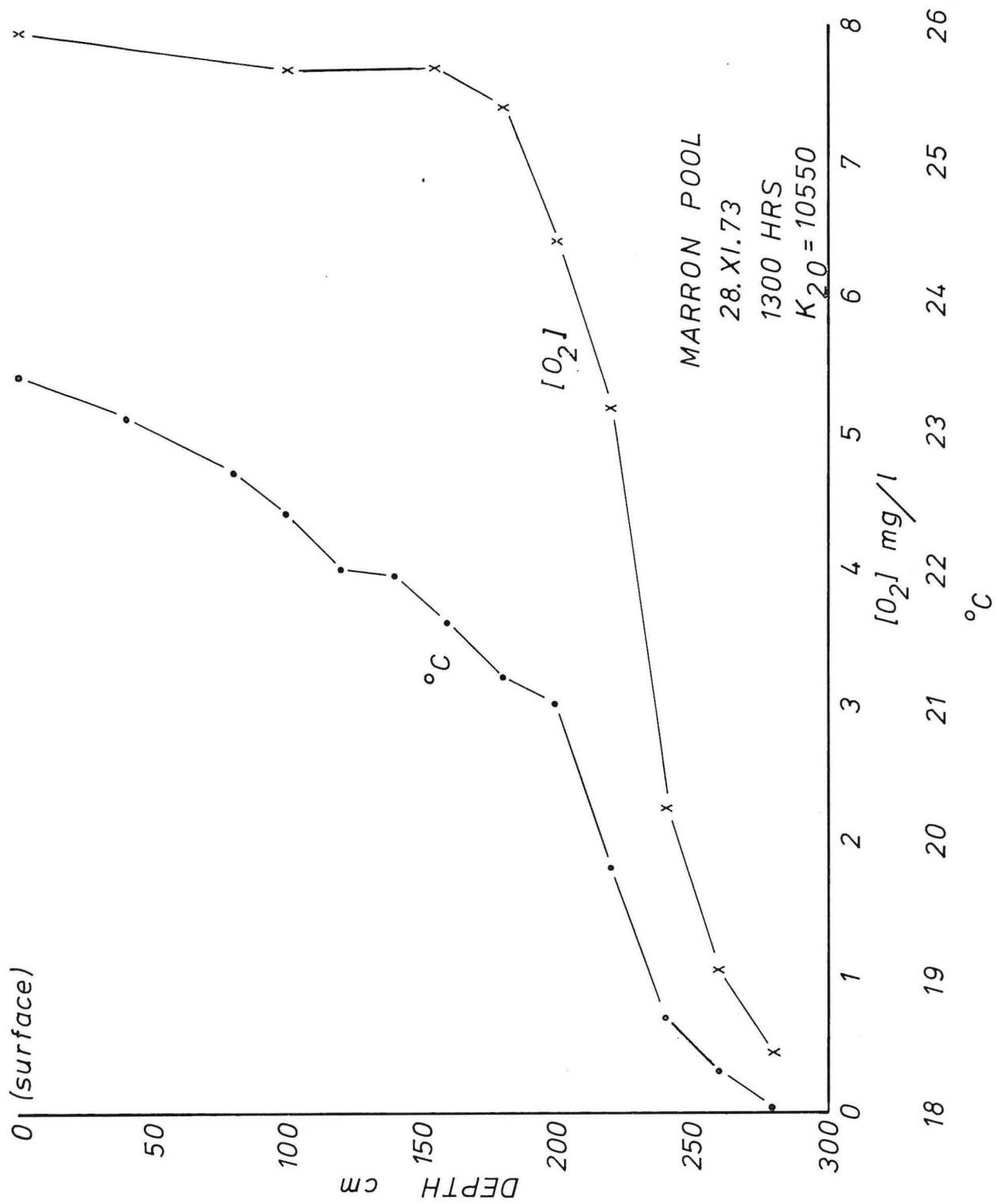


Figure 4—Oxygen-temperature profiles for a pool on the upper Blackwood River system near Kojonup.

MARRON POOL 28.XI.73 n = 0 K₂₀ = 10550

CHERRY TREE POOL 27.XI.73 n = 0 K₂₀ = 10100 0+ MARRON SEEN 1.II.73

BOKAL POOL 26.XI.73 24°C n = 0 K₂₀ = 8800

FORMATION POOL 28.XI.73 n = 0 K₂₀ = 7600

MOODIARUP POOL 29.XI.73 n = 0 K₂₀ = 7700 A MARRON SEEN

WINNEJUP FORD, CLARKES POOL 2.IV.74 22.3°C n = 0 K₂₀ = 8200

WINNEJUP BRIDGE POOL 3.IV.74 19.3°C n = 5 K₂₀ = 7800

BRIDGETOWN 10.X.74 16.4°C n = 48 K₂₀ = 5900

REVELLY ROAD 8.X.74 15.9°C n = 10 K₂₀ = 3750

SUES BRIDGE 9.X.74 15.7°C n = 42 K₂₀ = 2590

THE COLONELS, WARREN RIVER 16.5°C 3.XI.70 n = 286 K₂₀ ≈ 950

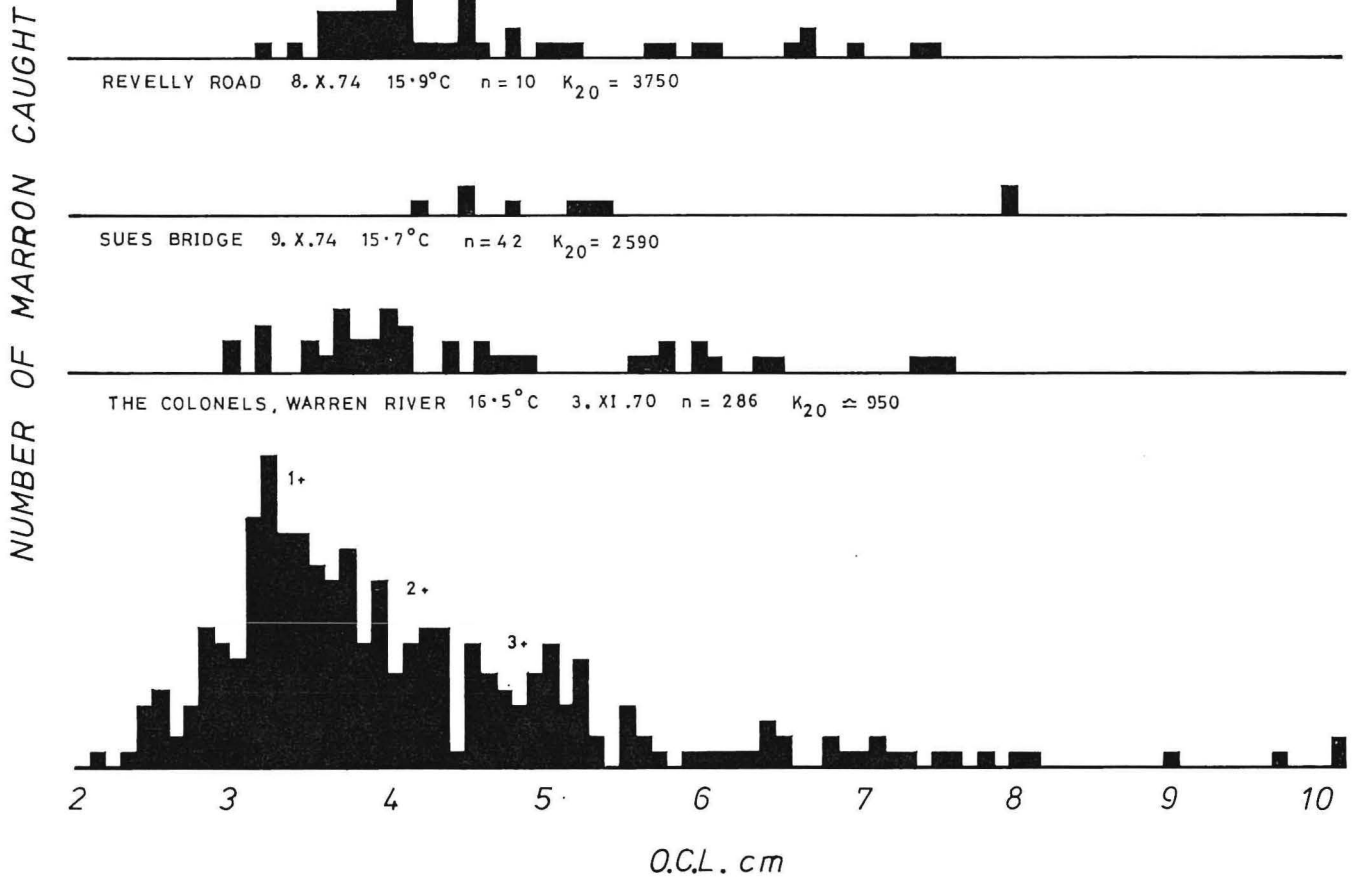


Figure 5—Results of drop net sampling along the course of the Blackwood River system. A catch from the lower Warren River is shown to illustrate a healthy stock.

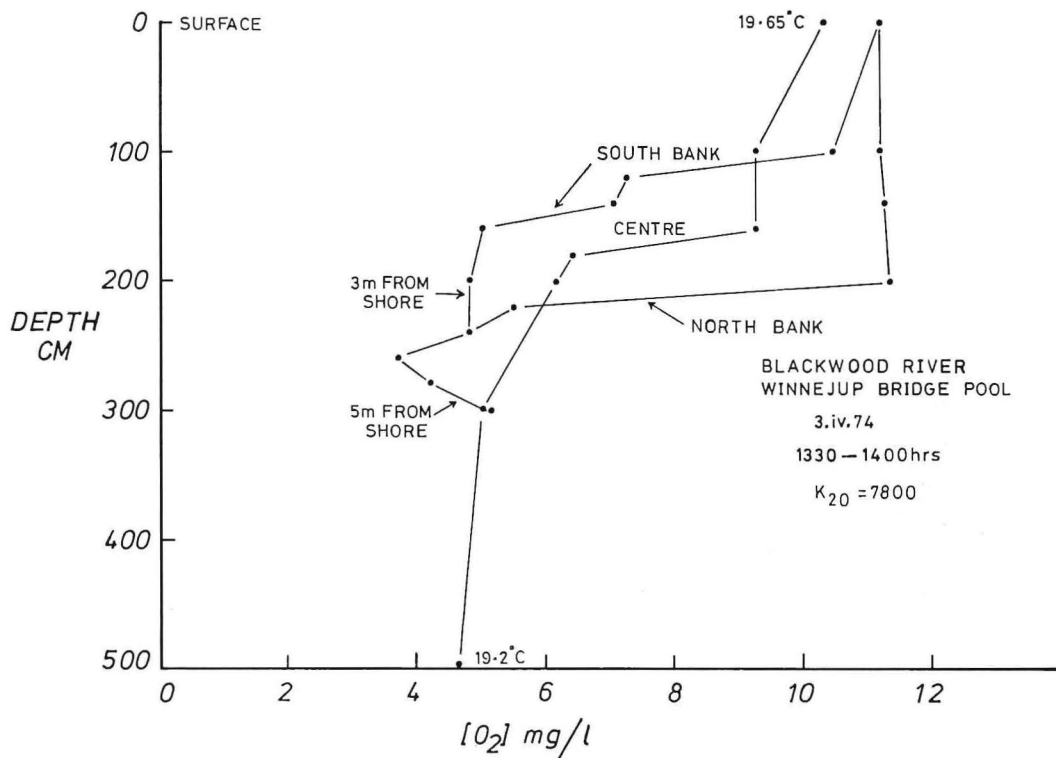
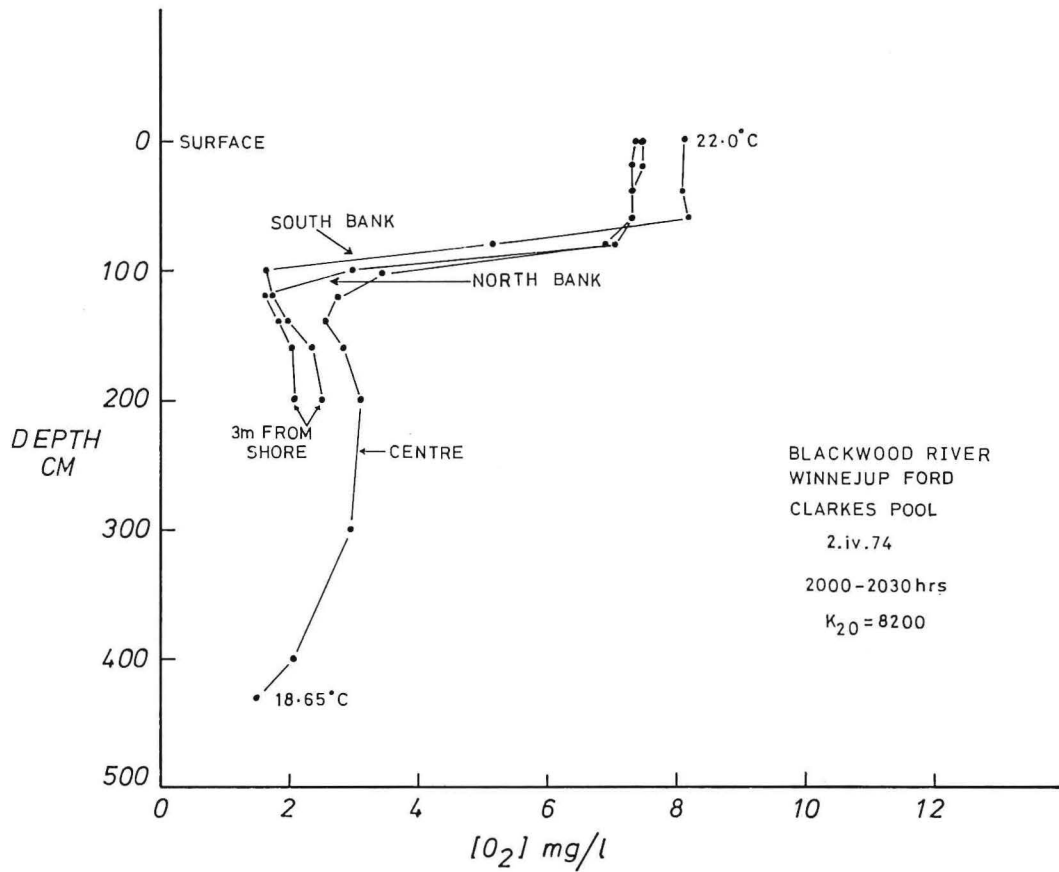


Figure 6—Oxygen profiles for pools on the middle course of the Blackwood River. “Bank” profiles refer to bottom readings moving out from the shoreline and “centre” profiles were measured vertically from the surface at the centre of the pool.

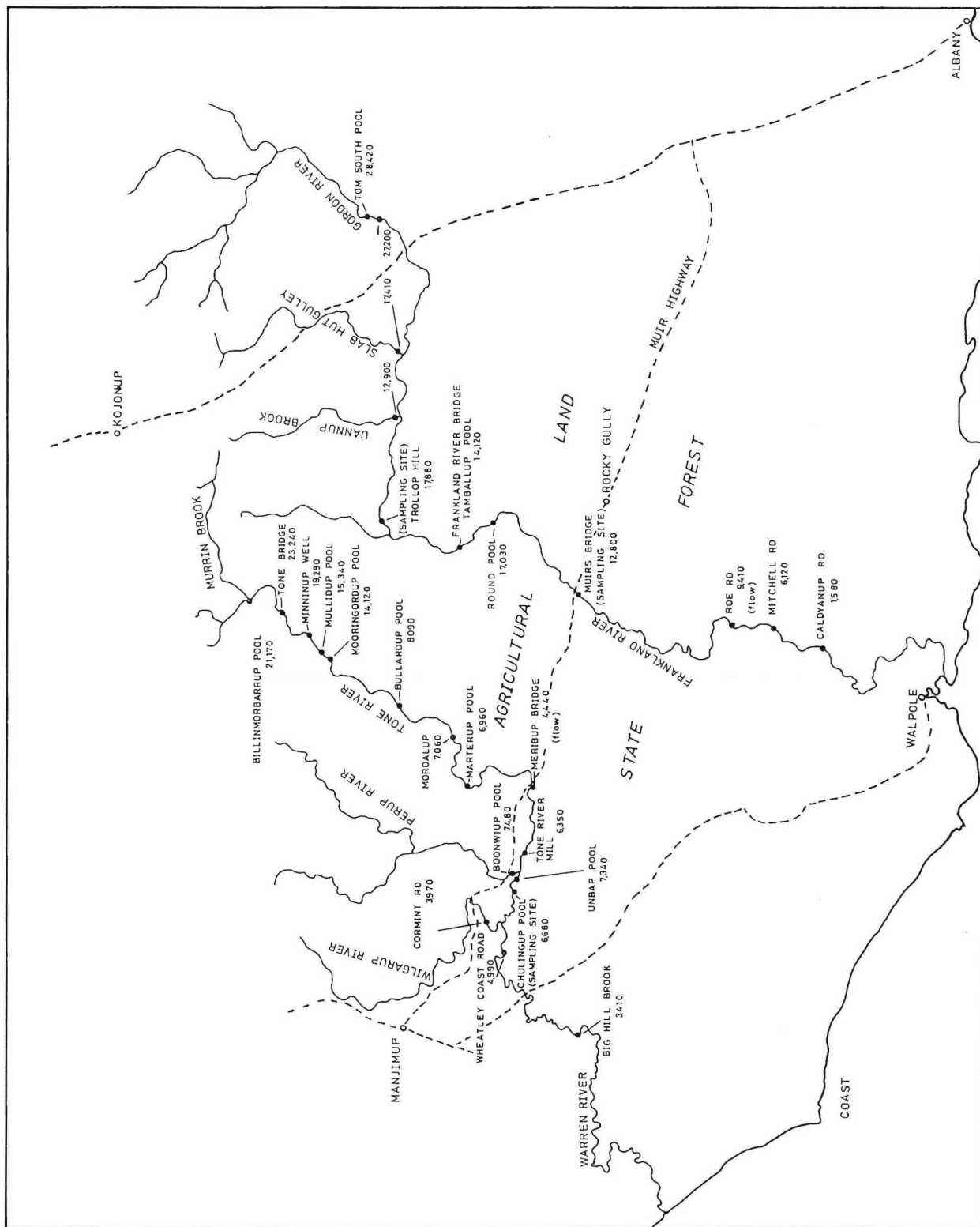


Figure 7—Conductivity values (K₂₀, S cm⁻¹) along the courses of the Frankland and Warren River systems sampled during February 1977.

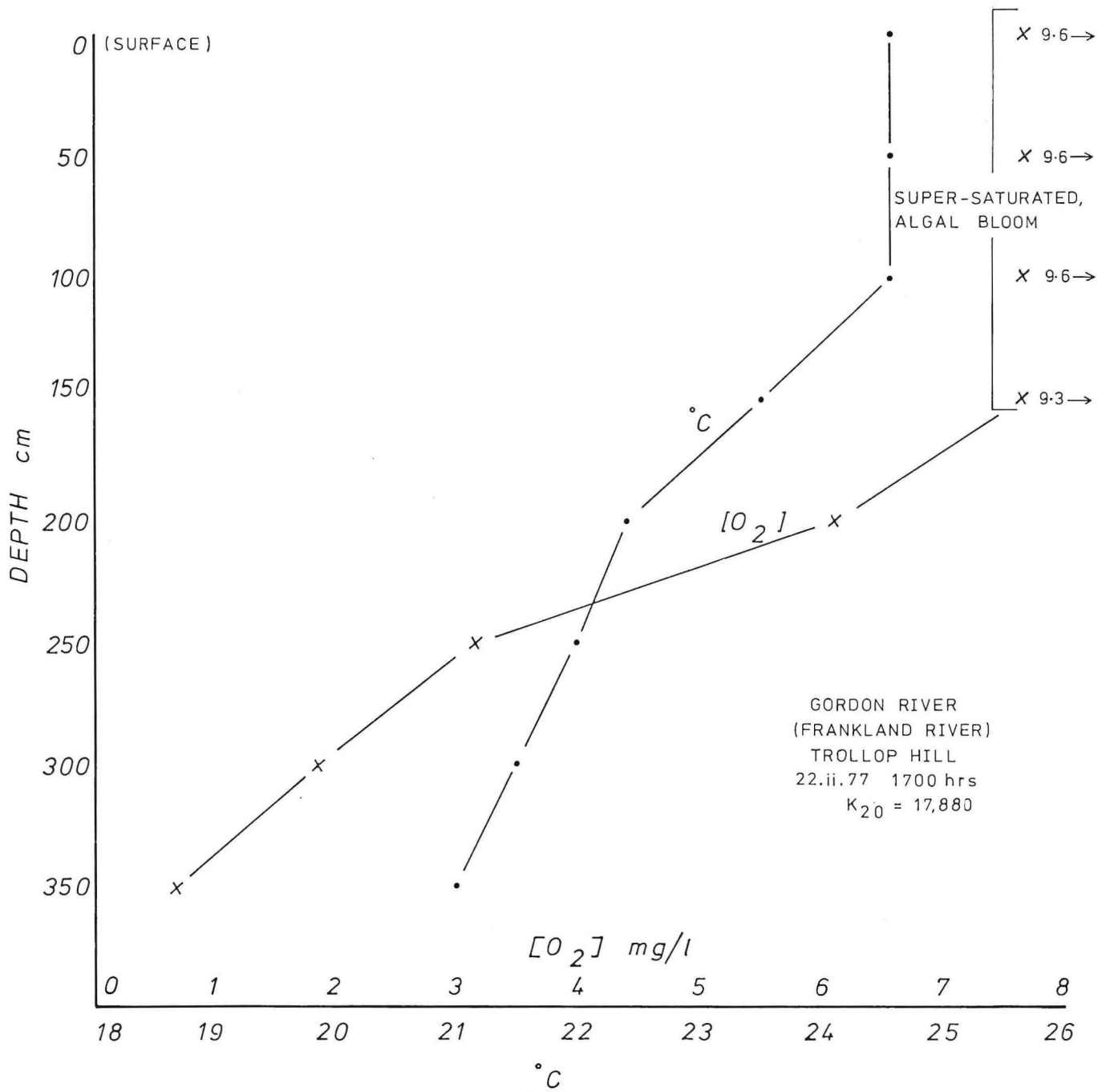


Figure 8—Oxygen-temperature profiles for a pool on the Gordon River.

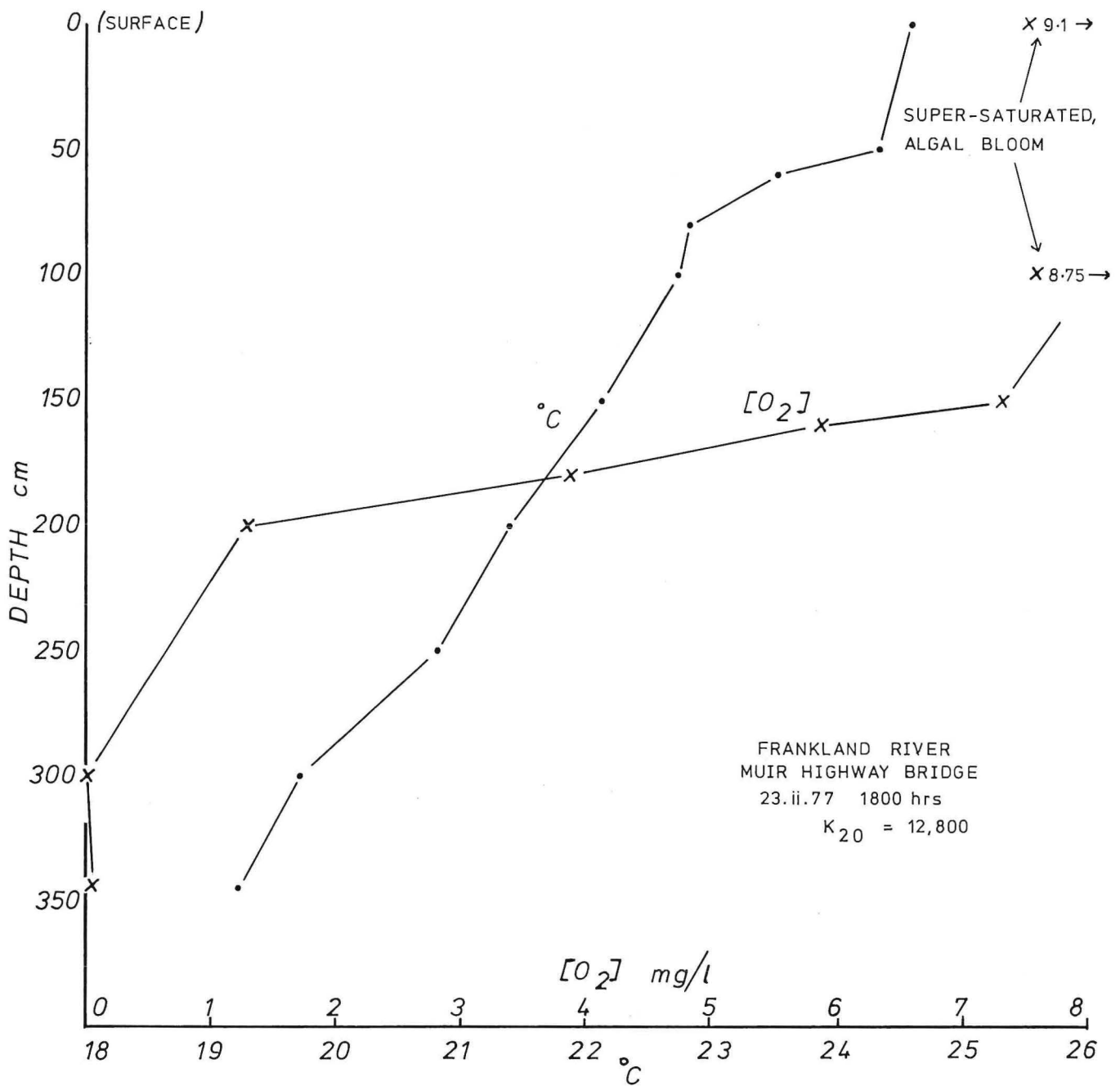


Figure 9—Oxygen-temperature profiles for a pool on the middle course of the Frankland River system.

MURRAY RIVER (HOTHAM RIVER) 17.iii.77 20°C $K_{20} = 10,770$ $n = 21$ (17 LEGAL SIZE)
 WEST OF BODDINGTON
 STONE CROSSING POOL (FARMERS)

830 →
 839 →
 823 →

MURRAY RIVER 17.iv.72 19.9°C $K_{20} = 1278$ $n = 401$ (19)
 ISLAND POOL

WARREN RIVER 24.ii.77 23.5°C $K_{20} = 6680$ $n = 40$ (6)
 CHULINGUP POOL

WARREN RIVER 23.ii.71 22.8°C $K_{20} = 1400$ $n = 232$ (13)
 COLONELS POOL

FRANKLAND RIVER 23.ii.77 22.1°C $K_{20} = 12800$ $n = 17$ (2)
 MUIRS BRIDGE

FRANKLAND RIVER 12.ii.75 24.2°C $K_{20} = 2496$ $n = 149$ (21)
 ABOVE CIRCULAR POOL

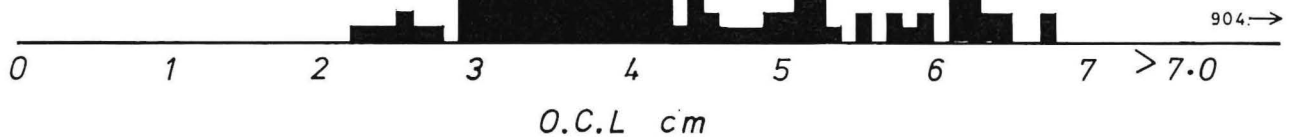


Figure 10—Catches of marron from the lower courses of the Frankland, Warren and Murray Rivers compared with ones taken later from the middle courses.

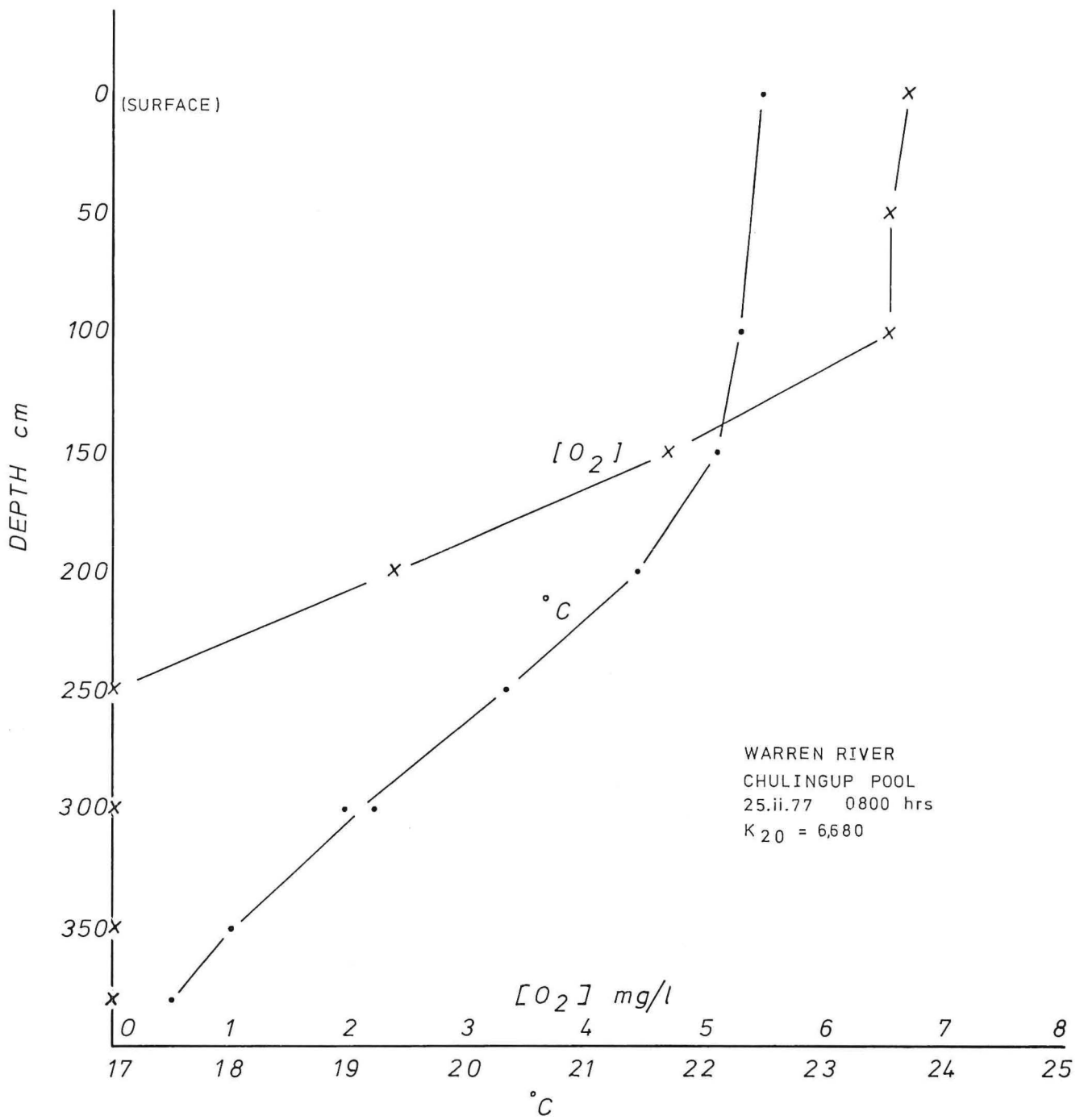


Figure 11—Oxygen-temperature profiles for a pool on the middle course of the Warren River.

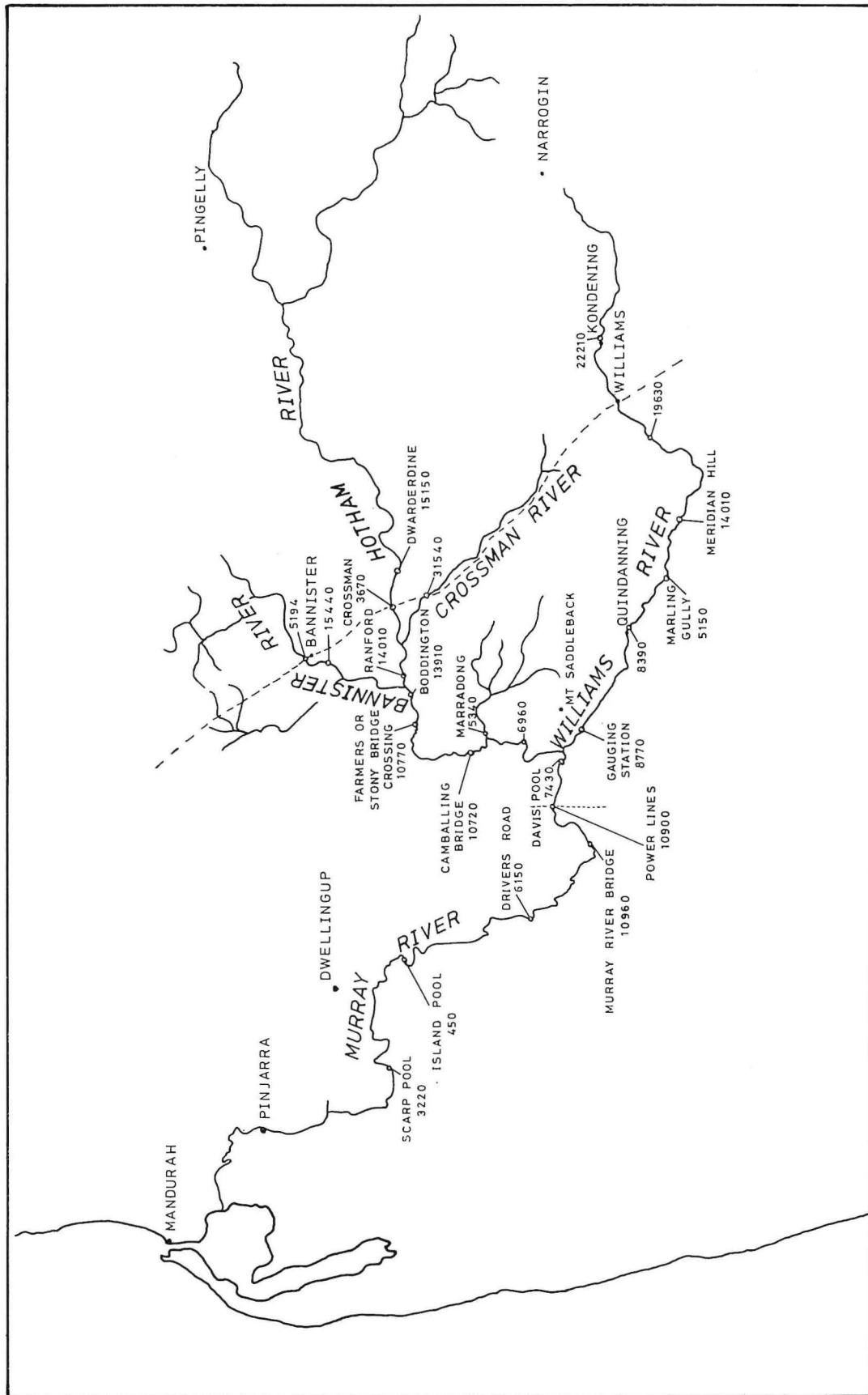


Figure 12—Conductivity values (K_{20} , $S\ cm^{-1}$) along the course of the Murray River system sampled in March 1977.

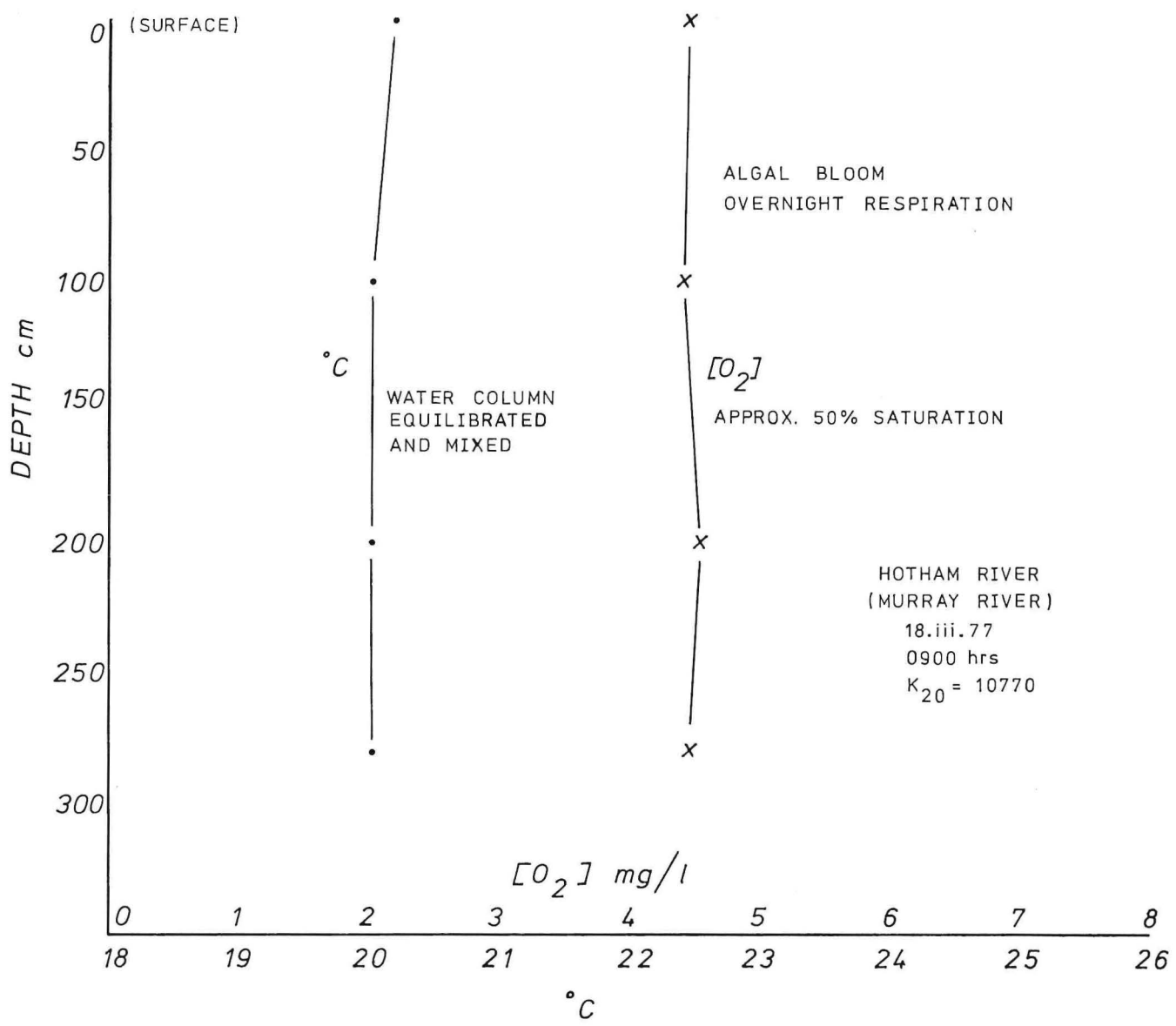
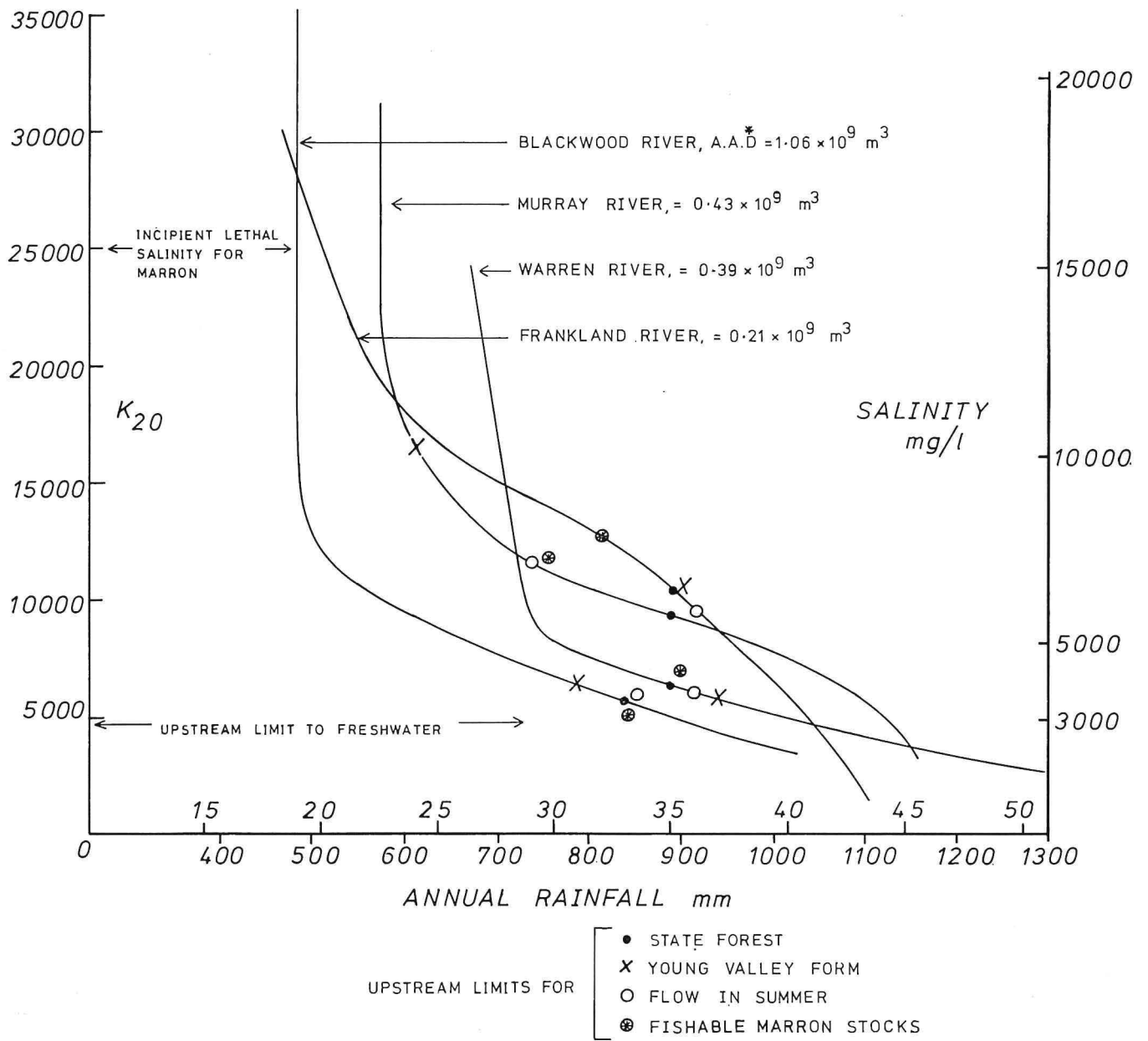


Figure 13—Oxygen-temperature profiles for a pool on the middle course of the Murray River.



* AVERAGE ANNUAL DISCHARGE AFTER COLLETT (1970)

Figure 14—Salinity (K_{20})-rainfall profiles of the four major rivers, showing the approximate upstream limits of fishable marron stocks, young valley form, flow in summer and State Forest.

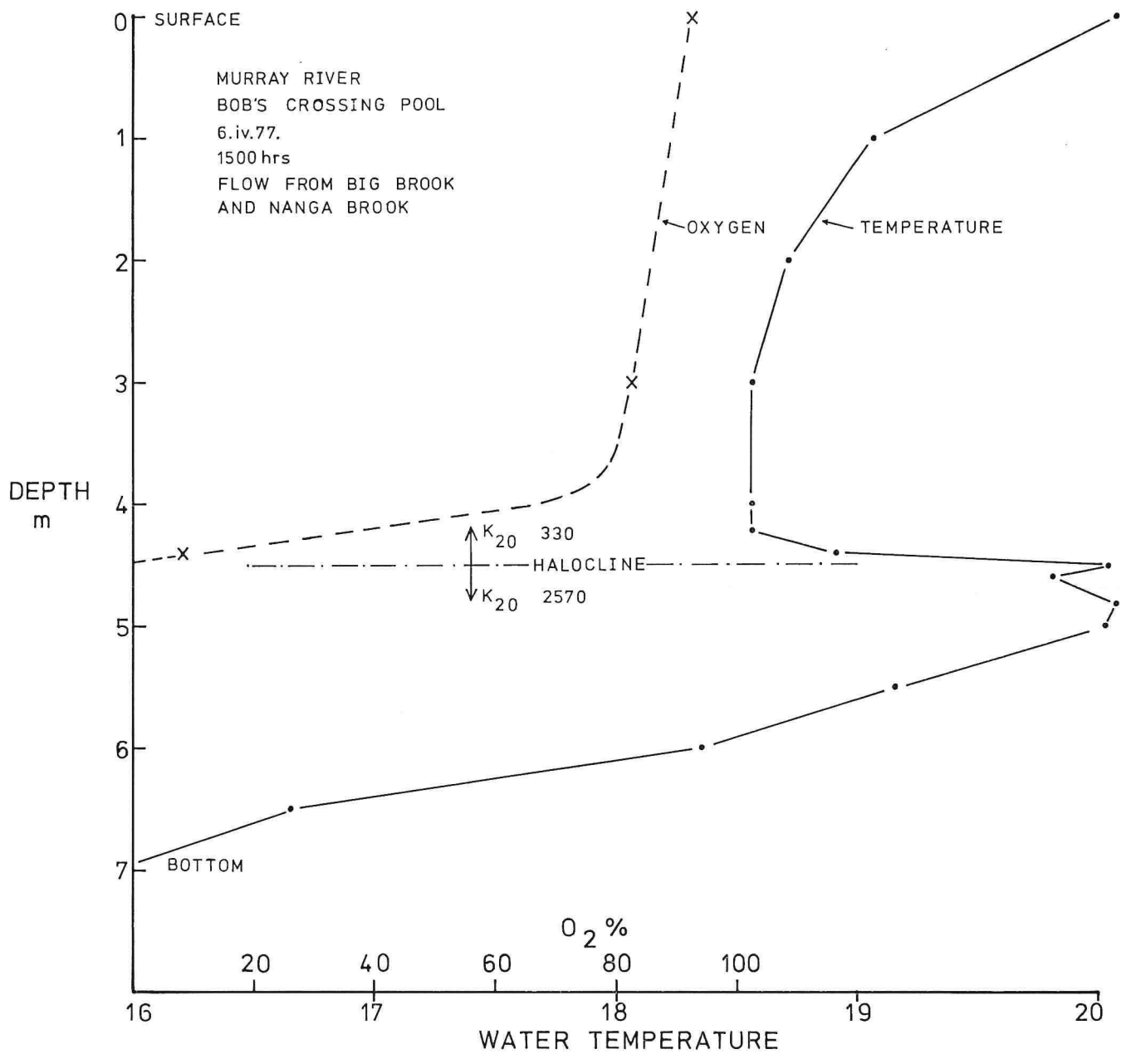


Figure 15—Oxygen-temperature profiles for a pool on the lower course of the Murray River showing a halocline.

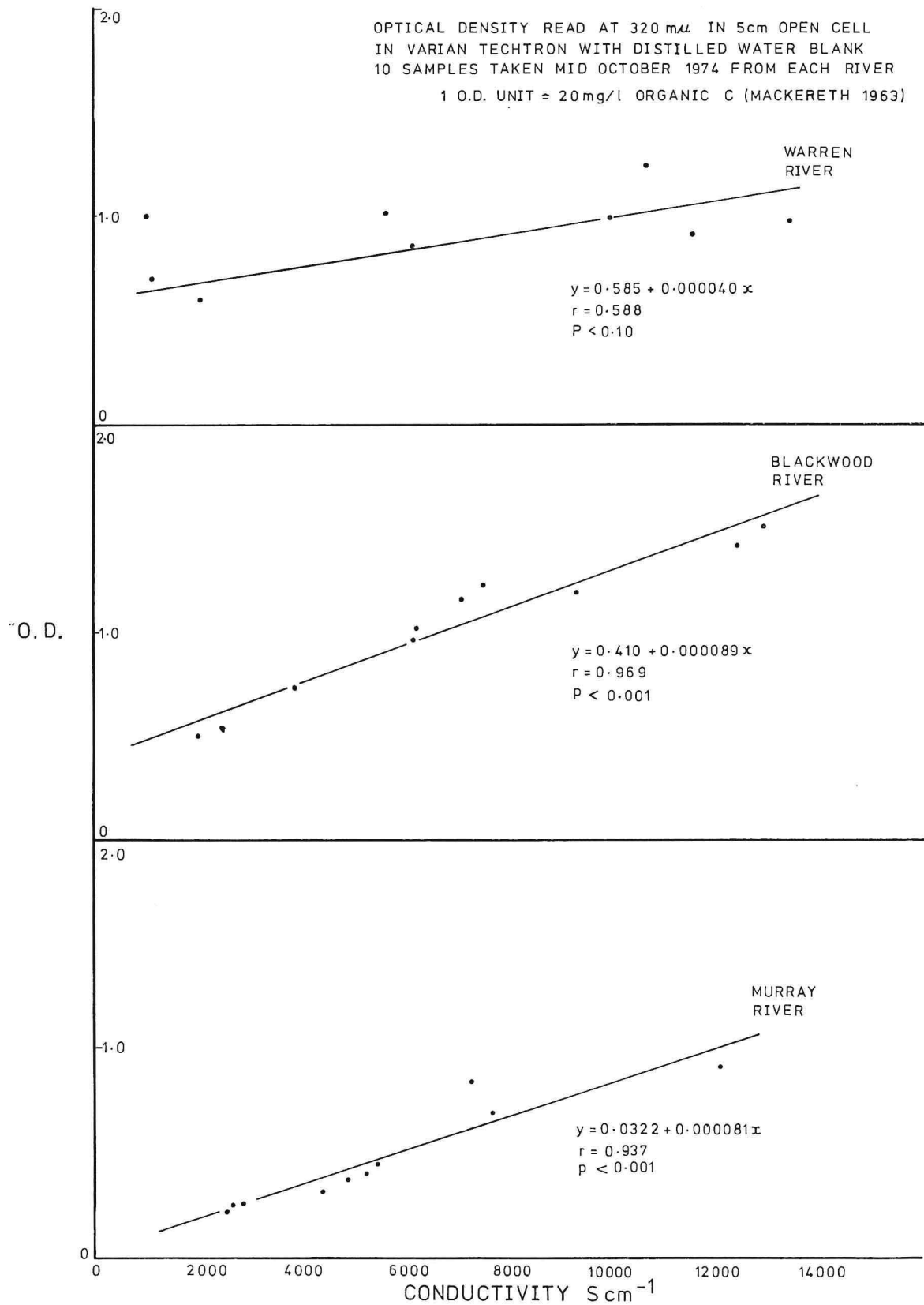


Figure 16—The relationship between dissolved organic matter, measured as the optical density at 320 μ, and salinity, as conductivity, along major rivers.

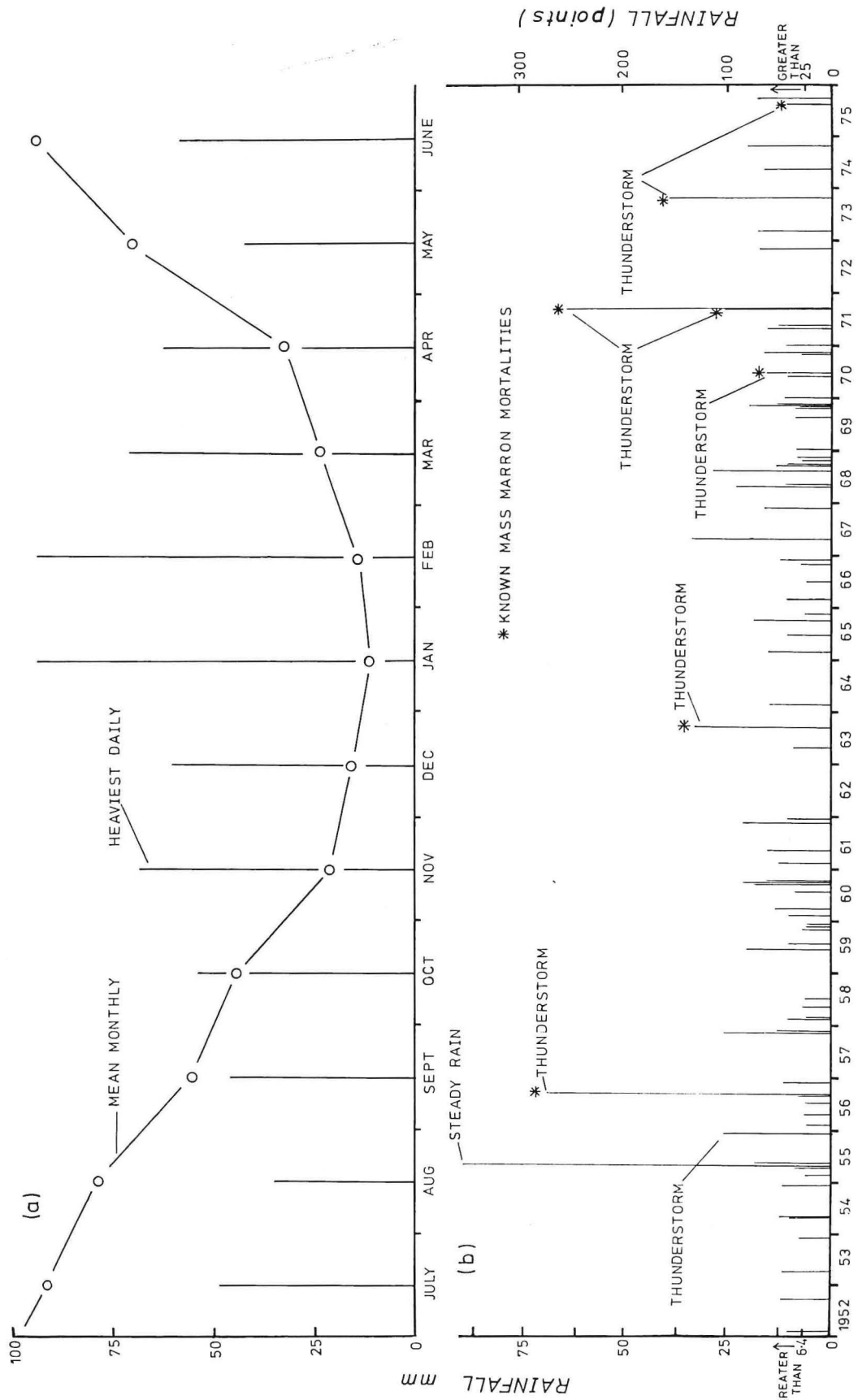


Figure 18—Kojonup rainfall statistics:
 (a) Mean monthly rainfall and heaviest daily rainfall.
 (b) Incidence of heavy daily rainfalls during the summer period, December to March inclusive, over the past 25 years.

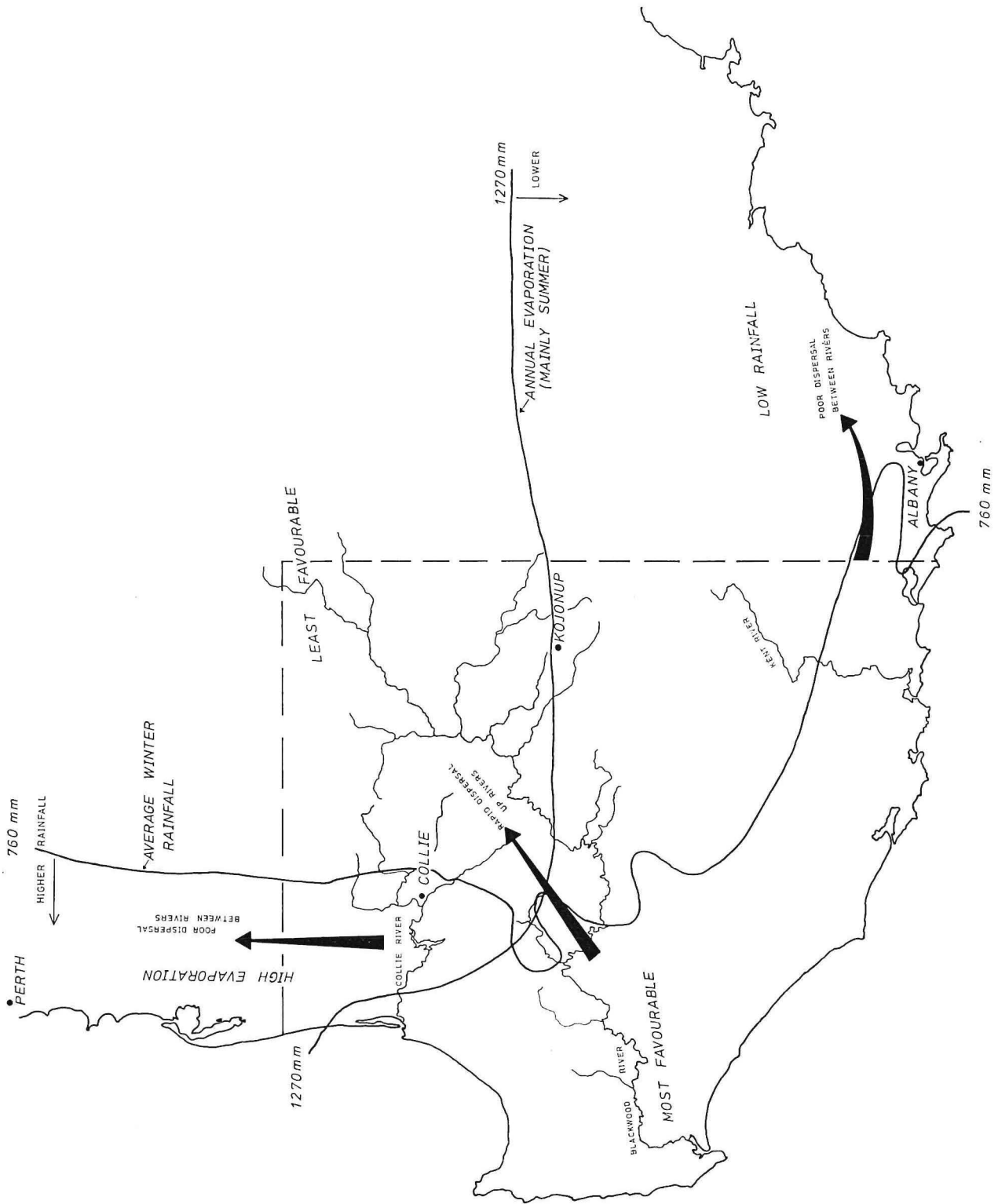


Figure 19—Arbitrarily chosen rainfall and evaporation boundaries illustrating the most probable long term influence of these factors on the distribution of marron,