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Distribution and environmental tolerances of aquatic macroinvertebrate families in the agricultural zone of southwestern Australia

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Abstract. The agricultural zone of southwestern Australia is an extensively modified landscape. Ninety percent of the perennial native vegetation has been cleared and replaced by annual cereal crops and pasture. Consequently, groundwater has risen and much of the region is affected by dryland salinity. River geomorphology and water quality have been severely impacted by land clearing, anthropogenic patterns of land use, and secondary salinization. The objectives of this study were to determine patterns of distribution of aquatic macroinvertebrates in the region, and to identify environmental variables influencing these patterns. Aquatic macroinvertebrates were sampled at 176 river sites during spring 1997 and a range of environmental data were collected at each site. Eighty-one families were collected, with the fauna being dominated by insects. At the family level, macroinvertebrate communities were homogeneous and depauperate, and consisted of families that tolerated a broad range of environmental conditions. The fauna was particularly resilient to high salinities, with some families tolerating salinities orders of magnitude greater than previously reported for lotic waters. The most significant environmental factors influencing the distribution of aquatic invertebrates were rainfall, salinity, land use, and instream habitat.

Key words: salinity, macroinvertebrates, agriculture, Western Australia, biomonitoring, land use, water quality, rainfall.

Secondary salinization is a global problem, occurring in Australia, North America, Africa, and the Middle East (Williams 1987). It is particularly acute in southwestern Australia where >70% of Australia's salt-affected land occurs. Approximately 90% of the agricultural zone in southwestern Australia has been cleared of native vegetation, mostly for wheat and wool growing (George et al. 1995). Land clearing has caused substantial increases in stream salinities, particularly where rainfall is <900 mm/y (Schofield et al. 1988).

Sea salt, transported to the inland regions by wind and rain, has been accumulating in the landscape for millennia (Schofield et al. 1988). Replacement of the deep-rooted, perennial native vegetation with shallow-rooted, annual agricultural species has altered the water balance of catchments and increased groundwater recharge. Consequently, groundwater levels have risen and salt previously stored in the soil is mobilized and brought to the valley surface or discharged directly into streams (Schofield et al. 1988). This process is sometimes referred to

as dryland salinization. Stream salinities have only marginally increased in cleared catchments where annual rainfall is >1100 mm, but have substantially increased where rainfall is <900 mm/y (Schofield et al. 1988). There is a clear trend for stream salinity to increase with proportion of catchment cleared and with decreasing annual rainfall. Agricultural clearing has changed the salt balance of catchments from a state of salt equilibrium or accumulation to a state of net salt export (Schofield et al. 1988).

Stream salinities have doubled in the medium-high rainfall zone (>700 mm/y) and increased up to 50-fold in the low-medium rainfall zone (300–700 mm/y) (Schofield et al. 1988). In the Avon River, there has been up to a 40-fold increase in salinity over the last century (Kendrick 1976). The ecological implications of such changes are poorly understood (Williams 1987). Although there is a universal trend for the number of plant and animal species in a waterbody to be negatively correlated with salinity over a broad range (300–300,000 mg/L), other factors often have more influence on species richness over smaller ranges of sa-

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linity (Williams et al. 1990). Nevertheless, Hart et al. (1990) suggested significant adverse biological effects would occur if salinities, in previously fresh Australian streams, exceeded 5000 to 7000 mg/L. A literature review by Hart et al. (1991) suggested some salt-sensitive species are deleteriously affected when salinities exceed 1000 mg/L.

In contrast to Hart et al. (1990, 1991), other recent Australian studies indicate that stream macroinvertebrates probably show little response to salinities $\leq 15,000$ mg/L (Williams et al. 1991, Bunn and Davies 1992, Mitchell and Richards 1992). Morrissy (1978) found that the large freshwater decapod *Cherax tenuimanus*, which is often regarded as salt-sensitive, tolerated salinities up to $\sim 17,000$ mg/L in laboratory experiments. It remains possible, however, that small increases in stream salinity remove a suite of salt-sensitive macroinvertebrates in the early stages of salinization. Kendrick (1976) documented the disappearance or decline of the molluscs *Westralunio carteri* and *Plotiopsis australis* from the Avon River at salinities $\leq 10,000$ mg/L, and Bunn and Davies (1992) suggested the dominance by crustaceans of macroinvertebrate communities of saline streams on the eastern Darling Scarp may reflect an earlier change from a salt-sensitive to a salt-tolerant community that was stable in the face of rising salinity.

In many parts of the world, macroinvertebrates are increasingly being used as indicators of river condition (Plafkin et al. 1989, Rosenberg and Resh 1993, Wright et al. 1993, Marchant et al. 1997). This use, however, requires pre-existing knowledge of the distribution patterns and environmental tolerances of macroinvertebrates, which is lacking for most of southwestern Australia other than some forested areas (e.g., Bunn 1986, Bunn et al. 1986, Storey et al. 1990). Compiling such information from small-scale studies can be misleading, especially when documenting environmental tolerances was not the study objective, because sites may not be representative of regional conditions. The aims of our study were: 1) to distinguish patterns in macroinvertebrate community composition in the agricultural zone, 2) to identify environmental variables associated with community patterns, and 3) to document the tolerances of common

families of macroinvertebrates to salinity and other water-quality parameters.

Methods

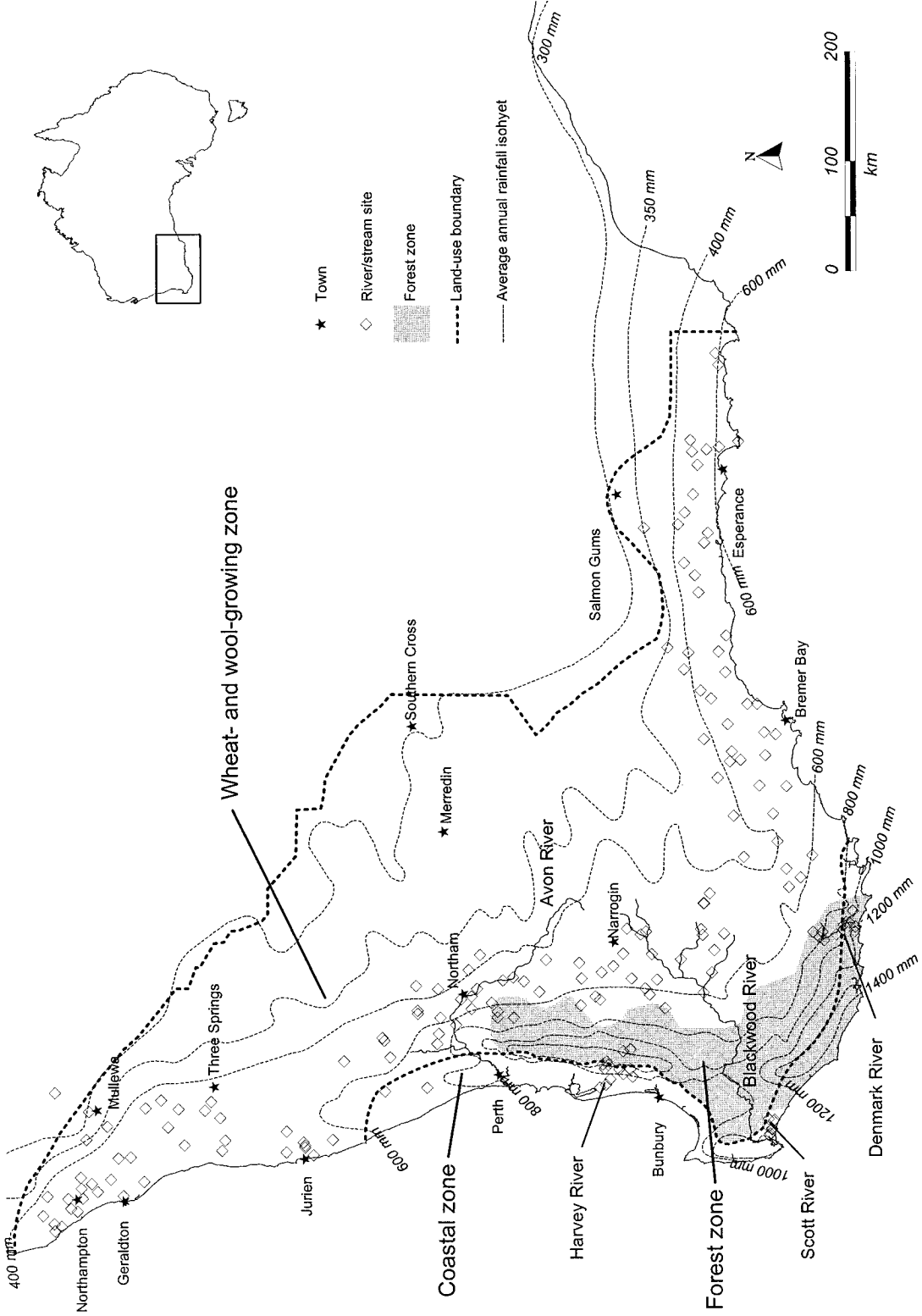
Study area

Southwestern Australia has a mediterranean climate consisting of hot, dry summers and cool, wet winters. Average annual rainfall ranges from 1400 mm on the southwestern coast to < 300 mm in the arid interior (Fig. 1). Seasonal drought occurs during the summer months when precipitation is insufficient to sustain plant growth. The dry period lasts from 3 to 4 mo in coastal regions to 7 to 8 mo in the interior agricultural zone (Beard 1990). An average annual rainfall of ~ 300 mm forms the lower limit for cereal crop cultivation (Fig. 1).

Western Australia is the oldest part of an old continent, which is reflected by a landscape of low relief, a deep mantle of weathering, and leached soils (O'Brien 1979). There are no high ranges that serve as major climatic barriers (Linacre and Hobbs 1977). Much of Western Australia is a plateau between 300 and 600 m above sea level (Australian Bureau of Statistics 1995), with most of the agricultural zone occupying a plateau 200 to 300 m above sea level (Beard 1990). The main influence of the topography is seen in the general decrease in rainfall with increasing distance from the coast (Fig. 1).

The flora of the region is diverse and highly endemic (Beard 1990). Vegetation varies considerably across the study area, ranging from tall forest on deep soils in the high-rainfall areas to heath on impoverished sandy soils in areas with low rainfall (Beard 1990). Forests and woodlands are dominated by *Eucalyptus* spp., whereas shrublands are heterogeneous and dominated by members of the families Proteaceae and Myrtaceae (Beard 1990). There is a complete absence of natural grasslands. In the drier agricultural zone, the native vegetation typically is composed of scrub-heath on sandplain; *Acacia-Casuarina* thickets on ironstone gravels; woodlands of York gum (*Eucalyptus loxophleba*), salmon gum (*E. salmonophloia*), and wandoo (*E. wandoo*) on loams; and halophytes on saline soils (Beard 1990).

Agricultural systems in the study area are dominated by wheat and wool production, which account for $\sim 35\%$ and $\sim 19\%$, respective-



ly, of the total value of agricultural commodities produced in the state (Australian Bureau of Statistics 1995). Wheat crops comprise ~70% of the area under cereal crop production (http://www.agric.wa.gov.au/technical_subjects/S/stat.htm). Clearing for agricultural purposes has been the single greatest anthropogenic impact on the environment in southwestern Australia (O'Brien 1979) and has resulted in salinization, water logging, siltation, nutrient enrichment, and weed invasion (Lane and McComb 1988, George et al. 1995). Dryland salinity currently affects ~10% of the agricultural region, which is estimated to cost Western Australia ~\$1.5 billion in lost agricultural productivity. If the problem is not effectively managed, it is estimated that as much as 30% of the agricultural region will become salt-affected (Anonymous 1996).

Highly impoverished soils are a characteristic feature of the Australian landscape and of Western Australia in particular (Beard 1990). About 850,000 tonnes of artificial fertilizers are applied to 8 million hectares of rural land per annum in southwestern Australia (Australian Bureau of Statistics 1995). Nutrient runoff has caused many rivers and wetlands to become eutrophic (Wrigley et al. 1988, Hillman et al. 1990).

Site selection

A total of 176 sites was sampled for macroinvertebrates in spring (August–November) 1997 (Fig. 1). Sampling approximately coincided with recessionary flows for rivers in the study area. Rainfall in 1997 was average to below average over most of the study area (Bureau of Meteorology 1997). Most sites (140) were located in wheat- and wool-growing areas of Western Australia, which we defined as agricultural land between the 750 and 350 mm/y isohyets. Thirty-six sites were located on the Scott, Harvey, and Denmark Rivers in the higher-rainfall, southwestern corner of the study area (Fig. 1).

The study area was subdivided into catch-

ments and the number of sites sampled in each catchment was proportional to catchment area. Liaison with local land-management agencies and land owners aided in selecting sites that were either the best examples of high-quality sites in conservation reserves or the worst examples of heavily impacted sites in farmland. The remainder of sites were randomly selected from topographic maps.

Environmental variables

Forty-four environmental variables were measured at each site (Table 1). Latitude and longitude were measured with a GPS. Altitude, slope, and distance from source were calculated from topographic maps. Data on river discharge were provided by the Water and Rivers Commission of Western Australia. Mean river width and all habitat variables were estimated visually except maximum and minimum flow, which were measured with a flow meter. Water temperature, pH, conductivity, and dissolved oxygen (DO) were measured in situ with WTW P4 portable meters. Color, alkalinity, turbidity, and nutrients were measured in the laboratory from water samples collected at each site. Conductivity was measured as an indicator of salinity, and throughout the paper we will use the term salinity (1000 mg/L \cong 2 mS/cm after Williams 1986).

Invertebrate sampling

Invertebrates were collected with a 250- μ m-mesh pondnet over 10 m² of the stream bed at depths <1 m using a sweep technique that disturbed the top few centimetres of substrate (Smith et al. 1999). Substrates in the study area were typically sandy. Kick sampling was used when flow was sufficiently high. Samples were collected along the edge and midstream of runs or pools. No samples were taken in macrophyte or riffle zones to avoid a confounding effect

FIG. 1. Locations of 176 river/stream sites sampled for macroinvertebrates during spring 1997. Towns, major rivers, broad land-use zones, and average annual rainfall isohyets are included. Boundaries of the coastal (mainly intensive industries such as horticulture, dairy, beef, and viticulture), forest (native hardwood timber production, water catchment, bauxite mining, and localized horticulture), and wheat and wool growing (mixed farming—cereal cultivation, grazing, meat, and wool production) zones are primarily determined by climate and landform.

TABLE 1. Environmental variables measured at each site.

Physical variables	Chemical variables
Latitude	pH
Longitude	Temperature (°C)
Altitude (m)	Conductivity (mS/cm)
Slope (m/km)	Color (TCU)
Distance from source (km)	Dissolved oxygen (% saturation) ^a
Discharge category (log discharge volume ML/y: 1 → 6)	Alkalinity (mg/L CaCO ₃)
Mean river width (m)	Turbidity (NTU)
Average annual rainfall (mm)	NH ₃ (mg/L)
Bedrock (% substrate that is bedrock)	NO ₃ /NO ₂ (mg/L)
Boulders (% substrate that is boulders; >256 mm)	Total N (mg/L)
Cobbles (% substrate that is cobbles; 64–256 mm)	Soluble reactive P (mg/L)
Pebbles (% substrate that is pebbles; 16–64 mm)	Total P (mg/L)
Gravel (% substrate that is gravel; 4–16 mm)	
Sand (% substrate that is sand; 1–4 mm)	
Silt (% substrate that is silt; <1 mm)	
Clay (% substrate that is clay)	
Habitat area (% component of reach)	
Mineral substrate (% surface area of habitat)	
Emergent macrophyte cover (% surface area of habitat)	
Emergent macrophyte density (1 → 5; 1 = sparse, 5 = dense)	
Submerged macrophyte cover (% surface area of habitat)	
Submerged macrophyte density (1 → 5; 1 = sparse, 5 = dense)	
Floating macrophyte cover (% surface area of habitat)	
Floating macrophyte density (1 → 5; 1 = sparse, 5 = dense)	
Algae cover (% surface area of habitat)	
Algae density (1 → 5; 1 = sparse, 5 = dense)	
Detritus cover (% surface area of habitat)	
Detritus density (1 → 5; 1 = sparse, 5 = dense)	
Riparian vegetation in water (% surface area of habitat)	
Maximum flow of area sampled (cm/s)	
Minimum flow of area sampled (cm/s)	

^a Dissolved oxygen measurements were taken at the top and bottom of the water column in the area sampled

from different habitats when making comparisons between sites (Chessman 1995, Humphries et al. 1996). Riffle and macrophyte habitats were rarely encountered in the agricultural zone.

Samples were emptied into a bucket of water where sand and gravel were removed by elutriation. Water containing the organic fraction was poured through a stack of 3 sieves (2-mm, 500- μ m, and 250- μ m mesh). The sieves were then clamped together and agitated in the water column to separate the remainder of the sample into different size fractions. Each fraction was emptied into a separate sorting tray. If a fraction contained a large amount of organic material, aliquots were placed in additional trays. Macroinvertebrates were picked live from the trays by 2 operators for 30 min

each (1 person-h), using pipettes and forceps, and then preserved in 70% alcohol. Time allocated to each tray was proportional to the amount of organic matter it contained. Animals were picked out with the aim of maximizing the number of families collected (Chessman 1995) rather than the number of individual animals. Animals were mostly identified to family using the keys listed by Hawking (1994), although a few were identified to higher taxonomic categories; Chironomidae were identified to subfamily. Qualitative abundance data for each taxon was estimated for the whole sample at the conclusion of picking using the following categories: 1 (1–10 animals), 2 (11–100), and 3 (>100). The method was aimed at collecting all taxa present in a sample

with a qualitative estimate of abundance for each taxon. All taxa are hereafter referred to as families.

Classification

Sites were classified using 8 of the water chemistry variables listed in Table 1 to identify patterns in water chemistry across the study area. Cluster analyses were performed using the PATN analysis package (L. Belbin, 1993. PATN: pattern analysis package, version 3.6, CSIRO, Canberra). Dissimilarities between sites were calculated using the Bray–Curtis algorithm. An agglomerative hierarchical fusion technique (unweighted pair-group method using arithmetic averages, UPGMA) was used and space distortion was controlled using a β value of -0.1 (PATN). Temperature was omitted because it varied with time of day, all sites were located in the same broad climatic region, and sampling was conducted over a period of 3 mo. Total N (TN) and total P (TP) were used as measures of nutrient status; other forms of N and P were excluded because they were correlated with the total measures and inclusion of several nutrient variables would bias the classification. Two DO measures were taken at each site and averaged for the classification. Values were range standardized from 0 to 1 so that variables with large values would not bias the analysis. The resulting dendrogram was well-structured, and water chemistry groups (WCs) were assigned by applying a uniform cut-level to the dendrogram.

Sites were also classified using macroinvertebrate families and qualitative abundance data for each family to identify patterns in macroinvertebrate community composition among sites. Families collected from only 1 site were not used in the classification (PATN). The resulting data set consisted of 176 sites and 70 families. A total of 29,164 invertebrates were processed for this data set with a mean of 166 ± 6 (± 1 SE) invertebrates collected per sample.

In a 3rd classification, families were classified by site to examine which families tended to occur together. The Two-Step association option was used in this classification because it is considered more robust when classifying taxa by site (Belbin 1991). Invertebrate community groups (ICs) and family groups (FGs) were assigned by comparing the structure of the dendrograms with a 2-way contingency table of

sites versus families before deciding on the cut-level.

Group and family profiles

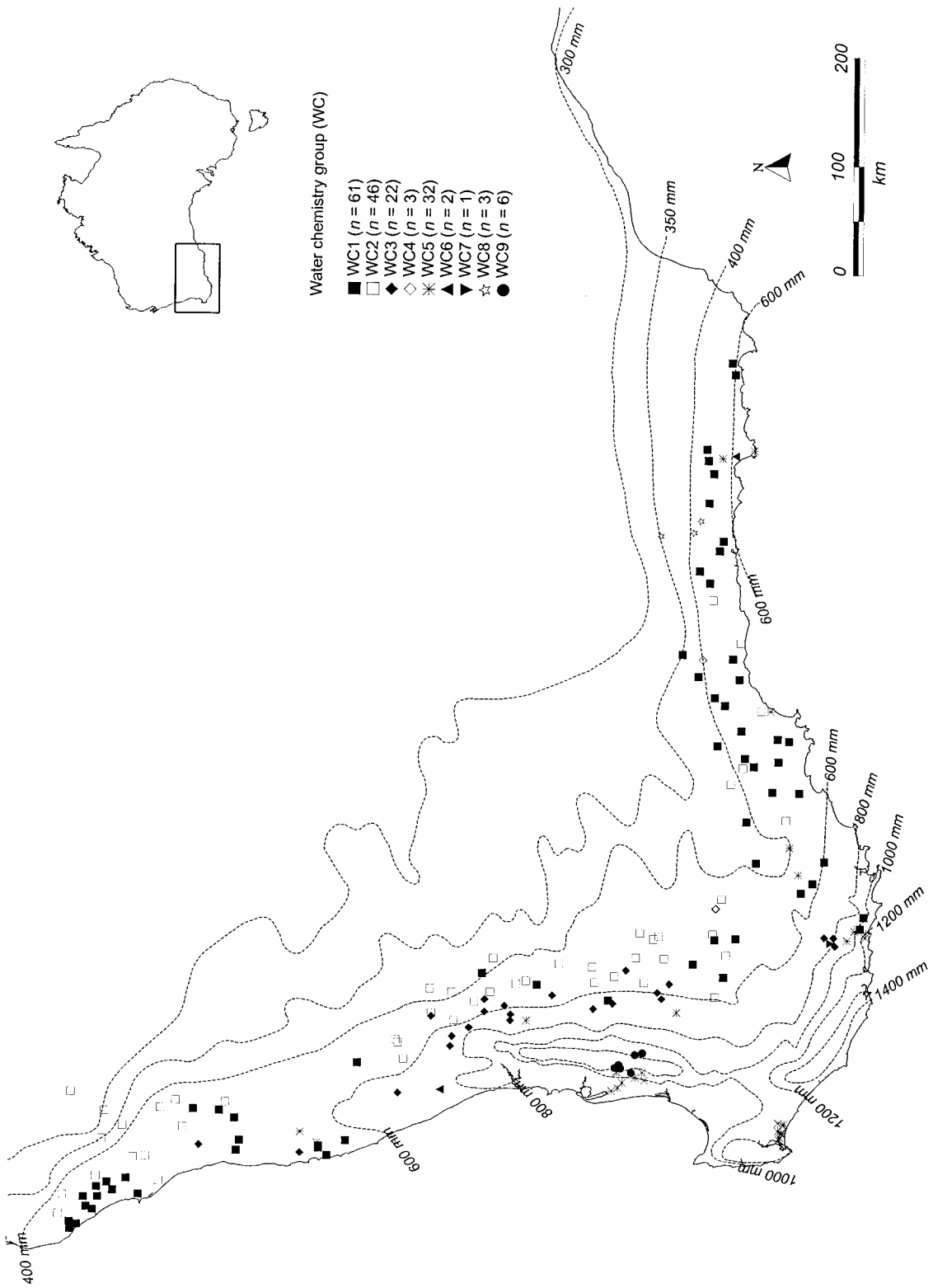
We examined 8 of the water chemistry variables by 1-way analysis of variance (ANOVA) to create profiles of WCs. The aim of this analysis was not to test for differences between the defined groups, but to define the characteristics of each group, and to identify those differences between the groups that were real. Data used in ANOVAs were tested for normality and homoscedasticity, and were log-transformed if necessary (Fry 1994). Values with studentized residuals >4 were regarded as highly atypical and excluded from analyses (Fry 1994). A Bonferroni correction was applied to the significance level to compensate for performing multiple comparisons (Fry 1994). Pairwise comparisons to determine which means were significantly different were done with Fisher's Least Significant Difference test. Univariate statistics were calculated for the 30 families most-frequently collected to examine the range of water-quality conditions over which they occurred. ANOVAs were done using PROC GLM, and univariate statistics were calculated using PROC UNIVARIATE from the SAS statistical package (release 6.12, SAS Institute Inc., Cary, North Carolina).

Relationships between environmental variables and ICs were examined with a Kruskal–Wallis test using the NPAR1WAY procedure in SAS. A nonparametric method was chosen to avoid making assumptions concerning normality and homogeneity of variance for the response variables (Siegel 1956). All variables listed in Table 1 were used in this ANOVA, and a Bonferroni correction was applied to the significance level.

Results

Water chemistry

Five large and 4 small groups of sites were identified by cluster analysis based on water chemistry variables (Fig. 2). Most sites in the wheat- and wool-growing areas grouped in WC1 or WC2. Both were saline (WC1: 17.9 ± 3.4 [mean ± 1 SE] mS/cm; WC2: 22.3 ± 2.2 mS/cm) and alkaline (WC1: 141 ± 11 mg/L CaCO_3 ; WC2: 184 ± 9 mg/L CaCO_3). WC1 sites usually



had more color (116 ± 8 TCU) than WC2 (38 ± 3 TCU). Most sites in both groups were located in areas where average annual rainfall was <600 mm (Fig. 2). Sites in WC3 were brackish (8.4 ± 0.7 mS/cm), colorless (15 ± 2 TCU), and had low alkalinity (64 ± 10 mg/L CaCO_3). Most WC3 sites were located in areas where average annual rainfall was 600–800 mm. Groups WC5 and WC9 were both fresh (1.1 ± 0.3 mS/cm and 0.2 ± 0.02 mS/cm, respectively), and were located in areas where average annual rainfall was >800 mm. Sites in the remaining groups tended to be atypical of regional conditions. WC4 consisted of 2 sites located downstream of sewage treatment plants and 1 site downstream of a stock saleyard. This group was characterized by high alkalinity (253 ± 7 mg/L CaCO_3), high nutrient levels (TN: 14.6 ± 6.8 mg/L; TP: 5.43 ± 2.05 mg/L), and low average DO ($7 \pm 7\%$ saturation). Sites in WC6 were fresh (2.4 ± 1.2 mS/cm), heavily colored (450 ± 50 TCU), and had elevated nutrient levels (TN: 3.2 ± 0.6 mg/L; TP: 0.20 ± 0.04 mg/L). WC7 consisted of a single site that was fresh (4.6 mS/cm) and turbid (66 NTU). Sites in WC8 were located in the southeastern part of the study area and were acidic (pH: 5.3 ± 0.6) and saline (56.2 ± 13.9 mS/cm). Rainfall significantly influenced surface-water characteristics in the study area (Figs 2, 3), especially salinity ($r = -0.41$; $p < 0.0001$).

Invertebrates

Eighty-one families were collected during the study. The fauna was dominated by insects, which accounted for 64% of families collected, followed by crustaceans (14%). The dominant insect orders were flies (31% of insect families) and beetles (21% of insect families). Eight groups of families that tended to co-occur were identified by cluster analysis (Appendix). FG4 formed a core group of families that was present at most sites (Table 2). However, only 12% of families were collected from $>1/2$ of the sites, and 13% of families were collected from 1 site only. Almost 60% of families were collected

from $<10\%$ of sites, indicating that the occurrence of families was irregular.

Families in FG4 were found across a broad range of environmental conditions (Table 3). They were salt-tolerant, nutrient-tolerant, and were collected at some sites when conditions were anoxic (Table 3). Dipteran families dominated FG5, which also tolerated high salinities, elevated nutrients, and low DO. Families in FG1 and FG3 tended to occur across a narrower range of environmental conditions, although some families within these groups tolerated a broad range of conditions. FG1 contained families that tended to occur at sites with lower TN, alkalinity, and salinity than the other FGs (Table 3). FG2, FG6, FG7, and FG8 contained families that were rarely collected. In summary, the commonly collected families tolerated a broad range of environmental conditions, especially salinity (Table 3).

Seven groups of sites were identified by cluster analysis based on their macroinvertebrate communities (Fig. 4). IC1 contained most of the sites in the wheat- and wool-growing regions, and members were widespread across the study area (Fig. 4). Low occurrences of families in FG1, FG2, and FG3, and patchy occurrences of families in FG5 characterized IC1 (Table 2). IC2 sites were predominantly located in the southeastern region of the study area and had a similar, but more depauperate, macroinvertebrate assemblage than IC1. The absence of the odonate families Corduliidae and Coenagrionidae and the hemipteran families Corixidae and Notonectidae from FG4 characterized IC2. IC3 was similar to IC1 and IC2 but was characterized by higher occurrences of families in FG1 and FG6 (Table 2). Sites in IC4 and IC5 had richer faunas than the other groups. IC4 sites were characterized by families in FG1 and were mostly located in areas that had intact native vegetation. IC5 was characterized by high occurrences of families in FG3. The 2 remaining groups (IC6 and IC7) contained only single sites that were depauperate and atypical.

There were significant differences in family

FIG. 2. Distribution of water chemistry groups identified by cluster analysis using 8 water chemistry variables measured from 176 river/stream sites in southwestern Australia during spring 1997. Average annual rainfall isohyets for the study area are included.

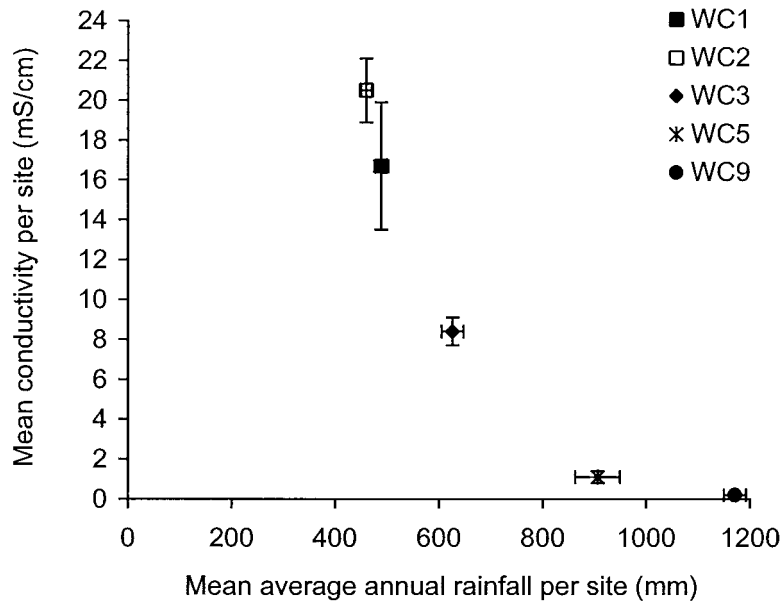


FIG. 3. Relationship between average annual rainfall and conductivity for the 5 major water chemistry groups (WCs) identified by cluster analysis. Values are means \pm 1 SE. Error bars for low SEs are sometimes obscured by symbols.

richness between ICs ($F = 26.91$; $p < 0.0001$). IC4 (16.8 ± 0.7 [mean \pm 1 SE] families) and IC5 (18.2 ± 0.9) were significantly different from IC1 (12.6 ± 0.3), IC2 (9.8 ± 0.5), and IC3 (11.3

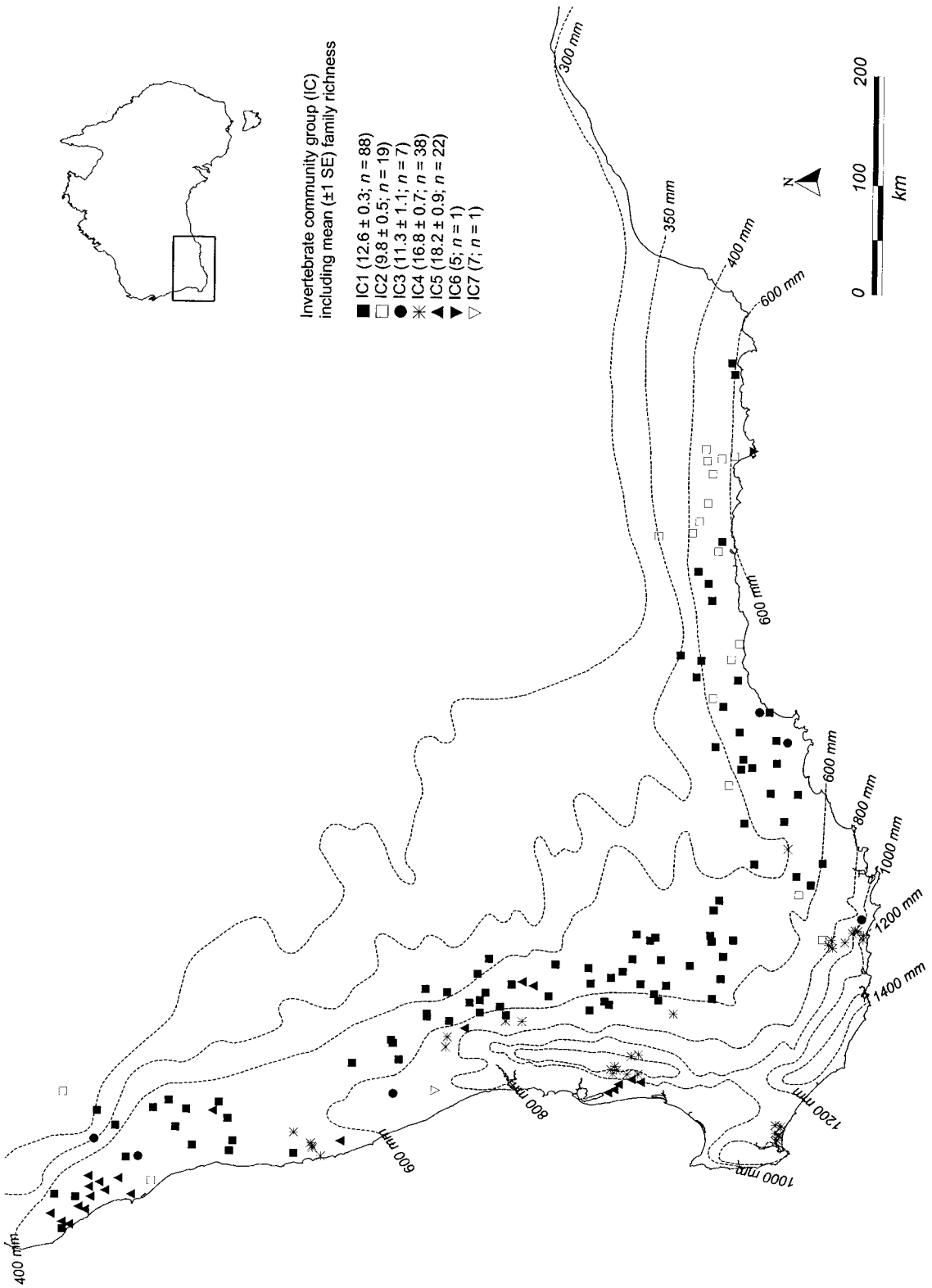
± 1.1). IC6 (5 families) and IC7 (7 families) were excluded from the ANOVA because they contained only single sites. Family richness tended to be higher in the higher rainfall, southwestern

TABLE 2. Simplified 2-way contingency table of sites versus families with cluster groups assigned. A value of 1.00 would result if all families in a family group (FG) occurred at all sites in an invertebrate community group (IC). Shading has been added to aid visual inspection and is weighted proportional to the constancy value.

IC	FG							
	1 (n = 14)	2 (n = 5)	3 (n = 6)	4 (n = 14)	5 (n = 16)	6 (n = 6)	7 (n = 7)	8 (n = 2)
1 (n = 88)	0.05	0.02	0.11	0.64	0.13	<0.01	0.02	0.00
2 (n = 19)	0.03	0.02	0.07	0.41	0.16	0.02	0.07	0.00
3 (n = 7)	0.15	0.00	0.10	0.49	0.03	0.14	0.02	0.00
4 (n = 38)	0.33	0.05	0.25	0.62	0.07	0.04	<0.01	0.09
5 (n = 22)	0.09	0.25	0.71	0.71	0.07	0.02	0.03	0.00
6 (n = 1)	0.00	0.00	0.17	0.07	0.19	0.00	0.00	0.00
7 (n = 1)	0.07	0.20	0.00	0.21	0.06	0.17	0.00	0.00

TABLE 3. Ranges of 8 selected water chemistry variables for the 30 most common aquatic macroinvertebrate families collected in southwestern Australia during spring 1997. Limits of detection for color, total N and total P were 5 TCU, 0.02 mg/L, and 0.01 mg/L, respectively. DO = dissolved oxygen.

Family group	Families	n	pH	Conductivity (mS/cm)	Color (TCU)	Alka- limity (mg/L CaCO ₃)	Turbidity (NTU)	Total N (mg/L)	Total P (mg/L)	Avg. DO (% satur- ation)
1	Aeshnidae	32	5.9-9.3	0.2-30.2	<5-230	8-290	1-66	0.05-1.70	<0.01-0.13	20-180
	Palaemonidae	39	6.1-8.8	0.2-34.1	8-190	13-350	1-22	0.16-1.70	<0.01-0.20	28-174
	Parastacidae	43	5.9-8.8	0.1-29.2	<5-500	10-280	1-66	0.08-3.90	<0.01-0.36	20-146
	Perithidae	26	5.4-9.0	0.2-7.6	<5-210	8-120	2-66	0.05-1.10	<0.01-0.13	20-132
	Scirtidae	28	5.9-12.9	0.1-36.7	<5-400	10-230	1-66	0.08-2.60	<0.01-0.25	20-148
	Baetidae	20	6.9-8.7	0.2-19.6	<5-120	8-300	2-32	0.5-2.60	<0.01-0.37	84-132
	Caenidae	46	6.4-9.0	0.1-18.6	<5-320	10-300	1-32	0.10-2.60	<0.01-0.37	31-142
	Gyrinidae	26	6.4-9.0	0.3-18.6	<5-120	20-280	1-32	0.30-2.60	<0.01-0.37	66-142
3	Libellulidae	30	6.4-9.3	0.4-30.2	<5-320	18-290	1-30	0.31-17.0	<0.01-9.00	20-279
	Simuliidae	55	5.9-12.9	0.2-14.8	<5-400	8-290	1-32	0.5-2.60	<0.01-0.37	42-180
	Tipulidae	43	5.4-12.9	0.2-192.0	<5-400	8-290	1-290	0.08-2.60	<0.01-0.25	62-180
	Acarina	93	4.6-12.9	0.1-33.6	<5-500	3-490	1-120	0.05-25.0	<0.01-5.40	0-236
	Ceimidae	115	4.9-12.9	0.1-69.1	<5-400	8-490	1-42	0.25-25.0	<0.01-5.40	0-279
	Ceratopogonidae	143	4.6-12.9	0.1-192.0	<5-400	3-490	1-290	0.08-25.0	<0.01-9.00	0-279
	Chironominae	166	4.6-12.9	0.1-192.0	<5-400	3-490	1-290	0.05-25.0	<0.01-9.00	0-279
	Coenagrionidae	36	6.7-9.3	0.2-30.2	<5-190	10-300	1-22	0.09-25.0	<0.01-5.40	0-236
4	Corduliidae	83	5.3-12.9	0.1-33.6	<5-320	8-300	1-66	0.05-17.0	<0.01-9.00	0-279
	Corixidae	56	6.1-12.9	0.2-23.1	<5-230	10-290	2-32	0.10-17.0	<0.01-9.00	4-279
	Dytiscidae	163	4.9-12.9	0.1-192.0	<5-500	8-490	1-120	0.05-25.0	<0.10-9.00	0-279
	Hydrophilidae	107	6.1-12.9	0.1-192.0	<5-320	10-320	1-120	0.09-25.0	<0.01-5.40	0-279
	Leptoceridae	117	4.9-12.9	0.1-69.1	<5-320	8-490	1-120	0.05-25.0	<0.01-9.00	0-180
	Notonectidae	41	5.3-9.3	0.1-26.9	<5-230	13-290	2-23	0.38-17.0	<0.01-9.00	4-279
	Oligochaeta	117	5.4-12.9	0.1-69.1	<5-400	8-490	1-290	0.05-25.0	<0.01-9.00	0-236
	Orthocladinae	115	4.6-12.9	0.1-74.4	<5-500	3-490	1-290	0.05-25.0	<0.01-5.40	0-250
	Tanytopinae	141	5.3-12.9	0.1-192.0	<5-400	8-490	1-290	0.05-25.0	<0.01-9.00	0-279
	Culicidae	56	4.6-9.3	0.1-192.0	<5-500	3-370	1-290	0.10-17.0	<0.01-9.00	4-279
	Dolichopodidae	21	4.6-9.1	1.1-192.0	<5-300	3-490	1-42	0.38-2.00	<0.01-0.18	4-167
	Ephydriidae	39	4.6-9.3	0.6-69.1	<5-300	3-370	1-290	0.25-25.0	<0.10-5.40	0-279
5	Hydraenidae	24	5.3-9.0	0.4-192.0	<5-180	13-260	1-66	0.29-1.90	<0.01-0.11	20-279
	Lestidae	33	5.3-9.3	3.4-36.7	5-230	13-300	1-66	0.31-25.0	<0.01-5.40	0-279



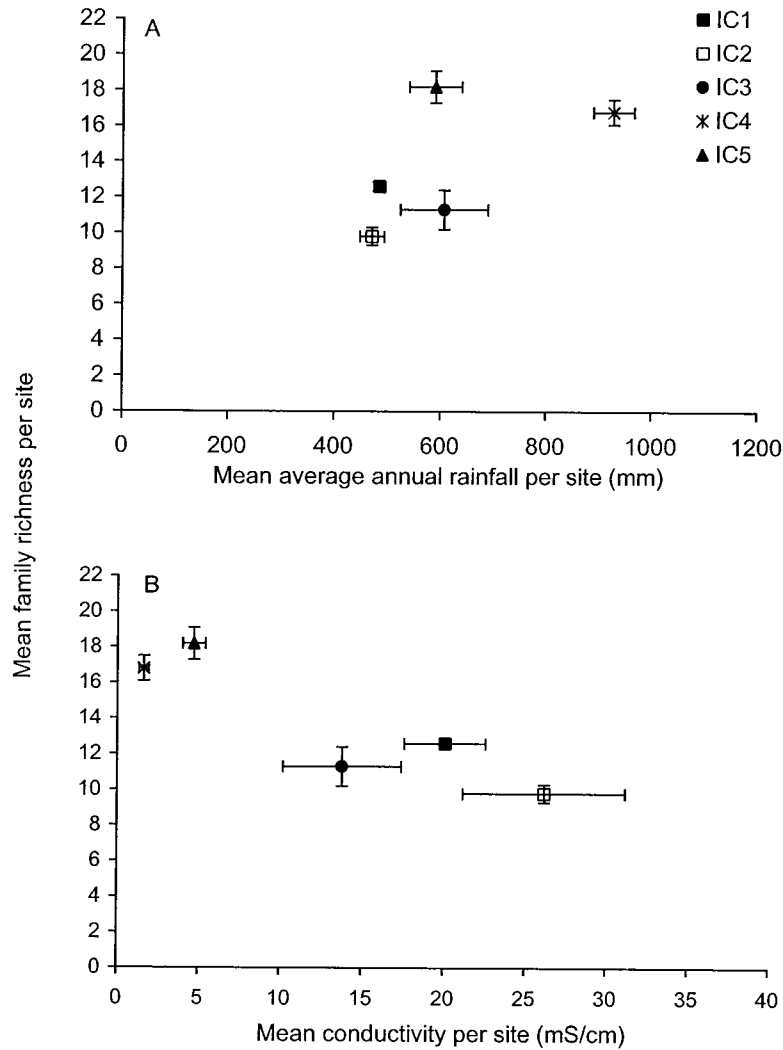


FIG. 5. Relationships between (A) rainfall and family richness, and (B) conductivity and family richness for the major invertebrate community groups (IC) identified by cluster analysis. Values are means ± 1 SE. Error bars for low SEs are sometimes obscured by symbols.

corner of the study area where land clearing was not as extensive as in the wheat- and wool-growing areas (Fig. 4). There was a general tendency for family richness to increase with rainfall (Fig. 5A; $r = 0.48$, $p < 0.0001$) and decrease

with increasing salinity (Fig. 5B; $r = -0.38$, $p < 0.0001$).

Twelve environmental variables were identified as significantly different among ICs (Table 4). One was a climatic descriptor, 3 were geo-

FIG. 4. Distribution of invertebrate community groups identified by cluster analysis using qualitative abundance data for 70 macroinvertebrate families collected in southwestern Australia during spring 1997. Average annual rainfall isohyets for the study area are included.

TABLE 4. Mean (± 1 SE) values for each invertebrate community group (IC) of the 12 most significant ($p < 0.0001$) environmental variables distinguishing the groups identified with a Kruskal–Wallis test. IC6 and IC7 were excluded from the ANOVA because they only contained a single site. The significance threshold was set at 0.001 ($\alpha = 0.05/44$ comparisons) after applying a Bonferroni correction to compensate for multiple comparisons. DO = dissolved oxygen.

Environmental variable	IC			
	1 ($n = 88$)	2 ($n = 19$)	3 ($n = 7$)	4 ($n = 38$)
Avg. annual rainfall (mm)	484 \pm 8	471 \pm 23	607 \pm 83	928 \pm 39
Latitude	32.32 \pm 0.20	33.22 \pm 0.38	32.37 \pm 1.09	33.30 \pm 0.25
Longitude	117.37 \pm 0.19	119.95 \pm 0.53	117.11 \pm 0.70	116.20 \pm 0.14
Altitude (m)	198 \pm 9	141 \pm 21	61 \pm 25	95 \pm 14
pH	8.1 \pm 0.1	7.4 \pm 0.3	7.7 \pm 0.3	7.0 \pm 0.1
Conductivity (mS/cm)	20.1 \pm 2.5	26.2 \pm 5.0	13.8 \pm 3.6	1.6 \pm 0.3
Surface DO (% saturation)	114 \pm 5	92 \pm 8	82 \pm 10	82 \pm 4
Bottom DO (% saturation)	110 \pm 6	93 \pm 8	75 \pm 15	79 \pm 5
Alkalinity (mg/L CaCO ₃)	148 \pm 9	113 \pm 20	134 \pm 34	36 \pm 5
Total N (mg/L)	1.39 \pm 0.33	1.35 \pm 0.14	0.91 \pm 0.16	0.63 \pm 0.06
Mineral substrate (% cover)	68 \pm 2	72 \pm 6	41 \pm 11	53 \pm 3
Detritus (% cover)	15 \pm 2	14 \pm 4	41 \pm 11	30 \pm 3

graphical descriptors, 6 were water-chemistry variables, and 2 were substrate variables.

Discussion

The wheat- and wool-growing region of Western Australia is an extensively modified landscape of which only 10% of the 20 million ha remains as remnant native vegetation, much of which is degraded (George et al. 1995). Processes associated with agricultural development appear to have resulted in a simplified aquatic ecosystem that has a homogeneous and depauperate macroinvertebrate community consisting of families that tolerate a broad range of environmental conditions (Table 3). Similar effects have been found in other studies of aquatic invertebrate communities in agricultural landscapes (Delong and Brusven 1998). Intensive agricultural land use is known to reduce the richness of stream invertebrates (Dance and Hynes 1980). Southwestern Australia is considered to have a naturally impoverished aquatic macroinvertebrate fauna (Bunn and Davies 1990), but the low family richness observed at IC1, IC2, and IC3 sites during our study appears to be partly attributable to agriculture. The disappearance of some sensitive species from rivers in the agricultural zone has been documented by Kendrick (1976).

Seasonality and biomonitoring

Southwestern Australia has a strongly seasonal climate with most rain falling in winter. The aquatic biota of the region has always had to cope with natural declines in water quality as salt, nutrients, and other pollutants, whether natural or anthropogenic, evapoconcentrated during the dry season. As a result, many families have adapted to tolerate a broad range of environmental conditions (Table 3). Consequently, family-level biotic indices that are widely used in biological assessment protocols elsewhere (Plafkin et al. 1989, Resh and Jackson 1993, Chessman 1995) may be insensitive in southwestern Australia. Indices are probably more sensitive at the species level but further investigation of species-level tolerances is required. However, it is unlikely that there will be sufficient information on the biota of this region to construct species-level indices in the short term.

Salinity tolerances

Salinity tolerances of the families collected during our study are generally higher than have been found in other studies of lotic waters. For example, mayflies and caddisflies are usually regarded as sensitive taxa that are restricted to well-oxygenated, fast-flowing rivers and streams and not commonly found in waters

TABLE 4. Extended.

IC		
5 (n = 22)	6 (n = 1)	7 (n = 1)
590 ± 50	600	750
30.07 ± 0.43	34.00	31.35
115.24 ± 0.17	122.16	115.74
100 ± 15	10	47
8.2 ± 0.1	7.1	6.3
4.7 ± 0.7	0.6	3.6
110 ± 4	93	39
107 ± 4	93	40
133 ± 17	18	38
1.18 ± 0.11	0.38	3.90
71 ± 5	70	0
9 ± 1	10	100

where salinities exceed 1000 mg/L (\cong 2 mS/cm) (Hart et al. 1991). We collected caenid and baetid mayflies at salinities of 18.6 and 19.6 mS/cm, respectively, and leptocerid caddisflies at salinities up to 69.1 mS/cm. The common families collected in our study typically occurred at salinities ranging from 0.1 to 30 mS/cm, with some families being collected at salinities up to 192.0 mS/cm (Table 3). These values are comparable with maximum tolerances for species within the same families that inhabit salt lakes (Hammer 1986).

Discharge of salt from groundwater into playa lakes and river systems has been occurring in southwestern Australia for hundreds of thousands of years (Salama et al. 1992, Salama 1997). Consequently, the region contains large numbers of lentic species such as brine shrimp adapted to hypersaline conditions (De Deckker 1983). Presumably, similar evolutionary processes have occurred among lotic species, although the processes are not well documented. Secondary salinization has occurred very rapidly (Wood 1924, Kendrick 1976, Schofield et al. 1988), and the wide salinity tolerances observed in our study must reflect pre-existing tolerances for much of the biota.

Environmental factors

Although salinity is important, other factors also influence the aquatic macroinvertebrate bi-

ota in the region (Table 4). Rainfall can influence the aquatic biota in 2 major ways: 1) by regulating water quality through dilution and flushing, and 2) by determining the quantity and persistence of surface water in a particular locality. The characteristics of surface waters in the study area are principally determined by local rainfall (Fig. 3). A confounding factor in southwestern Australia is that rainfall has largely determined patterns of land use and also the level of secondary salinization in streams (Schofield et al. 1988). Most sites in higher rainfall areas (IC4) had similar macroinvertebrate communities even though surrounding land use ranged from agriculture to conservation, probably because of similar surface water characteristics, especially low salinity. Family richness tended to increase with rainfall and decrease with increasing salinity (Figs 4, 5). Similar patterns have been observed in northwestern Australia where family richness increased as rainfall increased and became more predictable (Kay et al. 1999). Similarly, De Deckker (1983) concluded that species richness was greater in areas with high rainfall that had a consistent pattern.

IC5 sites were an exception to the general trends shown in Fig. 5. Even though these sites were located in low-rainfall, agricultural areas they were still comparatively fresh (4.7 ± 0.7 mS/cm). The high family richness was probably attributable to low salinity in conjunction with slightly elevated nutrient levels (IC5: TN = 1.18 ± 0.11 mg/L cf. IC4: TN = 0.63 ± 0.06 mg/L).

A number of other environmental variables also influenced the ICs (Table 4). In Fig. 6, we summarize how these variables interrelate with one another and the biota. Geographic descriptors such as latitude and longitude are surrogates for other factors such as land use and/or climate because the biota is unlikely to be responding to location. Environmental variables in Fig. 6 have only been associated with the links that are considered to be most influential. For example, conductivity (\approx salinity) is a component of the link between geology and water chemistry, but because large-scale clearing has mobilized salt stored in the soil, which has subsequently impacted the waterways, we consider it to be a more important component of the link between land use and water chemistry than geology and water chemistry.

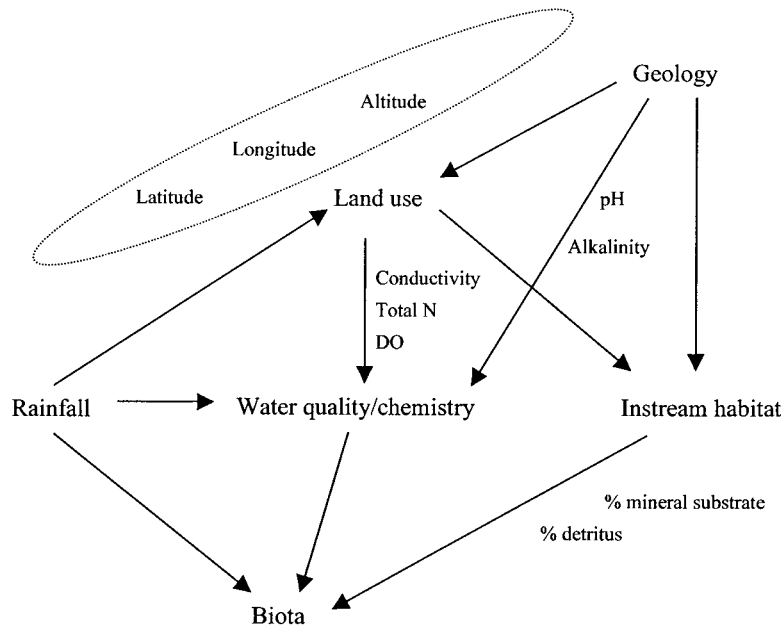


FIG. 6. Environmental variables influencing the distribution of aquatic macroinvertebrate families and the structure of macroinvertebrate communities in the agricultural zone of southwestern Australia. DO = dissolved oxygen.

Macroinvertebrate distributions and colonization

Most families collected in our study occurred throughout the study area, indicating there are no major physical barriers to dispersal. Macro- and mesoscale habitat preferences are unlikely to be influencing family distributions in the wheat- and wool-growing region given the homogeneous landscape, the broad environmental tolerances of many families (Table 3), and the fact that water chemistry of the rivers is fairly uniform (Fig. 2). Despite their wide distribution, however, the occurrence of most families was irregular (Table 2). Sampling error and/or the dispersal characteristics of the biota provide 2 possible explanations for the patchiness. Ten-metre sweeps only collect ~75% of the families present at a site (Kay et al. 1999), but similar patchiness has been found in other studies in Western Australia where a larger sampling effort has been used (Halse et al. 2000) or a number of samples have been combined (Kay et al. 1999).

Boulton (1989) described a number of different strategies used by aquatic invertebrates for surviving drought, and concluded that the dif-

ferential survival of fauna in various refuges undoubtedly influenced the community composition of streams, and had a profound effect on ecological succession during the ensuing period of flow. We propose the irregular occurrence of families in the study area relates to the seasonal nature of the aquatic habitats. Migration rates of arthropods are correlated with the type of habitat they occupy, with species occupying temporary habitats having higher rates of migration than species occupying permanent habitats (Brown 1951, Southwood 1962). Many of the streams in the study area dry seasonally because of the strongly seasonal pattern of rainfall and, thus, provide only temporary habitats. The irregular occurrences of some families would be the result of opportunistic colonization by highly migratory species when water is available. Permanent habitats such as perennial river pools or lentic wetlands would act as refugia from which migratory species could disperse and colonize temporary habitats. Consequently, permanent habitats in the study area are perhaps more significant than temporary habitats from a conservation perspective.

Acknowledgments

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APPENDIX. Macroinvertebrate taxa collected in southwestern Australia during spring 1997 with family group assignments as determined by cluster analysis.

Family group	Families	Family group	Families
1	Aeshnidae Empididae Gomphidae Gripopterygidae Hydroptilidae Hyriidae Leptophlebiidae Megapodagrionidae Palaemonidae Parastacidae Perthiidae Planorbidae Scirtidae Veliidae	5	Carabidae Culicidae Dolichopodidae Ephydriidae Haliplidae Hydraenidae Lestidae Muscidae Nematoda Oniscidae Paramelitidae Phreatoicidae Pomatiopsidae Staphylinidae Stratiomyidae Tabanidae
2	Ecnomidae Hydropsychidae Lymnaeidae Mesoveliidae Physidae	6	Ancylidae Psychodidae Richardsonianidae Sphaeromatidae Syrphidae Thiaridae
3	Baetidae Caenidae Gyrinidae Libellulidae Simuliidae Tipulidae	7	Branchipodidae Brentidae Curculionidae Dugesiidae Hebridae Pyalidae Sciomyzidae
4	Acarina Ceinidae Ceratopogonidae Chironominae ^a Coenagrionidae Corduliidae Corixidae Dytiscidae Hydrophilidae Leptoceridae Notonectidae Oligochaeta Orthocladiinae ^a Tanypodinae ^a	8 Single taxa ^b	Hydrobiosidae Temnocephalidea Atriplectidae Corbiculidae Gelastocoridae Gordiidae Heteroceridae Hydrobiidae Hydrometridae Hymenosomatidae Janiridae Neoniphargidae Sphaeriidae

^a Chironomid subfamily

^b Single taxa do not have a family group assignment because they were excluded from analysis