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From the mountains to the sea: assemblage structure and dynamics in Chironomidae (Insecta: Diptera) in the Clyde River estuarine gradient, New South Wales, south-eastern Australia

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Abstract Chironomidae (Insecta: Diptera: non-biting midges) were surveyed at five shallow riffle stations along the estuarine gradient of the Clyde River, southern New South Wales (35°45′S, 150°15′E). Benthic populations were sampled seasonally between April 2001 and January 2002, between an uppermost fully fresh station and 7 km south of the tidal limit at Shallow Crossing, encompassing a 23 km stretch. Biological structure and integrity of chironomid assemblages, which are essentially unknown in eastern Australia's estuarine environments, were elucidated. Assemblages were diverse: from 5732 chironomid larvae, 45 species belonging to four subfamilies were identified from riffles. All chironomid assemblages were strongly structured and non-random with respect to spatial position along the salinity gradient although relatively random with respect to temporal shifts between the five seasonal samples. Generally, the salinity gradient had strong effects on assemblage composition but no discrete brackish fauna was identifiable, and the abundance of many species declined gradually with distance from the freshest station. Dominant taxa in the brackish zone were *Parakiefferiella* '*variegatus*' and two species of *Cladotanytarsus*. Notably, the little-known *Semiocladius crassipennis* Skuse (Orthocladiinae) was abundant at the most marine-influenced station. Taxa present exclusively in freshwaters included several Tanypodinae notably absent from sites below Shallow Crossing at salinities normally tolerated in athalassic waters. Other species restricted to freshwaters included *Nanocladius* sp., *Demicryptochironomus (Irmakia)* sp., *Polypedilum vespertinus* (Skuse), *Zavrelliella fuscoguttata* (Kieffer), *Riethia stictoptera* (Kieffer) and *Podonomopsis* sp.

Key words Australia, Chironomidae, estuary, gradient, immature.

INTRODUCTION

Immature stages of Chironomidae (Diptera) are encountered in all freshwater aquatic systems and can be treated at refined taxonomic levels, especially for inventory and monitoring purposes (e.g. Johnson 1989; Rosenberg 1993). Furthermore, chironomids are among the few aquatic insects that span the length of estuarine gradients from fully fresh to marine conditions (Williams & Hamm 2002). The vast majority of ecological studies concern chironomid dominance in running (lotic) systems and freshwater (oligohaline) lakes. Larval Chironomidae undoubtedly are limited in saline athalassic waters (Kefford *et al*. 2003) and in marine environments. Ecological studies on some few mesohaline chironomid species exist (Palmén & Lindeberg 1959; Parma & Krebs 1977; Kokkin 1986) and there has been taxonomic interest in the 'marine', but probably essentially intertidal (Colbo 1996) taxa such as the subfamily Telmatogetoninae and *Clunio* and relatives (e.g. Hashimoto 1976). Common inhabitants of inland saline waters include species of *Chironomus*, *Cricotopus* and *Tanytarsus* species that tolerate pollution, extremely low oxygen levels, and high nutrient levels (Armitage *et al*. 1995; Bervoets *et al*. 1996). The estuarine salinity gradient balance also may affect bioaccumulation of heavy metals and transport of pathogens by sediment-dwelling invertebrates such as larval Chironomidae that are important components of fish and bird diets (Batzer & Wissinger 1996; Bendell-Young 1999; Broza & Halpern 2001). Understanding the interplay between halobiont biotas and those of freshwaters is important for the management of aquatic resources such as oysters (Wilber 1992).

Quite how halobiont Chironomidae might expand their distribution into marine environments has been addressed for Western Australia, where, as salinities increase with summer drying-out, several 'freshwater' species tolerate increased salinity (Edward 1986). This allows rapid exploitation of similarly saline habitats and populations may reach plague proportions. Thus, many adaptations developed in athalassic waters

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apply also to thalassic waters, which is especially appropriate in an Australian context because many athalassic water bodies are dominated by sodium chloride and have similar ionic compositions to seawater (Paterson & Walker 1974; Halse *et al*. 1998; Williams 1998). This correlation may be less significant along the eastern coastline of Australia, because there are fewer athalassic water bodies compared with the west and more permanent freshwater flow regimes. In eastern environments, chironomid populations may not exhibit the salinity tolerance observed elsewhere in Australia, but such patterns have never been tested explicitly (Pinder 1995). We assess these ideas in a pristine estuary, the Clyde River (35°45′S, 150°15′E) before systems such as this succumb to pollution resulting from Australia's rapidly expanding population in coastal regions, estimated already at 85% of the total population (West *et al*. 1985; Kench 1999; Birch 2000). We assess these ideas in a pristine estuary, the Clyde River (35°45′S, 150°15′E). With an estimated 85% of Australia's rapidly expanding population living in coastal regions (West *et al*. 1985; Kench 1999; Birch 2000) such estuarian systems inevitably face an insecure future.

Australian Chironomidae can be incorporated into such studies because substantial taxonomic work (summarised: Cranston 2000b) allows identification of immature stages in both larval and pupal stages (e.g. Hardwick *et al*. 1995a). Globally, analyses of larval distributions correlate with environmental characteristics, with relative abundance distributions of species determined largely by climatic and physicochemical variables, particularly with salinity, temperature and oxygen (Rossaro 1991; Brooks & Birks 2001; Dimitriadis & Cranston 2001; Ruse 2002).

Considerable progress has been made regarding the understanding of chironomid diversity and assemblage structure in Australia's athalassic waters (Timms 1983, 1992, 1993) compared with the documentation of estuarine Chironomidae. Chironomid assemblages inhabiting fresh and saline inland waters clearly are delimited: the salinity dividing these macroinvertebrate faunas is considered widely to be 30 mg/L (Williams 1998). Given the ionic similarity between athalassic and thalassic Australian waters, the estuarine gradient provides an ideal test for a more precise definition of the division between fresh and fully saline/marine assemblages of Chironomidae. This information contributes to improving our knowledge of their ecology and the nature of rates of turnover and types of transitions between inland, coastal and marine habitats.

Our study at the Clyde River estuary in south-east New South Wales aimed to establish the identity of chironomid larval assemblages and their relationship with estuarine environmental attributes. We aimed also to assess whether a discrete brackish water chironomid fauna exists and to what extent ecologically equivalent species tend to replace one another at stations along the estuarine gradient. The assemblage structure and composition of the Clyde fauna with the Chironomidae of athalassic waters and estuaries along the west coast of Australia allows testing of the hypothesis that salinity tolerance develops in athalassic waters.

METHODS

Study area

The study was conducted at the Clyde River (35°42′S, 150°15′E) in south-eastern Australia. The Clyde catchment area totals 1791 km^2 with only 5% of vegetation cleared and a waterway area of around 20 km^2 (West *et al*. 1985; Roy *et al*. 2001). Riparian vegetation is characterised by pockets of temperate closed forest and tall open forest particularly in the uppermost reaches (Austin & Cocks 1978). From its sources in the Sassafras Tableland north of the Buddawang Range to the coast (~80 km), the Clyde maintains relatively high flow. Sampling stations (Fig. 1), labelled 1–5, were located ~40, 56, 58, 59.5, 63 km south of the source. Uppermost reaches comprise a narrow steep-sided valley cut into bedrock aligned approximately parallel with the coast through highly folded Early Ordovician geology (Brown 1931). After an eastward turn, the river broadens and slows towards the coastal town of Nelligen. Most of the Clyde's length can be divided into sections of deep pools mostly scoured to bedrock and with little accumulated sediment, extensive runs and short cobbled riffle zones. The climate is temperate with average mean daily temperatures reaching 25°C in February or 4°C in July and the highest maximum temperature recorded is 44.8°C and lowest minimum −3°C (Australian Bureau of Meteorology 2007). Local topography affects precipitation, particularly in winter when moisture-laden westerly winds prevail and deliver precipitates to the western slopes where orographic lift is between 600 and 1200 m. Mean annual precipitation is 1029 mm, with a range of 690–1660 mm and most falls in late summer and early autumn, although river discharge displays little seasonal variation and recurrent flooding throughout the year is a feature (Briggs *et al*. 1980). Maximum spring tidal range at the coast is 2.0 m and tides are semidiurnal (Roy *et al*. 2001). The tidal limit is slightly upstream of Shallow Crossing at station 2. The slope of the salinity gradient changes daily with tidal cycles and seasonally with some minor variation in freshwater inflow between winter and summer. Despite small seasonal differences, the Clyde is consistently mixed, with virtually no change in salinity between the surface and bottom waters. The transport of freshwaters seaward and of salt water landward is accomplished primarily by horizontal eddy diffusion and the net flow at all depths is seaward.

Sampling procedure and analyses

Larval chironomid was sampled and associated physicochemistry measured at five riffle stations (Fig. 1) along the estuarine gradient approximately every 2 months between April 2001 and January 2002. Zonation corresponded with a previous survey of salinity and sediment (Cotter 1996) such that station 1 matched the head of the river where freshwater enters the estuary above the tidal limit and maximum salt penetration at the highest tide does not exceed 5 mg/L NaCl. Station 2 corresponded with the upper reaches of the river where some

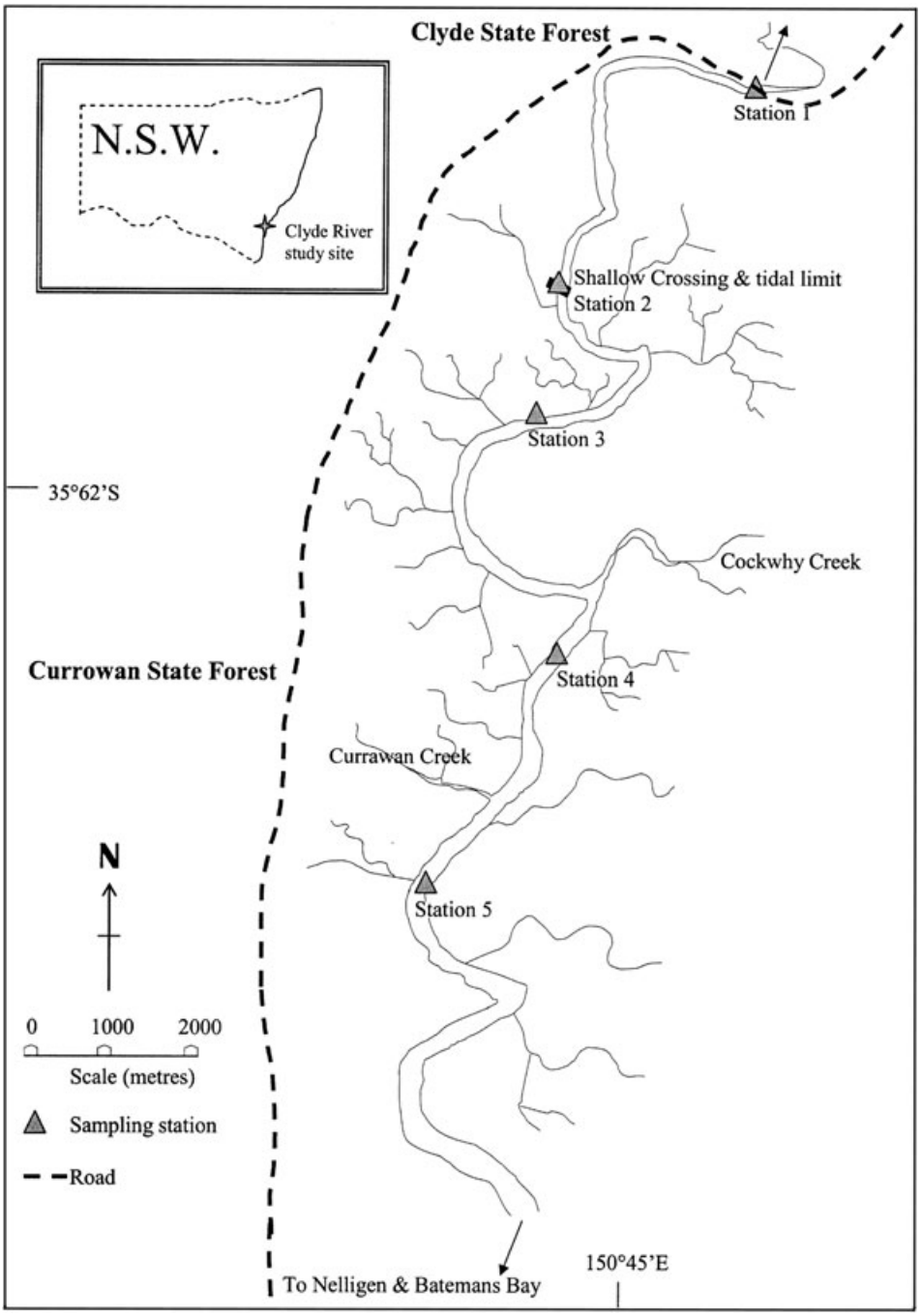

Fig. 1. Map of the Clyde River estuary showing location of sites. N.S.W., New South Wales.

mixing of fresh and saltwater occurs due to tidal influence, with salinities ranging between 5 and 18 mg/L NaCl. Stations 3 and 4 represented the middle reaches of the river with faster current speeds and salinities between 18 and 25 mg/L NaCl and station 5 represented the lower reaches of the river where salinities are between 25 and 35 mg/L NaCl. Rock washes and kick-sweep netting allowed comparison and assessment of sampling effects (Hardwick *et al*. 1995b; Bradley & Ormerod 2002). Rock washes recovered larvae from seven medium-sized cobbles with an average circumference of 40 cm using a 100 µm sieve. Kick sweeping, with a 500 µm mesh net, sampled larvae over the breadth and width of riffles for a set period of 5 min (Frost *et al*. 1971). Samples were placed in plastic containers or cliplock bags and transported live to the laboratory where they were refrigerated overnight before processing.

Chironomid larvae, pupae and exuviae were sorted and picked using fine forceps, grid-marked Petri dishes or Bogorov sorting trays under a stereomicroscope. All larvae were mounted in Hoyer's on glass slides and identified using a compound microscope. The association between larva, pupa and adult chironomids necessary for full taxonomic description was attempted for most morphospecies, including by rearing individual live larvae in glass vials containing river

water and stopped with cotton/polyester wool according to methods outlined by Cranston and Edward (1999). Identifications were made in reference to taxonomic keys to the Australian fauna (Cranston 2000b) and voucher specimens maintained in the Australian National Insect Collection, CSIRO, Canberra. Formally unpublished voucher names in quotes (e.g. *Cricotopus* '*parbicinctus*') and codes (e.g. unknown genus 'SO3') used here follow Cranston (2000b) and do not constitute nomenclatural actions.

Water samples were collected in Nalgene bottles before sampling larvae and physicochemistry was recorded at the same time. Conductivity readings were taken using an ACTIVON pocket conductivity meter with a carbon plate dip probe. Temperatures were measured using a max/min thermometer and standard thermometer for air temperatures in the shade. Alkalinity of the water was measured with pH paper and compared with laboratory measurements at standard temperature. An Orbeco Hellige water analysis system Model 975 MP was used to determine ammonia (nitrogen) using the Nessler technique for high concentrations and the Indophenol technique for low concentrations. Chloride concentrations were measured using the silver nitrate turbidimetric technique. Iron levels were measured using the colorimetric 3-(2-pyridyl)-5, -bis(4-phenyl-sulfonic acid)-1, 2, 4-triazine (PPST) technique for low concentrations or the o-pheranthroline technique for high concentrations, and phosphates were measured using hot oxidation and hydrolysis with molybdenum blue according to Orbeco-Hellige (2000).

Efficiency of sampling regimes was evaluated using species accumulation curves to extrapolate species richness to an asymptote of total expected richness (Soberón & Lorente 1993; Christen & Nakamura 2002). These were plotted as a function of kick-sweep and rock-wash collection effort using EstimateS ver. 5.0, and Primer ver. 5 software packages (Colwell & Coddington 1994; Clarke & Gorley 2001). Standard diversity measures and estimators also available in these packages were employed. Matches between the assemblage patterns observed at each station and expectations from models were evaluated using rank abundance distribution curves plotted as $\log_{10}$ of abundance as a function of species rank order using the program PAST (Hammer 2002). A total of 999 simulations were made for each model and relative abundances were expressed as mean values of these replications. If *P*-values were <0.05, distributions for models were considered not significantly different at the 5% level. Data sets also were $\log(x + 1)$ transformed to scale down very abundant species and used to generate Bray Curtis similarity coefficient matrices; this index was chosen for its invariance to changes in scale. These data then were classified hierarchically and examined visually by non-metric multidimensional scaling (NMDS) ordination plots (Clarke & Gorley 2001). This technique enabled the data points for each station and sampling period (Q mode) to be ordered in two dimensions according to the differences among larval chironomid communities that later were related directly to the accompanying physicochemistry. Finally, cluster analyses with between-group average linking were carried out to determine groupings among taxa and sites.

RESULTS

From the 50 samples taken from the five stations along the estuarine gradient at five seasons using two sampling techniques, 5735 chironomid larvae were recovered belonging to 44 species (Table 1). Species richness declined towards riffle station 5 from a maximum of 41 species at station 1 to a maximum of seven species at station 5. Most species abundances declined with distance from riffle station 1, notable exceptions being *Semiocladius crassipennis* (Skuse) and certain *Cladotanytarsus* species that dominated brackish station 5. Individuals collected per station declined with distance from station 1 with numbers ranging from 2780 to 243. Species richness (diversity) increased at all five stations as sample size increased towards fresher stations, but richness increased more rapidly at station 1 than at stations 3–5 indicating that sampling the full complement of species was more likely at stations 3–5 than at station 1. Plots of percentage cumulative abundance against species rank on logarithmic scales (k dominance plots) showed that station 3 followed by 2 and 1 was the most diverse (Fig. 2).

Average numbers of midge larvae per square metre at each riffle as sampled by rock washes were ~820, 230, 120, 60 and 40 individuals for stations 1–5, respectively. K dominance plots showed that kick-sweep samples were more diverse than rock washes (Fig. 2). Initially for every 1000 individuals sampled by rock washes, 10 species were identified and as sampling increased to 4000 individuals, about 40 species were collected. Species not recovered using the rock wash technique included *Demicryptochironomus (Irmakia)* sp., *Djamabatista* sp., *Stictochironomus* sp. 'K2', *Stempellina johni* Glover, *Tanytarsus* sp. nr 'M1' and *Zavreliella* nr 'S1'. Kick-sweeping netted fewer (1807) individuals, but with 20 species recovered, species diversity was higher. From kick-sweep samples, five species were sampled for every 20 individuals and 14 species for every 50 individuals. Species unsampled by kick-sweep netting were: *Ablabesmyia hilli* Freeman, *A. notabilis* (Skuse), *Nilotanypus* sp., *Botriocladius grapeth* Cranston & Edward, unknown genus 'SO3', *Cardiocladius australiensis* Freeman, *Corynoneura* sp., three species of *Cricotopus*, *Nanocladius* sp., three species of *Parakiefferiella*, *S. crassipennis*, *Conochironomus* sp., *Cryptochironomus griseidorsum* (Kieffer), *Demicryptochironomus (Irmakia)* sp., *Dicrotendipes leei* Freeman, *Parachironomus* sp., *Nilothauma* sp., three species of *Cladotanytarsus* and *Tanytarsus* nr 'M1'. While kick-sweep netting captured individuals less efficiently compared with rock washes, both sampling regimes recovered approximately 10 species per 1000 individuals. Most importantly, the taxon confined to station 5, *S. crassipennis*, was undetected by kick-sweep netting alone.

For efficient sampling along the Clyde River we combined techniques, because pooled samples from both techniques and all seasons showed that variation due to sampling artefacts was minimised. These pooled individuals from seasonal samples show similar species accumulation curves for each station along the gradient (Fig. 2). The maximum number of species sampled according to these curves was about 45 species for around 2000

Table 1 Larval Chironomidae collected per station along the Clyde River

	Station 1	Station 2	Station 3	Station 4	Station 5	Sum total
Podonominae						
Podonomopsis sp.	24	0	0	0	0	24
Tanypodinae						
Ablabesmyia hilli	9	10	4	0	0	23
Ablabesmyia notabilis	12	0	2	0	0	14
Djalmabatista sp.	2	0	0	0	0	2
Nilotanypus sp.	55	0	1	0	0	56
Paramerina sp.	12	0	0	0	0	12
Paramerina sp. 2	4	0	0	0	0	4
Orthocladiinae						
Botriocladius grapeth	181	66	17	0	0	264
Cardiocladius australiensis	36	2	1	0	1	40
'Genus Australia' sp. B	477	0	0	0	2	479
Corynoneura sp.	36	0	0	0	0	36
Cricotopus '*albitarsus*'	457	26	2	2	0	487
Cricotopus '*brevicornis*'	140	77	21	0	0	238
Cricotopus '*parbicinctus*'	70	62	9	2	1	144
Echinocladius martini	43	25	1	0	0	69
Nanocladius sp.	6	0	0	0	0	6
Parakiefferiella '*variegatus*'	5	364	742	317	69	1497
Parakiefferiella sp. 1	10	1	0	0	0	11
Parakeifferiella sp. 2	30	84	20	4	0	138
Rheocricotopus sp. 1	64	1	0	0	1	66
Rheocricotopus sp. 2	3	0	0	0	0	3
Semiocladius crassipennis	0	0	0	0	165	165
Thienemanniella sp.	339	7	0	0	0	346
Unknown genus 'SO3'	17	152	27	5	0	201
Chironominae						
Conochironomus sp.	2	1	0	0	0	3
Cryptochironomus griseidorsum	3	2	1	0	0	6
Demicryptochironomus sp.	1	0	0	0	0	1
Dicrotendipes leei	482	321	10	3	0	816
Parachironomus sp.	7	0	0	0	0	7
Polypedilum vespertinum	6	0	0	1	0	7
Nilothauma sp.	1	4	3	0	0	8
Stictochironomus 'K2'	2	2	0	0	0	4
Xenochironomus sp.	1	0	0	0	0	1
Zavreliella nr 'S1'	2	0	0	0	0	2
Riethia stictoptera	13	3	0	0	0	16
Cladotanytarsus unilinearis	0	35	45	23	10	113
Cladotanytarsus sp. 2	1	58	20	6	0	85
Cladotanytarsus sp. 3	0	3	1	1	0	5
Cladotanytarsus sp. 4	10	1	0	0	0	11
Paratanytarsus jeffereyi	6	3	3	0	0	12
Rheotanytarsus juliae	197	79	15	0	0	291
Stempellina johni	6	2	0	0	0	8
Tanytarsus nr M1	1	3	0	0	0	4
Tanytarsus nr *bispinosus*	7	2	1	0	0	10

Taxon names, including vouchers, follow Cranston (2000b).

individuals at station 1 and sampling appeared sufficient at all stations. Using EstimateS (Colwell & Coddington 1994), Chao 1, a simple estimator of the true number of species in an assemblage based on the number of rare species in the sample, indicates a maximum of around 42 species. Chao 2, applied to the distribution of species among samples and requiring only presence–absence data, predicts around 43 species but greatly overestimates species richness at station 1. When mean species accumulation curves were compared with the expected curve and individuals in all pooled samples had been assigned randomly (Coleman's curve) a significantly steeper rise from the origin was seen compared with the mean curves. Thus, samples are more heterogeneous in species composition than the contribution due to sampling errors. An asymptotic model for species accumulation curves, the Michaelis–Menten two-parameter hyperbola approach, suggests that around 40 species is the upper expected limit of richness for Clyde River riffles stationed along the estuarine gradient. Given that Coleman's curve is equivalent to rarefaction techniques, these models indicate that taxonomic diversity is sampled adequately at the

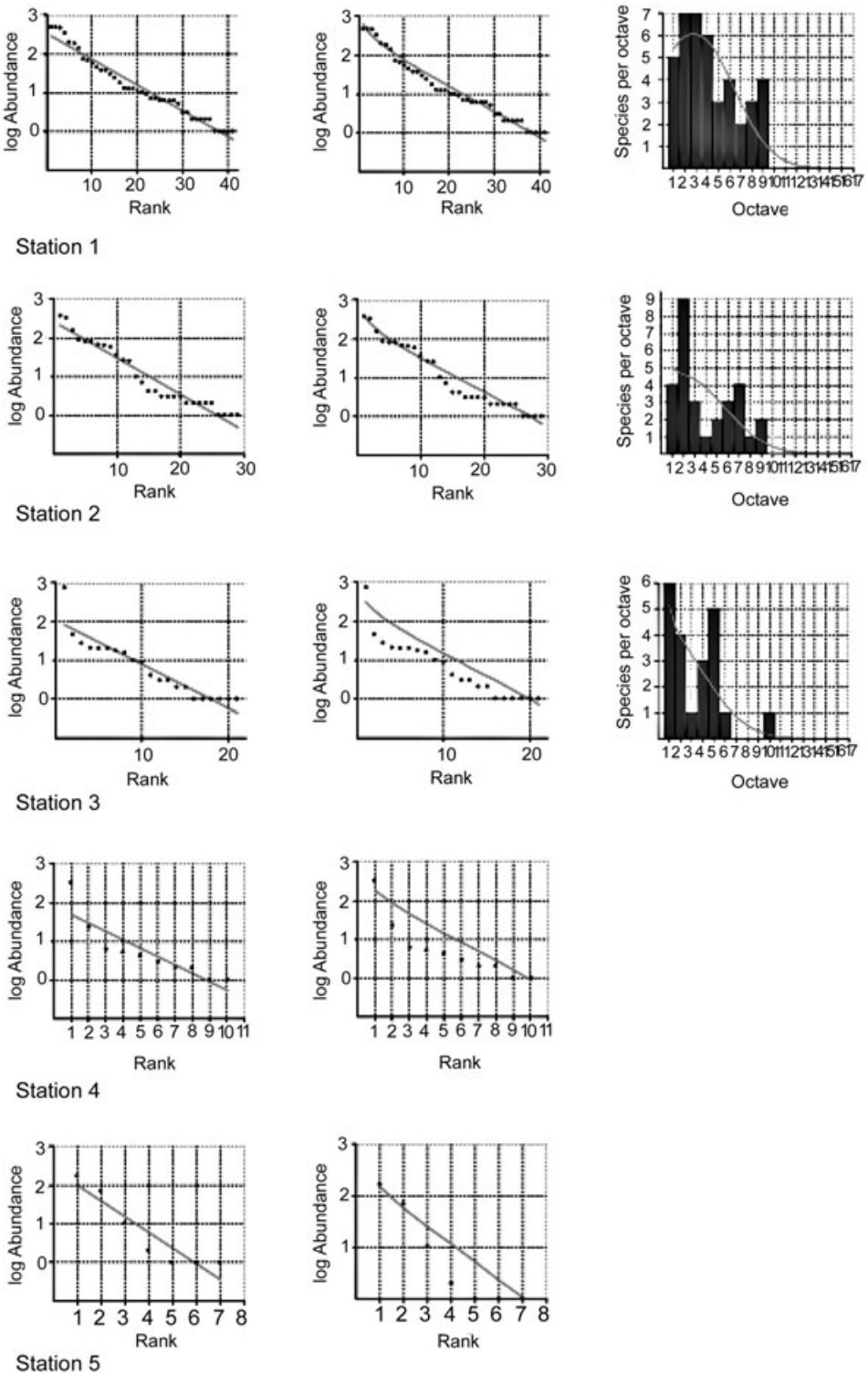

Fig. 2. K dominance plots for kick-sweep samples pooled from all stations compared with rock washes and plots of percentage cumulative abundance of chironomidae larvae collected from the five riffles stationed along the Clyde River estuarine gradient against species rank on logarithmic scales (k dominance plots).

Clyde, being a compromise between overestimation (rock washes) and underestimation (kick/sweep) samples.

Concerning physicochemical parameters, the mean minimum and maximum water depth for stations 1–5 was 61 and 173 cm, respectively, and the difference between stations was significant (52%) with a gradual increase in water depth towards station 5. The increase from a maximum water depth of 57–232 cm showed only minor differences between

Table 2 The fit of three types of species abundance models for larval chironomid distributions stationed along the Clyde River estuarine gradient

Geometric series model	*P*-value	*K*-value
Station 1	0.00*	0.14
Station 2	0.00*	0.20
Station 3	0.00*	0.22
Station 4	0.00*	0.39
Station 5	1.12	0.60
All stations	0.00*	0.13
Log series model	***P*-value**	**α-value**
Station 1	6.82	6.81
Station 2	1.08	4.96
Station 3	0.00*	3.80
Station 4	0.00*	1.90
Station 5	3.72	1.33
All stations	1.94	6.48
Log normal model	***P*-value**	**Mean & variance**
Station 1	0.87	0.91, 0.93
Station 2	0.07	0.66, 1.11
Station 3	0.10	0.23, 1.14
All stations	0.27	1.33, 0.82

*Represents a significant fit. There were insufficient sample sizes to adequately test the fit of the log normal model for stations 4 and 5.

sampling dates. Mean pH was 5.5 with a variance of 0.2 and mean range of 5.1–6.2 from station 1–5 that was significant (68% correlation), though apparently with little seasonal variation (18%). Mean water temperature averaged across all months and stations was 17.7°C with a variance of 29.4°C and with a standard deviation of 5.4°C. Temperatures varied seasonally from 11°C to 23°C and water and air temperatures consistently correlated closely at all stations. Conductivities recorded at stations along the gradient differed significantly (71%) and mean field conductivity was 4.9 mS/cm with a variance of 20.5 mS/cm. Similarly, sodium chloride concentrations differed significantly between stations (67%) with a mean of 7.8 mg/L and mean concentrations varied from 0.05 mg/L at station 1 to 24.0 mg/L at station 5 with non-significant correlative variation between seasons (19%). Ammonia/nitrogen concentrations increased towards station 5 with significant differences between stations (59%), but only slight correlation with sampling date (higher values in summer). Iron decreased in concentration towards station 5 with significant differences between stations (64%), but no correlation with sampling date (23%): iron precipitation usually was present at stations 3 and 4. Phosphorus levels were below detectable levels.

Comparison of larval chironomid rank abundance patterns from the Clyde River with the three models available in the PAST program (Hammer 2002) gave patterns that differed in their correspondence at stations down the gradient (Table 2). Overall, a satisfactory fit was achieved with the geometric series model, although this declined down the gradient such that log series was best fit at stations 3 and 4. By comparison, the log normal model poorly fitted the data sets and was affected strongly by the absence of scarcer species below station 3.

Results from NMDS ordinations indicate that stations cluster strongly according to position along the gradient, such that rock wash and kick-sweep samples from station 1 were located in the lower left of the ordination and samples from station 5 in the upper right (Fig. 3). This pattern was reflected in the hierarchical cluster diagram using Bray Curtis similarities with $\log(x + 1)$ transformation. For example, *S. crassipennis* was associated with rock washes at station 5, whereas *Xenochironomus* was more likely to be present in kick-sweep samples at station 1 (Fig. 3).

DISCUSSION

The species richness across the entire estuarine gradient of the Clyde is typical of many freshwater streams across the Australian continent, perhaps especially those of the wet tropics that range from 40 to 59 species per stream with an estimated regional species pool between 110 and 158 species (Cranston 2000a). Diversity is comparable to the 60 species identified from 3929 larvae from 44 localities in the Blue Mountains (Hardwick *et al*. 1995b). Species numbers from permanent waters approach the richness of large inland river systems such as the Murray Darling (17 to around 43 species) (Sheldon & Walker 1998). However, the Clyde's fauna contains few taxa typical of turbid, eutrophic and less permanent inland rivers as taxa belonging to the tribe Chironomini, such as species belonging to the genera *Chironomus*, *Stenochironomus*, *Paratendipes*, *Cladopelma*, *Harnischia* and *Kiefferulus*, were not recovered. However, the river does share certain cosmopolitan elements with inland waters such as *A. notabilis*, *Cricotopus* spp., *Nanocladius* spp., *C. griseidorsum* and *Parachironomus* spp. These eurytolerant taxa are present even at the variably saline Lake Gregory in north-western Western Australia (Halse *et al*. 1998). Other genera shared with other high conductivity lakes of the Western Australian coastal plain include *Corynoneura*, *Thienemanniella* and *Nilothauma* (Edward *et al*. 1994). Notably, among the species of *Cricotopus*, *Cricotopus* '*albitarsus*' is considered to be a pollution indicator, although at the Clyde its tolerance of naturally saline conditions is narrower than that of *Parakiefferiella* '*variegatus*'.

The Clyde shares few species with the saline inland lakes of the Paroo (Timms 1993), which are colonised by taxa in the subfamily Tanypodinae, especially species of *Procladius* (Clair & Paterson 1976; Timms 1983; Kokkin 1986). Although tanypod species occur in moderately saline athalassic waters (1–13 g/L NaCl), none were found in the lower reaches of the Clyde. Within the localised region of the south-eastern subcoastal Australia, the small, permanent, shallow, freshwater sand-dune McKenzie Lake, near Jervis Bay, southern New South Wales, shares 14 species with the Clyde River (Wright & Cranston 2000).

Complementarity between sampling months generally was high with the greatest number of shared species observations between the months of June and August and least between October and January. The Jaccard and Sorenson indices

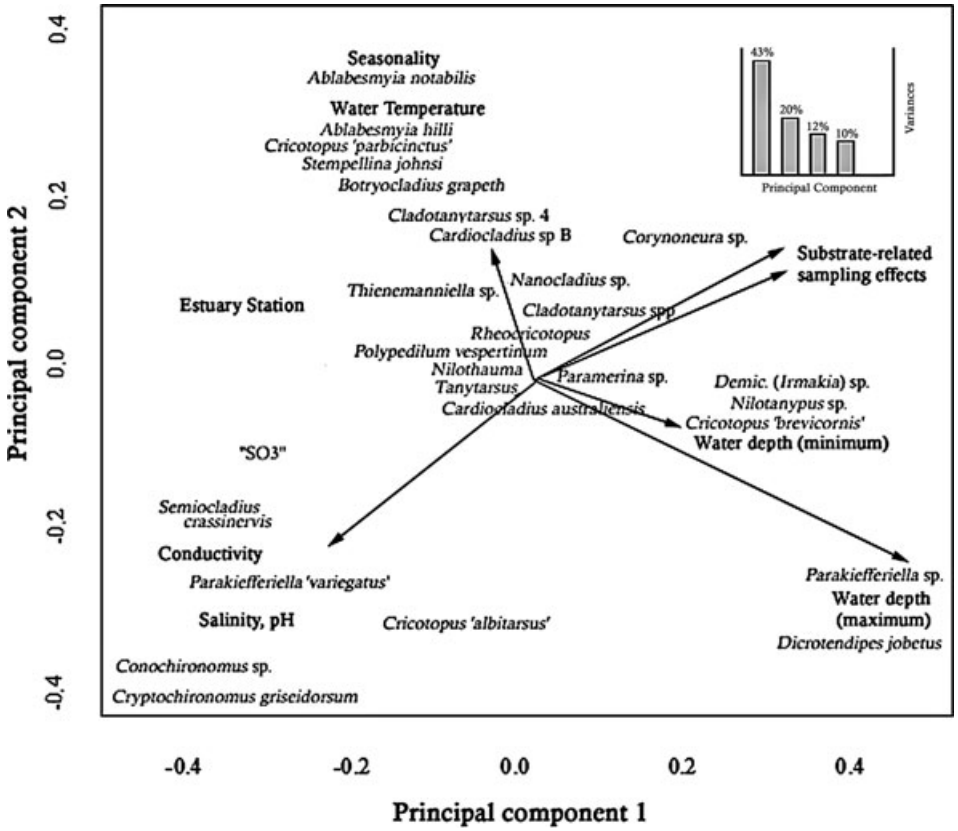

Fig. 3. Non-metric multidimensionally scaled ordination (NMDS) for Chironomidae larval species sampled along the Clyde River estuarine gradient with the corresponding ordination of environmental variables. Derived from combined kick-sweep and rock-wash samples collected at the five riffle stations at five separate sampling dates between April 2001 and January 2002, based on hierarchically clustered Bray Curtis similarities with $\log(x + 1)$ transformation and with group average linking to generate a dendrogram (not shown). Insert shows variation associated with principal components: 1, which explains 43% is interpreted as water depth; 2, explaining 20%, reflects salinity.

showed that the highest complementarity occurred between June and August whereas the Moriset–Horn index indicated that this occurred between April and August with the lowest complementarity between October and January.

Overall, species relative abundance patterns and plots such as k dominance curves appear to be more informative than presence/absence data or standard diversity indices (e.g. richness). The emergent pattern shows gradually intergrading assemblages of species behaving individualistically with no discrete brackish fauna. In the intermediate transitional zone, an assemblage of *Chironomus*, *Cricotopus* and *Tanytarsus* species represents taxa that are widely distributed in fresh habitats, including those that are polluted (Edward *et al*. 2001). The notable exception is stenohaline *S. crassipennis* found in large numbers at station 5 (Cranston & Dimitriadis 2005).

These chironomid abundance patterns observed at the Clyde are unlikely to result entirely from effects of sampling or scaling, as complementary distribution patterns are observed in unrelated organisms in different trophic groups. For example, benthic Foraminifera are absent from Clyde sites equivalent to stations 2, 3 or 4 but occur near station 5, where a low-diversity assemblage of six species dominated by benthic Textulariids was sampled, with much higher diversities and abundances further downstream (Cotter 1996). Station 5 is transitional where neither brackish, marine or freshwater taxa are completely dominant and only few specialist taxa occur.

Matching larval abundance patterns against theoretically based models reveals several findings of interest. A fit with the geometric series model at stations 1–4 indicates that sequential niche apportionment may underlie the observed patterns. This finding is somewhat surprising as geometric series patterns are observed most frequently in severe environments or early in succession. Stations 1–3 might be least stressful for freshwater chironomid taxa and climax communities therefore are expected. An equally good fit at stations 3 and 4 is provided by the log series model – station 3 being the most diverse according to k dominance plots, although station 1 was the most diverse according solely to the univariate measure of richness. The poor fit with the log normal model was expected as assemblages were strongly delimited by the riffle zones and by increasing salinity. However, in this environment, strongly individualistic specific behaviour was expected. Our findings are consistent with studies that examine sampling effects in which inclusion of rarer species has significant influence on both the discrepancy between real and observed patterns (Cao *et al*. 1998) and the interpretation of underlying processes (Underwood *et al*. 2000). This is especially relevant in the context of studies that recognise that trends may be influenced, by somewhat arbitrary spatiotemporal scales (Guisan & Zimmermann 2000; Lande *et al*. 2000), which is of particular relevance for monitoring changes along pollution gradients (Waterhouse & Farrell 1985; Ricotta 2004).

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