Hydrobiologia (2010) 652:89–100
DOI 10.1007/s10750-010-0321-9

PRIMARY RESEARCH PAPER

Native and alien macroinvertebrate richness in a remnant of the former river Rhine: a source for recolonisation of restored habitats?

Aurelia Wirth · Denes Schmera · Bruno Baur

Received: 14 December 2009 / Revised: 25 May 2010 / Accepted: 12 June 2010 / Published online: 26 June 2010

Abstract Rivers are among the most endangered ecosystems of the world with dramatically decreasing biodiversity. Rehabilitation programmes aiming at restoration of riverine ecosystems rely on the recolonisation of native macroinvertebrates from refuges. We examined whether a relatively natural remnant of the former river Rhine (Altrhein) harbours a higher richness of benthic macroinvertebrates than two sites of the modified Rhine with artificial and semi-natural embankments near Basel. All three sites were bimonthly sampled between May 2007 and May 2008 using three techniques: Kick and Sweep, drifting animals collected from pieces of stone turned by hand, and animals collected from stone surfaces. Taxa richness was higher in the Altrhein than in the two sampling sites in the river Rhine, but it was mainly a result of the large number of individuals sampled at this site. Despite 17% of taxa recorded were alien, the three sampling sites differed neither in the number of alien taxa nor in their abundances. However, lower percentages of both alien taxa and individuals were recorded in the Altrhein than at the other two sites in the Rhine. Indicator value analysis showed that the macroinvertebrate community of the Altrhein maintains several native and specific taxa. Multivariate analyses supported the separation of the communities collected at different sampling sites and also the uniqueness of the community in the Altrhein. The observed patterns, however, strongly depended on the sampling method applied, thereby calling the attention to the application of standard sampling methods and also to the restriction of result comparisons on projects using identical sampling methodology. Our study shows that the remnant of the former river Rhine serves as a refuge for macroinvertebrates which may facilitate future restoration of the river embankment.

Keywords Alien taxa · Richness · Conservation value · Macroinvertebrates · River Rhine

Handling editor: B. Oertli

A. Wirth · D. Schmera (✉) · B. Baur
Section of Conservation Biology, Department of Environmental Sciences, University of Basel, St. Johanns-Vorstadt 10, 4056 Basel, Switzerland
e-mail: denes.schmera@unibas.ch

D. Schmera
Balaton Limnological Research Institute, Hungarian Academy of Sciences, Klebelsberg K. u. 3, Tihany 8237, Hungary

Introduction

Man-made alterations of the environment have caused major changes in the global distribution of organisms (Vitousek et al., 1997). Many species have been eliminated from areas dominated by human beings as a consequence of habitat destruction or alteration, pollution, over-harvesting, introduction of alien species and climate change (Chapin et al., 2000). The current rates of species extinction are estimated to be 10–100 times greater than the pre-human rates (Pimm et al., 1995) and there is increasing evidence of declining biodiversity both in terrestrial (Haddad et al., 2009) and aquatic ecosystems (Roberts & Hawkins, 1999). Freshwater ecosystems are among the most endangered ecosystems in the world (Dudgeon et al., 2006) as they suffer from water pollution, habitat degradation, flow modification, overexploitation and species invasion (Giller & Malmqvist, 1998; Dudgeon et al., 2006), all of which affect the diversity and integrity of river biota (Karr et al., 1985; Poff et al., 1997). Recent studies have also shown that hydromorphological degradation of watercourses decreased riverine diversity (Malmqvist & Rundle, 2002; Lorenz et al., 2004). As a result of the intensive human impact, natural or semi-natural conditions occur only in a few rivers with species-rich floodplains (Ward et al., 1999, 2002). These species-rich sites could act as sources for future colonisation of more degraded and thus species-poor sites following habitat restoration.

The river Rhine is a good example on how a combination of different factors structures benthic communities (Baur & Schmidlin, 2007). River modification deteriorated certain habitats but also created new habitats. Prolonged pollution changed the original communities and caused a loss of certain species, simultaneously creating open niches for pollution-tolerant alien species (Tittizer et al., 1991; Van der Brink et al., 1996). Major disturbances enabled the invasion of alien species, and the Rhine-Main-Danube Canal, opened in 1992–1993, provided additional opportunities for this process (Tittizer, 1997; bij de Vaate et al., 2002). After reduction of the pollution in the Rhine, recolonisation seemed to favour alien, rather than native species. These alien species suppress the development of populations of native species. At the present day, the number of invaders is still increasing (Baur & Schmidlin, 2007; Leuven et al., 2009).

Despite profound alterations of river characteristics, the Rhine still has natural and semi-natural banks, and areas of floodplain, with abandoned meanders, brooks, backwaters, sand and gravel pits; and remnants of riparian forest still harbour a high richness of plants and animals, and are therefore of high conservation value (e.g. LfU, 2000; Baur et al., 2002). Furthermore, in the past decades, the water quality of the Rhine has improved considerably (Sacher et al., 2008).

Management agencies are increasingly attempting to reverse degradations to rivers through ecosystem restoration (Ardon & Bernhardt, 2009). In the framework of the "Integrated Rhine Programme" (Integriertes Rheinprogram) large areas for water retention during floods will be created by removing the existing dams and widening the riverine area of the upper Rhine and other by-passed remnants of the river between Basel and Mannheim (Umweltministerium Baden-Württemberg, 2007). Increasing flood retention is being coupled with ecological restoration of the banks in this large project and near natural river sections are assumed to serve as species pool for the recolonization of restored sites.

In the present study, we examined whether a remnant of the river Rhine, which is characterised by a natural river bed and extreme fluctuations in discharge and water level, could serve as a source for species colonisation of sites with degraded communities in future river restorations. In particular, we asked (1) whether the relatively natural remnant of the former Rhine harbours a higher richness of benthic macroinvertebrates than two sites of the modified river Rhine with artificial and semi-natural embankments and (2) whether these sites differ in richness, abundance and biomass of native and alien macroinvertebrate taxa. From a methodological perspective, we addressed these questions by comparing the performance of three sampling methods of benthic macroinvertebrates.

Materials and methods

The river Rhine

With a length of 1,320 km and a catchment area of 185,000 km^2, the river Rhine is one of the largest rivers in central Europe (Friedrich & Müller, 1984). The deterioration of the river started in the Middle Ages (Nienhuis & Leuven, 1998) and continued by straightening, reduction of channel networks to a single channel and disconnection from the floodplain (Baur & Schmidlin, 2007). In the early 1800s, for instance, the Upper Rhine north of Basel showed a natural, up to 6-km wide river system with numerous branches, including runs and riffles and slow flowing meanders associated with numerous sand and gravel flats. In the Tulla-correction, carried out between 1817 and 1874, and in a subsequent canalisation (Grand Canal d'Alsace), the Upper Rhine was transformed into a 130-m wide, artificial fast flowing sealed canal. Nowadays, the Rhine is a completely man-manipulated river, more intensively used than ever before (Tittizer & Krebs, 1996).

Study sites

The Altrhein is a remnant of the former river Rhine running parallel to the Grand Canal d'Alsace (Fig. 1). The Altrhein has a close to natural river bed and is fed with water from the Rhine with a minimum discharge of 10–50 m^3/s. However, when the water level of the river Rhine exceeds 1,400 m^3/s, the surplus water is released through the Altrhein, thereby causing extreme fluctuations in discharge and water level. The first sampling site is located near Märkt (Germany) approximately 1 km downstream of the weir of the hydroelectric power plant Kembs (Rhine km 175; 47°37′32.302″N, 7°34′17.440″E). The bank of the sampling site is covered with a dense

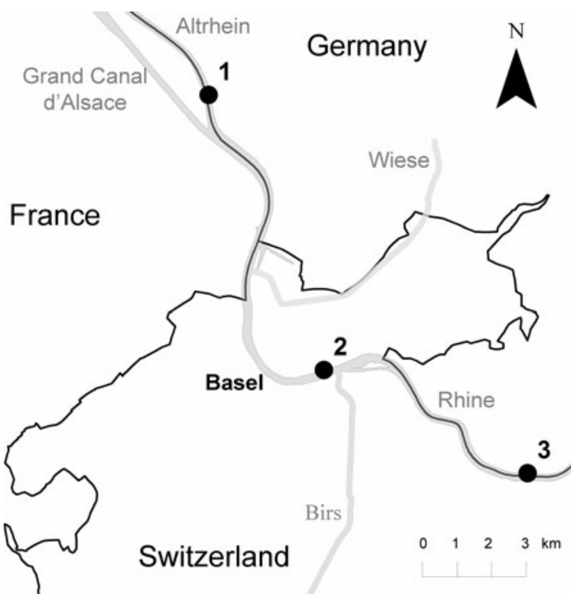

Fig. 1 The map of the study area with the three sampling sites (*1*: Altrhein, *2*: Schwarzwaldbrücke, *3*: Grenzach)

riparian vegetation of trees and shrubs. The riverbed provides a wide variety of mesohabitats like pools, riffles and runs. The substrata of the riverbed are dominated by rocks, stones and gravel. The second sampling site Schwarzwaldbrücke is situated in the city of Basel (Rhine km 164.8; 47°33′31.280″N, 7°36′46.219″E). This sampling site is embanked and the riverbed consists of stones and gravel. The water current is constantly fast at the site (mean discharge 1,033 m^3/s). The third sampling site Grenzach (Rhine km 157.8; 47°32′00.162″N, 7°41′09.247″E) is situated close to the village Grenzach-Wyhlen (Germany). The bank of the sampling site shows natural characteristics with trees and shrubs. The river contains several mesohabitat patches with fast and slow flowing sections. The substrata of the riverbed are dominated by coarse gravel and stones of variable size (mean discharge approximately 1,000 m^3/s). Detailed hydrological data on the river Rhine in Basel (close to the sampling site Schwarzwaldbrücke) are available at http://www.hydrodaten.admin.ch/e/2289.htm.

Field survey and laboratory protocols

Each site (30-m river length) was sampled every 2 months between May 2007 and May 2008 (altogether seven sampling occasions). Kick and Sweep sampling technique was applied using a hand net (opening: 155 × 130 mm, mesh size: 0.5 mm). At each site, eight replicate samples were taken by disturbing the substratum of the riverbed in an area of approximately 0.5 m^2 per sample. However, the occurrence of large pieces of stone at the sampling sites decreased the efficiency of the Kick and Sweep sampling technique. Therefore, we decided to apply two additional sampling techniques. First, single pieces of stone were turned by hand and the drifting animals were collected by the net (hereafter Stone drift). At each sampling site and on each sampling occasion eight Stone drift samples were collected. Second, at each site pieces of stone with an approximate surface area of 0.02 m^2 were randomly chosen and all animals were collected from the surface (five replicates per site and sampling occasion, hereafter Stone surface). Macroinvertebrates were preserved in 75% ethanol and later identified using the keys of Eggers & Martens (2001), Tachet et al. (2006) and Glöer & Meier-Brook (2003). Taxa were assigned to functional groups following Tachet et al. (2006). Altogether 32,896 individuals were collected. However, 3,826 juvenile individuals could not be classified into any taxonomical group and were therefore omitted from the analyses. Taxa were classified as alien or native following DAISIE (2008).

The wet weight of each taxon per sample was measured to the nearest 0.1 mg. To reduce the influence of conservation fluid on the wet weight, each sample was put into water for 10 min prior to weighing and then dried on paper towelling for 1 min. External material like cases of caddisflies was removed before weighing (shells of molluscs were included).

Statistical analyses

Our study design included two categorical factors (sampling site and sampling method) and several dependent variables (taxa richness, number of individuals, biomass, alien [non-native] taxa richness, percentage of alien taxa, number of alien individuals, percentage of alien abundance, alien biomass and percentage of alien biomass). Linear models were fitted to the data using the individual and joint effects of site and sampling method on each dependent variable separately. The final model was selected based on Akaike's Information Criterion (AIC). If the final model revealed significant differences, then Tukey test (Zar, 1999) was used as multiple comparison method. The individual-based rarefaction, originally proposed by Sanders (1968) and corrected by Hurlbert (1971) and Simberloff (1972), was used to compare taxa richness among sampling sites. Individual-based rarefaction controls for differences in abundance, thus allowing a comparison of taxa richness among sampling sites which differed in the number of individuals collected. For rarefaction analyses, both seasonal and replicate abundance data were pooled.

Indicator value analyses (Dufrene & Legendre, 1997) were performed to identify taxa characterising sampling sites. The significance level of indicator value was defined by randomisation with 1,000 runs. Analysis of Similarity (ANOSIM; Clarke, 1993) with 1,000 runs was used to examine whether the three sampling sites differed in the composition of macroinvertebrates. ANOSIM was performed separately for each sampling method (Kick and Sweep, Stone drift and Stone surface) with three different input data sets (presence–absence of taxa, abundance and biomass). For presence/absence data the Jaccard similarity index was used, whereas for abundance and biomass data the Bray–Curtis similarity index was applied (Podani, 2000). For all analyses, we used the R statistical computing environment (R Development Core Team, 2006) using the vegan (Oksanen et al., 2009), multcomp (Hothorn et al., 2008) and MASS packages (Venables & Ripley, 2002), an exception being a web-based software for the rarefaction curves (Brzustowski, 2009).

Results

Altogether 52 taxa were found among the 29,069 identified individuals. Taxa richness was significantly influenced by both individual and joint effects of sampling site and sampling method (Table 1, Fig. 2). Independent of the sampling method used, taxa richness was higher in the Altrhein than in the two sampling sites in the river Rhine. When the absolute values were compared, a larger number of individuals was collected at the Altrhein site than at the Schwarzwaldbrücke and Grenzach sites (Table 1). A higher biomass was recorded at the Altrhein site than at the two sampling sites in the river Rhine. Nine of the 52 taxa (17.3%) were considered to be alien. However, the three sampling sites did not differ in the number of alien individuals (Table 1). In contrast, the percentage of alien taxa, the number of alien individuals and their biomass differed among sampling sites (Table 1, Fig. 2). Tukey test showed that the Altrhein is relatively (in percentage) less affected by invasive taxa (considering their richness, abundance and biomass) than the two other sites in the river Rhine (Table 1, Fig. 2). Rarefied taxa richness revealed that the higher taxa richness in the Altrhein was mainly a result of the larger number of individuals sampled at this site (Fig. 3). This finding was significant in data obtained by the Stone drift method, and tended to be significant in data from the two other sampling methods (Fig. 3).

Considering the three sampling methods separately, our analyses revealed that the sampling method used strongly influenced the results (Table 1). In general, with the Kick and Sweep method the

Table 1 Summary of linear models (F values and significance levels) and multiple comparisons (Tukey test) examining the effects of sampling site and sampling method on various measures of taxa richness, abundance and biomass of macroinvertebrates in the river Rhine

Response variable	Sampling site (L)		Sampling method (M)		$L \times M$
Taxa richness	55.04***	A > S > G	107.55***	KS, SS > SD	9.60***
Number of individuals	44.23***	A > S, G	89.57***	SS > KS > SD	24.04***
Biomass	8.39***	A > G, S	7.54***	KS > SD, KS = SS, SD = SS	ns
Alien taxa richness	3.23*	A > S, A = G, S = G	77.54***	KS > SS, SD	3.48**
Number of alien individuals	ns		33.04***	KS > SS > SD	ns
Alien biomass	3.64*	A > S, A = G, S = G	12.51***	KS > SS, SD	ns
Percentage of alien taxa	17.56***	S, G > A	38.76***	SD, KS > SS	ns
Percentage of alien abundance	36.36***	S, G > A	61.29***	KS, SD > SS	ns
Percentage of alien biomass	13.26***	G, S > A	101.73***	KS, SD > SS	ns

Sampling sites were Altrhein (A), Schwarzwaldbrücke (S) and Grenzach (G). Sampling methods included Kick and Sweep (KS), Stone drift (SD) and Stone surface (SS). Significance levels were * $P = 0.05$, ** $P = 0.01$, *** $P = 0.001$ and *ns* non significant. In multiple comparisons, the significance level was set at $P = 0.05$

largest numbers of taxa (both native and alien) were collected (Table 1). However, the Stone surface method exceeded the Kick and Sweep method in the number of individuals collected. This can be explained by the fact that several thousands of Chironomidae individuals were collected with the Stone surface method, mainly at the Altrhein site. Three of nine interactions between sampling sites and sampling methods were significant (Table 1).

Indicator value analysis based on data from the Kick and Sweep method revealed 21 indicator taxa (Table 2). Fifteen taxa were indicators of the Altrhein site, and two of them were alien. At the sites Schwarzwaldbrücke and Grenzach, the numbers of indicator taxa were 4 and 2, and out of these 2 and 1 were aliens. Indicator value analysis based on the Stone drift method resulted in only seven indicator taxa: five native taxa in the Altrhein and two alien taxa at the site Grenzach. Finally, indicator analysis based on data from the Stone surface samples revealed nine indicator taxa for the Altrhein (all of them being native) and one indicator taxon for the site Grenzach (alien). Independently on the sampling method used, the majority of the indicator taxa in the Altrhein belonged to the functional group of the filter feeders. In contrast, at the two other sites, none of the indicator taxa was a filter feeder. ANOSIM revealed differences in the composition of aquatic macroinvertebrates at the three sampling sites in all nine comparisons (Table 3).

Discussion

Rivers belong to the most endangered ecosystems of the world (Malmqvist & Rundle, 2002; Ward et al., 2002; Dudgeon et al., 2006). Identifying river sections which still harbour species-rich communities is one of the first steps in conserving riverine biodiversity (Sutherland, 2000). Our results show that a relatively natural remnant of the former river Rhine (Altrhein) has both a higher richness and abundance and a larger biomass of benthic macroinvertebrates and is less dominated by alien taxa than two sites of the modified Rhine with artificial and semi-natural embankments near Basel. These findings suggest that the Altrhein may serve as a source-habitat from which native macroinvertebrates may recolonise degraded and thus species-poor sites of the river Rhine following habitat restoration.

Our study indicates that the higher taxa richness found in the Altrhein is associated with a larger number of individuals and higher biomass. As high taxa richness, abundance and biomass are special features of natural floodplain rivers (Ward et al., 1999, 2002), we interpret these characters as surrogates of conservation value. Considering individual-based taxa richness, rarefaction analyses showed that the Altrhein did not differ from the other sites. In this case, however, we consider sample-based (raw) estimates of taxa richness more informative because habitat modifications might also influence the

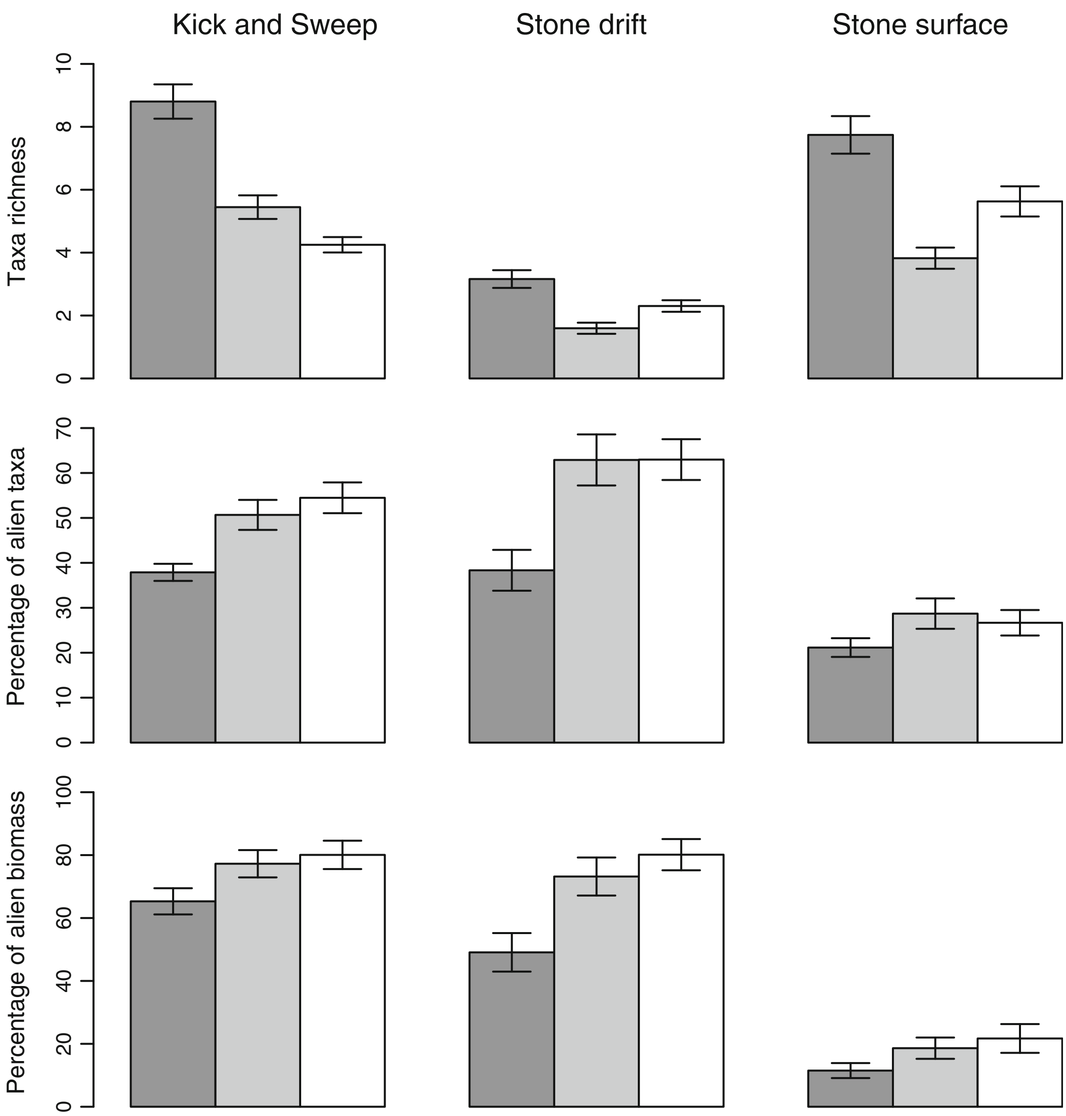

Fig. 2 Effect of sampling site (Altrhein [*dark grey*], Schwarzwaldbrücke [*light grey*] and Grenzach [*white*]) and sampling method on the taxa richness (*top*) on the percentage of alien taxa (*middle*) and on the percentage of alien biomass (*bottom*) in the river Rhine. Columns show mean values, whiskers indicate standard errors

abundance and biomass of the taxa. It is very likely that the separation of the Altrhein from the modified sections of the river Rhine contributed to the preservation of a high richness of macroinvertebrates. Furthermore, the extreme fluctuations in water level in the Altrhein provide a linkage between the water and the surrounding terrestrial landscape. The temporal and spatial variability in river flow is generally recognised as a fundamental control on instream habitat structure and riverine biodiversity (Monk et al., 2008).

We found the highest taxa richness in the Altrhein, although this river section is exposed to extreme fluctuations in discharge and water level. It seems that the effects of these human-induced impacts on the richness and composition of benthic macroinvertebrates are weaker that at the two other sampling sites; or the fluctuation in discharge and in water level is not associated with other stressors at this site.

A recent review showed that alien taxa accounted for 11.3% of the total taxa richness of benthic macroinvertebrates in the river Rhine, with slightly

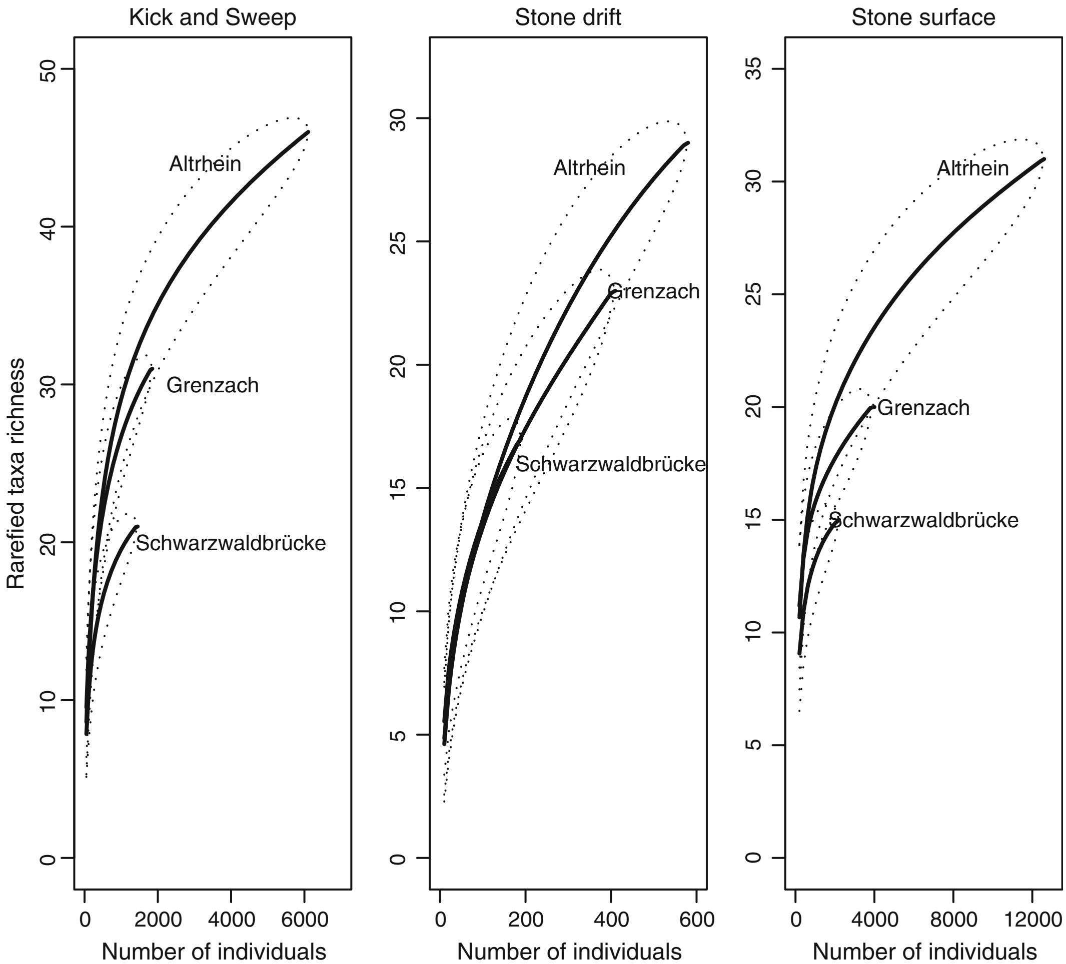

Fig. 3 Rarefied taxa richness (*solid line*) of the study sites and their 95% confidence intervals (*dotted lines*) in relation to the number of individuals

higher percentages in the Delta Rhine and Upper Rhine (Leuven et al., 2009). Another detailed field study revealed that 24.8% of the macroinvertebrate taxa were alien in the Upper Rhine between Karlsruhe and Mannheim (Bernauer & Jansen, 2006). Our finding of 17.3% of alien taxa is in the range of the previous records. However, this value may increase because the current rate of colonisation of alien species averages 1.27 new species per year in the river Rhine (Baur & Schmidlin, 2007). Considering abundance or biomass, approximately 80% of the macroinvertebrates were alien. However, the proportions of alien abundance and biomass show considerable variation in space (Tittizer et al., 2000; Haas et al., 2002; Bernauer & Jansen, 2006; Mürle et al., 2008). For instance, in a habitat restoration project in the Rhine Delta, the percentage of alien abundance varied considerably between habitats within the same locality (bij de Vaate et al., 2007). We found a similar variation on a larger spatial scale: the percentage of alien biomass and abundance varied between sampling sites 7 and 17.2 km apart: the Altrhein was less impacted by alien abundance and biomass compared to the other two sites. From a conservation point of view, identification and protection of sites less impacted by alien taxa and rich in native taxa are essential as these sites are the potential sources for species colonisation of other sites with degraded communities in future river restorations. Unfortunately, sites with high biodiversity values are also influenced by alien taxa, as it was observed in the Rhine Delta (bij de Vaate et al., 2006).

Table 2 Macroinvertebrate taxa found at the three study sites in the river Rhine with indicator values for the three sampling methods

Group	Taxon	Sampling method		
		Kick and Sweep	Stone drift	Stone surface
Crustacea	***Dikerogammarus villosus***	G 46.4**	G 43.5*	
	Echinogammarus ischnus			
	Echinogammarus trichiatus	S 9.6*		
	Gammarus fossarum			
	Gammarus roeseli			
	Corophium curvispinum	A 22.15**		
Ephemeroptera	*Baetis* sp.	A 36.8***	A 13.3**	A 33.7***
	Ephemera sp.	A 17.8***	A 12.3**	
	Heptagenia sp.	S 10.4*		
	Potamanthus luteus	S 11.1*		
	Caenidae	A 10.5*		
	Ephemerella sp.			
Trichoptera	*Psychomyia* sp.			
	Tinodes sp.			
	Hydroptila sp.	A 19.6***		A 30.4**
	Cheumatopsyche sp.			
	Hydropsyche sp.	A 30.5***	A 11.8**	A 23.7*
	Rhyacophila sp.	A 8.1*		A 17.1**
	Glossosoma sp.			
	Ceraclea sp.			
	Athripsodes sp.			
	Goera pilosa			
	Polycentropus sp.			
	Lepidostoma sp.			
Diptera	Simuliidae	A 17.8***		A 13.5*
	Chironomidae	A 82.4***	A 51.5**	A 75.8***
	Empididae	A 22.9***		A 24.8**
	Anthomyiidae			
	Psychodidae			
	Stratomyidae			
	Ceratopogonidae			
	Limoniidae	A 18.4***		A 35.4***
Coleoptera	*Elmis* sp. (larvae)			
	Esolus sp.			
	Limnius sp. (larvae)	G 12.5**		
	Oulimnius sp. (larvae)			
	Riolus sp. (larvae)			
Odonata	*Calopteryx splendens*			
Plecoptera	*Amphinemura* sp.			
	Leuctra sp.			
Heteroptera				
Bivalvia	***Dreissena polymorpha***			
	***Corbicula* sp.**			

Table 2 continued

Group	Taxon	Sampling method		
		Kick and Sweep	Stone drift	Stone surface
Gastropoda	*Ancylus fluviatilis*	A 24.6***		
	Potamopyrgus antipodarum		G 11.2*	G 26.4*
	Radix sp.			
	Gyraulus sp.			
Polychaeta	***Hypania invalida***	S 14.5*		
Oligochaeta		A 70.3***	A 15.1**	
Isopoda	***Jaera istri***	A 41.6***		
Hirudinea				
Acari		A 7.8*		A 21.5***

A Altrhein, *S* Schwarzwaldbrücke, *G* Grenzach, * Significant at $P = 0.05$, ** $P = 0.01$, and *** $P = 0.001$). Alien taxa are highlighted by bold

Table 3 *R* values of Analysis of Similarity (ANOSIM), expressing the separation of the macroinvertebrate communities collected at the three sampling sites in the river Rhine for each combination of data set and sampling method

Response variable	Kick and Sweep	Stone drift	Stone surface
Presence–absence data	0.125***	0.036***	0.090***
Abundance data	0.036*	0.077***	0.196***
Biomass data	0.043***	0.053***	0.145***

The Jaccard similarity index was used for presence–absence data, the Bray–Curtis index for abundance and biomass data (* $P = 0.05$, *** $P = 0.001$)

Although the proportion of alien taxa at the Altrhein site was significantly lower than at the other sampling sites, there was no difference in the number of alien individuals among the sites examined. Cargo shipping strongly contributes to the spread of alien species (Riccardi & MacIsaac, 2000). In the river Rhine, the number of alien taxa decreases upstream of Rheinfelden, where cargo shipping ends (Rey et al., 2004). The Altrhein is not used for cargo shipping, but it is fed by water from the river Rhine. During floods the surplus water is released through the Altrhein facilitating the colonisation of alien taxa, especially those, which have only an aquatic mode of dispersal (all of the alien taxa in this study).

Indicator value analyses were performed to identify taxa with high site specificity and fidelity. Indicator taxa often determine the uniqueness of a site or a habitat. Thus, their number is frequently associated with a high conservation value (Schmera & Kiss, 2004; Erős, 2007). In this context, the Altrhein harbours the highest number of specific taxa, which appear with high fidelity in the samples. Consequently, this type of analysis also supports the importance of the Altrhein in maintaining macroinvertebrate richness in the river Rhine. Moreover, in the Altrhein only a low percentage of the indicator taxa was alien in contrast to the two other sampling sites in the river Rhine. This indicates that a few alien taxa are only locally distributed but show a high fidelity in the samples. Specific taxa, their abundance and biomass might be responsible for the observed separation of the three communities as well as for the separation of the community in the Altrhein from the other sites. We assume that the combination of special habitat features of the Altrhein (lateral separation from the altered river Rhine, natural embankment, preservation of a high diversity of habitat, extreme fluctuations in discharge and water level, and strong linkage with the terrestrial ecosystem) maintain a unique and diverse macroinvertebrate community. However, the by-passed section of the Altrhein is fed with water from the Rhine. This enables alien taxa to colonise this diverse ecosystem.

Sampling is the first and most critical point in designing and conducting both basic and applied ecological research (Norris et al., 1992; Vinson & Hawkins, 1996; Friberg et al., 2006). For aquatic invertebrates, it is well known that several factors influence the properties of the samples, including the diversity of the habitat (Beisel et al., 1998), the spatial scale of the sampling (Schmera & Erős, 2008), the experience of the investigator (Metzeling et al., 2003) and the sampling method applied (Elliott & Drake, 1981; Drake & Elliott, 1982; Blocksom & Flotemersch, 2005). Our results show that differences in response variables (for instance taxa richness) among sampling sites strongly depended on the sampling method applied. This fact calls the attention to the application of standard sampling methods and also to the restriction of result comparisons on projects using identical sampling methodology. The high number of interactions between sampling site and method makes the interpretation of the results more complex.

It should be noted that the taxonomical level of our identification shows considerable variability: several taxonomic groups were identified only to genus or family level (Oligochaeta: class). Some of these taxonomic groups (e.g. Chironomidae or Oligochaeta) might strongly contribute to the species richness of the community (Marchese et al., 2005; Koperski, 2010). Our conclusions are therefore restricted to the taxonomical resolution used.

In summary, our study shows that the Altrhein can be considered as a biodiversity refuge of native aquatic macroinvertebrates. The Altrhein is less dominated by alien taxa compared to other sites on the river Rhine near Basel. Therefore, we suggest that aquatic conservation should consider the Altrhein as a source for colonisation of sites with degraded communities in future Rhine restoration projects (e.g. Integrated Rhine Project; LfU, 2000; Umweltministerium Baden-Württemberg, 2007).

Acknowledgements We would like to thank Verena Lubini (Zürich) for her help in checking the identification of the macroinvertebrate taxa, and Anette Baur, Stephanie Schmidlin and anonymous reviewers for their comments on the manuscript.

References

Ardon, M. & E. S. Bernhardt, 2009. Restoring rivers and streams. In: Encyclopedia of Life Sciences (ELS). Wiley, Chichester. doi:10.1002/9780470015902.a0020148.

Baur, B. & S. Schmidlin, 2007. Effects of invasive non-native species on the native biodiversity in the river Rhine. In Nentwig, W. (ed.), Biological Invasions. Ecological Studies, Vol. 193. Springer, Berlin: 257–273.

Baur, B., S. Zschokke, A. Coray, M. Schläpfer & A. Erhardt, 2002. Habitat characteristics of the endangered flightless beetle *Dorcadion fuliginator* (Coleoptera: Cerambycidae): implications for conservation. Biological Conservation 105: 133–142.

Beisel, J. N., P. Usseglio-Polatera, S. Thomas & J. C. Moreteau, 1998. Stream community structure in relation to spatial variation: the influence of mesohabitat characteristics. Hydrobiologia 389: 73–88.

Bernauer, D. & W. Jansen, 2006. Recent invasions of alien macroinvertebrates and loss of native species in the upper Rhine River, Germany. Aquatic Invasions 1: 55–71.

bij de Vaate, A., K. Jazdzewski, H. A. M. Ketelaars, S. Gollasch & G. Van der Velde, 2002. Geographical patterns in range extension of Ponto-Caspian macroinvertebrate species in Europe. Canadian Journal of Fisheries and Aquatic Sciences 59: 1159–1174.

bij de Vaate, A., R. Breukel & G. van der Velde, 2006. Long-term developments in ecological rehabilitation of the main distributaries in the Rhine delta: fish and macroinvertebrates. Hydrobiologia 565: 222–242.

bij de Vaate, A., A. G. Klink, M. Greijdanus-Klaas, L. H. Jans, J. Oosterbaan & F. Kok, 2007. Effects of habitat restoration on the macroinvertebrate fauna in a foreland along the river Waal, the main distributary in the Rhine delta. River Research and Applications 23: 171–183.

Blocksom, K. A. & J. E. Flotemersch, 2005. Comparison of macroinvertebrate sampling methods for nonwadeable streams. Environmental Monitoring and Assessment 102: 243–262.

Brzustowski, J., 2009. Rarefaction Calculator. Available at http://www2.biology.ualberta.ca/jbrzusto/rarefact.php. Accessed date 12 September 2009.

Chapin, F. S., E. S. Zavaleta, V. T. Eviner, R. S. Naylor, P. M. Vitosek, H. L. Reynolds, D. U. Hooper, S. Lavorer, O. E. Sala, S. E. Hobbie, M. C. Mack & S. Diaz, 2000. Consequence of changing biodiversity. Nature 405: 234–242.

Clarke, K. R., 1993. Non-parametric multivariate analysis of changes in community structure. Australian Journal of Ecology 18: 117–143.

DAISIE, 2008. European Invasive Alien Species Gateway. http://www.europe-aliens.org. Accessed date 26 September 2009.

Drake, C. M. & M. J. Elliott, 1982. A comparative study of three air-lift samplers used for sampling benthic macroinvertebrates in rivers. Freshwater Biology 12: 511–533.

Dudgeon, D., A. H. Arthington, M. O. Gessner, Z. I. Kawabata, D. J. Knowler, C. Leveque, R. J. Naiman, A. H. Prieur-Richard, D. Soto, M. L. J. Stiassny & C. A. Sullivan, 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. Biological Review 81: 163–182.

Dufrene, M. & P. Legendre, 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67: 345–366.

Eggers, T. O. & A. Martens, 2001. Bestimmungsschlüssel der Süsswasser-Amphipoda (Crustacea) Deutschlands. Lauterbornia 42: 1–68.

Elliott, J. M. & C. M. Drake, 1981. A comparative study of seven grabs used for benthic macroinvertebrates in rivers. Freshwater Biology 11: 99–120.

Erős, T., 2007. Partitioning the diversity of riverine fish: the role of habitat type and non-native species. Freshwater Biology 52: 1400–1415.

Friberg, N., L. Sandin, M. T. Furse, S. E. Larsen, R. T. Clarke & P. Haase, 2006. Comparison of macroinvertebrate sampling methods in Europe. Hydrobiologia 566: 365–378.

Friedrich, G. & D. Müller, 1984. Rhine. In Whitton, B. A. (ed.), Ecology of European Rivers. Blackwell, Oxford: 265–315.

Giller, P. S. & B. Malmqvist, 1998. The Biology of Streams and Rivers. Oxford University Press, Oxford.

Glöer, P. & C. Meier-Brook, 2003. Süsswassermollusken. Deutscher Jugendbund für Naturbeobachtung. 13. Auflage, Hamburg.

Haas, G., M. Brunke & B. Streit, 2002. Fast turnover in dominance of exotic species in the Rhine river determines biodiversity and ecosystem function: an affair between amphipods and mussels. In Leppäkoski, E., S. Gollasch & S. Olenin (eds), Invasive Aquatic Species of Europe. Distribution, Impacts and Management. Kluwer, Dordrecht: 426–432.

Haddad, N. M., D. M. Crutsinger, K. Gross, J. Haarstad, J. M. H. Knops & D. Tilman, 2009. Plant species loss decreases arthropod diversity and shifts trophic structure. Ecology Letters 12: 1029–1039.

Hothorn, T., F. Bretz & P. Westfall, 2008. Simultaneous inference in general parametric models. Biometrical Journal 50: 346–363.

Hurlbert, S. H., 1971. The non-concept of species diversity: a critique and alternative parameters. Ecology 52: 577–586.

Karr, J. R., L. A. Toth & D. R. Dudley, 1985. Fish communities of Midwestern rivers: a history of degradation. Bioscience 35: 90–95.

Koperski, P., 2010. Diversity of macrobenthos in lowland streams: ecological determinants and taxonomic specificity. Journal of Limnology 69: 88–101.

Leuven, R. S. E. W., G. van der Velde, I. Baijens, J. Snijders, C. van der Zwart, H. J. R. Lenders & A. bij de Vaate, 2009. The river Rhine: a global highway for dispersal of aquatic invasive species. Biological Invasions 11: 1989–2008.

LfU, 2000. Vom Wildstrom zur Trockenaue: Natur und Geschichte der Flusslandschaft am südlichen Oberrhein. Landschaft für Umweltschutz Baden-Württemberg. Verlag Regionalkultur, Ubstadt-Weiher.

Lorenz, A., D. Hering, C. K. Feld & P. Rolauffs, 2004. A new method for assessing the impact of hydromorphological degradation on the macroinvertebrate fauna of five German stream types. Hydrobiologia 516: 107–127.

Malmqvist, B. & S. Rundle, 2002. Threats to the running water ecosystems of the world. Environmental Conservation 29: 134–153.

Marchese, M. R., K. M. Wantzen & I. E. de Drago, 2005. Benthic invertebrate assemblages and species diversity patterns of the Upper Paraguay River. River Research and Applications 21: 485–499.

Metzeling, L., B. Chessman, R. Hardwick & V. Wong, 2003. Rapid assessment of rivers using macroinvertebrates: the role of experience, and comparison with quantitative methods. Hydrobiologia 510: 39–52.

Monk, W. A., P. J. Wood, D. M. Hannah & D. A. Wilson, 2008. Macroinvertebrate community response to inter-annual and regional river flow regime dynamics. River Research and Applications 24: 988–1001.

Mürle, U., J. Ortlepp & P. Rey, 2008. Koordinierte biologische Untersuchungen im Hochrhein 2006/2007. Makroinvertebraten. Umweltwissen Nr. 822. Bundesamt für Umwelt, Bern.

Nienhuis, P. H. & R. S. E. W. Leuven, 1998. Ecological concepts for the sustainable management of lowland river basins: a review. In Nienhuis, P. H., R. S. E. W. Leuven & A. M. J. Ragas (eds), New Concepts for Sustainable Management for River Basins. Backhuys, Leiden: 7–33.

Norris, R. H., E. P. McElravy & V. H. Resh, 1992. The sampling problem. In Calow, P. & G. E. Petts (eds), Rivers Handbook: Volume I. Blackwell Scientific Publications, Oxford: 282–306.

Oksanen, J., R. Kindt, P. Legendre, B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens & H. Wagner, 2009. Vegan: Community Ecology Package. R Package Version 1.15-4. http://CRAN.R-project.org/package=vegan.

Pimm, S. L., G. J. Russell, J. L. Gittleman & T. M. Brooks, 1995. The future of biodiversity. Science 269: 347–350.

Podani, J., 2000. Introduction into the Exploration of Multivariate Biological Data. Backhuys Publishers, Leiden.

Poff, N. L., D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegaard, B. D. Richter, R. E. Sparks & J. C. Stromberg, 1997. The natural flow regime. A paradigm of river conservation and restoration. BioScience 47: 769–784.

R Development Core Team, 2006. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org.

Rey, P., J. Ortlepp & D. Küry, 2004. Wirbellose Neozoen im Hochrhein. Ausbreitung und ökologische Bedeutung. BUWAL, Bern, Schiftenreihe Umwelt 380: 1–88.

Riccardi, A. & H. J. MacIsaac, 2000. Recent mass invasion of the North American Great Lakes by Ponto-Caspian species. Trends in Ecology and Evolution 15: 62–65.

Roberts, C. M. & J. P. Hawkins, 1999. Extinction risk in the sea. Trends in Ecology and Evolution 14: 241–246.

Sacher, F., M. Ehmann, S. Gabriel, C. Graf & H.-J. Brauch, 2008. Pharmaceutical residues in the river Rhine—results of a one-decade monitoring programme. Journal of Environmental Monitoring 10: 664–670.

Sanders, H. L., 1968. Marine benthic diversity: a comparative study. American Naturalist 102: 243–282.

Schmera, D. & T. Erős, 2008. Linking scale and diversity partitioning in comparing species diversity of caddisflies in riffle and pool habitats. Fundamental and Applied Limnology 172: 205–215.

Schmera, D. & O. Kiss, 2004. A new measure of conservation value combining rarity and ecological diversity: a case study with light trap collected caddisflies (Insecta: Trichoptera). Acta Zoologica Academiae Scientiarum Hungaricae 50: 195–210.

Simberloff, D. S., 1972. Properties of the rarefaction diversity measurement. American Naturalist 106: 414–418.

Sutherland, W. J., 2000. The Conservation Handbook. Research, Management and Policy. Blackwell Science, Oxford.

Tachet, H., P. Richoux, M. Bournaud & P. Usseglio-Polatera, 2006. Invertébrés d'eau douce: systematique, biologie, ecologie. CNRS Editions, Paris.

Tittizer, T., 1997. Ausbereitung aquatischer Neozoen (Makrozoobenthos) in den europäschen Wasserstrassen, erläutert am Beispiel des Main-Donau Kanals. In Güteentwicklung der Donau, Rückblick und Perspektiven. Schriftenreihe des Bundesamtes für Wasserwirtschaft (Wien) 4: 113–134.

Tittizer, T. & F. Krebs (eds), 1996. Ökosystemforschung: Der Rhein und seine Auen—eine Bilanz. Springer, Berlin.

Tittizer, T., F. Schöll, M. Dommermuth, J. Bahte & M. Zimmer, 1991. Zur Bestandsentwicklung des Zoobenthos des Rheins im Verlauf der letzten 9 Jahrzehnte. Wasser und Abwasser 35: 125–166.

Tittizer, T., F. Schöll, M. Banning, A. Haybach & M. Schleuter, 2000. Aquatische Neozoen im Makrozoobenthos der Binnenwasserstrassen Deutschlands. Lauterbornia 39: 1–172.

Umweltministerium Baden-Württemberg, 2007. Das Integrierte Rheinprogram. Stuttgart.

Van der Brink, F. W. B., G. Van der Velde, A. D. Buijse & A. D. Klink, 1996. Biodiversity in the Low Rhine and Meuse river-floodplains: its significance for ecological river management. Netherlands Journal of Aquatic Ecology 30: 129–149.

Venables, W. N. & B. D. Ripley, 2002. Modern Applied Statistics with S, 4th ed. Springer, New York.

Vinson, R. M. & C. P. Hawkins, 1996. Effects of sampling area and subsampling procedure on comparisons of taxa richness among streams. Journal of the North American Benthological Society 15: 392–399.

Vitousek, P. M., H. A. Mooney, J. Lubchenco & J. M. Melillo, 1997. Human domination of Earth's ecosystems. Science 277: 494–499.

Ward, J. V., K. Tockner & F. Schiemer, 1999. Biodiversity of floodplain river ecosystems: ecotones and connectivity. Regulated Rivers: Research and Management 15: 125–139.

Ward, J. V., K. Tockner, D. B. Arscott & C. Claret, 2002. Riverine landscape diversity. Freshwater Biology 47: 517–539.

Zar, J. H., 1999. Biostatistical Analysis, 4th ed. Prentice Hall, New Jersey.