Tweedley, J.R., Bird, D.J., Potter, I.C., Gill, H.S., Miller, P.J., O'Donovan, G. and Tjakrawidjaja, A.H. (2013) Species compositions and ecology of the riverine ichthyofaunas in two Sulawesian islands in the biodiversity hotspot of Wallacea. Journal of Fish Biology, 82 (6). pp. 1916-1950.

Journal of Fish Biology

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--Manuscript Draft--

Manuscript Number:	
Full Title:	Species compositions and ecology of the riverine ichthyofaunas on two Sulawesian islands in the biodiversity hotspot of Wallacea
Short Title:	Freshwater fish ecology in Sulawesi
Article Type:	Regular paper
Keywords:	adaptive radiation; ecology; endemic and native; riverine and lacustrine fish; Sulawesi; Wallacea
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Abstract:	This account of the riverine ichthyofaunas of the islands of Buton and Kabaena, off south-eastern mainland Sulawesi, represents the first detailed quantitative checklist and ecological study of the riverine fish faunas in the biological hotspot of Wallacea. The results are based on analysing samples collected by electrofishing at a wide range of sites in July to September of 2001 and 2002. While the fauna was diverse, with the 2179 fish caught comprising 64 species and representing as many as 43 genera and 22 families, the catches were dominated by the Gobiidae (26 species and 25% by numbers), Eleotridae (7 species and 27% by numbers), Zenarchopteridae (3 species and 22% by numbers) and Anguillidae (2 species and 12% by numbers). The most abundant species were the eleotrids Eleotris aff. fusca-melanosoma and Ophieleotris aff. aporos, the anguillid Anguilla celebesensis, the zenarchopterids Nomorhamphus sp. and Nomorhamphus ebrardtii, and the gobiids Sicyopterus sp. and Glossogobius aff. celebius-kokius. The introduced catfish Clarias batrachus was moderately abundant at a few sites. Cluster analysis, allied with the SIMPROF routine, identified seven discrete groups, which represented samples from sites entirely or predominantly on either Buton (five clusters) or Kabaena (two clusters). Species composition was related to geographical location, distance from river mouth, % contribution of sand and silt, altitude and water temperature. The samples from the two islands contained only one species definitively endemic to Sulawesi, i.e. Nomorhamphus ebrardtii, and another presumably so, i.e. Nomorhamphus sp., contrasting starkly with the 57 fish species that are endemic to Sulawesi and most notably its large central and deep lake

	systems on the mainland. This accounts for the ichthyofaunas of these two islands, as well as those of rivers in northern mainland Sulawesi and Flores, being more similar to each other than to those of the central mainland lake systems. This implies that the major adaptive radiation of freshwater fishes in Sulawesi occurred in those lacustrine environments rather than in rivers.

Species compositions and ecology of the riverine ichthyofaunas on two Sulawesian islands in the biodiversity hotspot of Wallacea

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Running headline: Freshwater fish ecology in Sulawesi

ABSTRACT

This account of the riverine ichthyofaunas of the islands of Buton and Kabaena, off south-eastern mainland Sulawesi, represents the first detailed quantitative checklist and ecological study of the riverine fish faunas in the biological hotspot of Wallacea. The results are based on analysing samples collected by electrofishing at a wide range of sites in July to September of 2001 and 2002. While the fauna was diverse, with the 2179 fish caught comprising 64 species and representing as many as 43 genera and 22 families, the catches were dominated by the Gobiidae (26 species and 25% by numbers), Eleotridae (7 species and 27% by numbers), Zenarchopteridae (3 species and 22% by numbers) and Anguillidae (2 species and 12% by numbers). The most abundant species were the eleotrids *Eleotris aff. fusca-melanosoma* and *Ophieleotris aff. aporos,* the anguillid *Anguilla celebesensis*, the zenarchopterids *Nomorhamphus* sp. and *Nomorhamphus ebrardtii*, and the gobiids *Sicyopterus* sp. and *Glossogobius aff. celebius-kokius*. The introduced catfish *Clarias batrachus* was moderately abundant at a few sites. Cluster analysis, allied with the SIMPROF routine, identified seven discrete groups, which represented samples from sites entirely or predominantly on either Buton (five clusters) or Kabaena (two clusters). Species composition was related to geographical location, distance from river mouth, % contribution of sand and silt, altitude and water temperature. The samples from the two islands contained only one species definitively endemic to Sulawesi, *i.e. Nomorhamphus ebrardtii*, and another presumably so, *i.e. Nomorhamphus* sp., contrasting starkly with the 57 fish species that are endemic to Sulawesi and most notably its large central and deep lake systems on the mainland. This accounts for the ichthyofaunas of these two islands, as well as those of rivers in northern mainland Sulawesi and Flores, being more similar to each other than to those of the central mainland lake systems. This implies that the major adaptive radiation of freshwater fishes in Sulawesi occurred in those lacustrine environments rather than in rivers.

Key words: Sulawesi; Wallacea; riverine and lacustrine fish; endemic and native; ecology; adaptive radiation

INTRODUCTION

Wallacea, which comprises a group of islands between Asia and Australasia, is one of 25 biodiversity hotspots identified by Myers *et al*. (2000) on the basis that it contained very high concentrations of endemic species and was undergoing exceptional loss of habitat. The western and eastern boundaries of Wallacea are essentially defined by Wallace's line and Lydekker's line, respectively (Michaux, 2010; Fig. 1a). The islands of Wallacea, among which mainland Sulawesi is the largest, thus lie between the land masses on the Sunda Shelf, comprising the Malay Peninsula, Sumatra, Borneo and Java to the west, and those of the Sahul Shelf, including Australia and New Guinea, to the south and east (Fig. 1).

The 'barrier' produced by the deep ocean trenches that separate Wallacea from the land masses on the Sunda and Sahul continental shelves help account for the high level of endemism in the fauna of Wallacea (Wallace, 1863; Myers *et al.*, 2000). A collation of the species recorded in Wallacea emphasises the extent of this remarkable endemicity, with nearly 70% of its amphibians, nearly 60% of its mammals and over 40% of its reptiles and birds endemic to this region (Conservation International, 2012). Although the level of endemicity among freshwater fishes (20-25%) is not as great, it still represents a substantial number of species. Furthermore, the endemicity of freshwater fishes has been known, for some time, to be particularly high on mainland Sulawesi (Kottelat *et al.*, 1993). Indeed, Parenti (2011) has recently estimated that the freshwater ichthyofauna of Sulawesi contains as many as 56 endemic species, to which a recently-described species is now added (Huylebrouck *et al.*, 2012). Among these 57 species, 45 are atherinomorphs (represented by the orders Atheriniformes and Belonifomes), with the remainder comprising perciforms, *i.e.* gobioids and a single terapontid species. Most of these species were described, however, from the large central tectonic lake systems (Kottelat, 1990a,b,c, 1991; Herder *et al.*, 2006b).

Several authors have emphasised that the endemic fish species, of particularly the above lake systems of Sulawesi, are becoming increasingly threatened from a range of anthropogenic effects, especially those brought about by the destruction or alteration of habitats, the introduction of exotic species, the collection of fish for the aquarium trade, overfishing and pollution, and that these effects have undoubtedly led to the extinction of certain species (Whitten *et al.*, 1987; Kottelat *et al.*, 1993; Parenti, 2011; Herder *et al.*, 2012). The need to conserve the remarkable freshwater ichthyofaunas of Sulawesi requires a thorough understanding of the compositions of these fish communities and the factors that influence their structure. Remarkably, however, there have been no detailed quantitative ecological studies of the fish communities of either the rivers or lakes of Sulawesi.

The islands of Buton and Kabaena, which occupy 4,640 and 873 km^2, respectively, are located off the south-eastern coast of mainland Sulawesi (Fig. 1b). The mountainous regions of both islands contain areas of relatively undisturbed forest, within which the river sources are located. The composition of the substrata of the rivers of these two islands ranges from mainly large boulders and pebbles in faster-flowing regions to fine sands and silts where the current is slowest. Michaux (2010) has stated that the satellite islands of Sulawesi, such as Buton, share many endemic species with its mainland, or have their own subspecies of Sulawesian endemics, and that these islands and the mainland thus constitute a common area of endemism. It should be recognised, however, that it is not clear whether this generalisation applies to the fishes in the fresh waters of Buton and Kabaena as these ichthyofaunas have not been sampled intensively and these islands differ from mainland Sulawesi in not possessing the large tectonic lake systems that contain most of the endemic freshwater fish species of Sulawesi (Parenti, 2011).

The aims of this study were as follows. 1) Compile the first quantitative checklist of the fish species of the rivers on Buton and Kabaena and thus ascertain which are the most abundant species, genera and families and whether any of the species are endemic to one or both of these satellite islands of Sulawesi or to Sulawesi in general. 2) Determine the structure of the ichthyofaunal communities of those two islands by identifying statistically the groups of sites at which the ichthyofaunal compositions were similar and which differed from those of all other such groups. 3) Determine the extent of the relationships between the ichthyofaunal compositions of the different groups identified above and a suite of environmental variables and thus identify the characteristics of the typical habitats of the main species and particularly of those that are endemic to Sulawesi. 4) Compare the species compositions of the riverine ichthyofaunas of Buton and Kabaena with those recorded elsewhere in Wallacea, placing particular emphasis on exploring the extent to which any differences among locations are related to whether the faunas are in rivers or lake systems. To achieve the above aims, fishes were sampled at sites chosen to encompass a wide range of the environmental characteristics found in the rivers of Buton and Kabaena and the resultant ichthyofaunal data are compared with those previously published for the fish faunas of the freshwaters of Wallacea as a whole.

MATERIALS AND METHODS

SAMPLING AND ENVIRONMENTAL MEASUREMENTS

The fishes in rivers on the islands of Buton and Kabaena, off the south-eastern corner of mainland Sulawesi (Fig. 1c,d), were sampled by electrofishing (Electrocatch International, Model WFC911-96) between mid-July and mid-September in both 2001 and 2002. Thirty seven sites were sampled in 2001 (27 on Buton and 10 on Kabaena) and 26 in 2002 (18 on Buton and 8 on Kabaena), with the sites being chosen so that they encompassed a range of the environmental characteristics found within the rivers of the two islands. Sampling was confined to the freshwater reaches of the rivers, as defined by an upper limit in conductivity of 600 µS.

The latitude, longitude and altitude of each site were recorded from a Global Positioning System (GPS; Garmin 12X model). The first two variables were then employed to map the location of each site in a Geographical Information System (GIS) using ArcGIS 10 software (ESRI, California, USA), thereby enabling the distance from each site to the coast in a straight line to be measured. A straight line measure, rather than the course of the river, was used because the precise paths of some of the rivers sampled were not available in a GIS format.

The following environmental variables were measured at each site on each sampling occasion. 1) Minimum and maximum widths and depths of the stream or river, 2) water temperature and pH (Hanna Instruments Ltd.; HI-9023C portable waterproof temperature and pH meter), 3) flow rate in the water column at a point *c.*60% of the distance from the substrate to the water surface (MJP Geopacks Flow Meter) and 4) conductivity (Hanna Instruments Ltd.; HI-9033 multi range waterproof conductivity meter). Although problems were frequently encountered with the oxygen meter (Hanna Instruments Ltd.; HI-9142), which could not readily be rectified due to the isolation of the sampling sites, the reliable measurements recorded at *c.* two thirds of the sites sampled in 2002 typically corresponded to percentage saturation values in excess of 80%.

The diameters of sub-samples of the larger components of the substratum and of particles of varying coarseness >2 mm in diameter were measured at each site on each sampling occasion. Following the Wentworth Classification scale (Wentworth, 1922), components with diameters >256 mm comprised boulders, whereas those with diameters of 65-256, 17-64 and 3-16 mm represented cobbles, pebbles and gravel, respectively. The smallest particles in the sediment were broadly separated visually into sand and silt according to whether they were light in colour and dropped out of suspension rapidly or darker in colour and settled more slowly after disturbance. The approximate percentage contributions of the different components of the substrate at each site were then calculated.

From the above, it follows that values were obtained for 18 variables for determining the types of environmental factor considered likely to influence the composition of the ichthyofaunas in the rivers of Buton and Kabaena.

SAMPLING OF FISH FAUNAS

The fish fauna at each site was sampled by moving the electrofisher slowly upstream for *c.*1h in a zigzag manner so that the full width of the river or stream came within the operational range of the electrodes. Two assistants used hand nets to catch the immobilised fish, which, as the water was always clear, could readily be detected, irrespective of their body size and position in the water column. Each fish was lightly anaesthetised in a weak solution of Benzocaine and, using Kottelat *et al.* (1993), identified to the lowest taxonomic level possible, which was usually species, except with many of the gobiids and eleotrids, *i.e.* gobioids. The standard lengths (SL) of the vast majority of the fish caught were measured to the nearest 1 mm. All of the fish identified to species were transferred to a large bucket containing fresh, well-aerated water and, when fully recovered, most were returned to the river or stream. A reference collection of all retained taxa was lodged with the Museum Zoologicum Bogoriense in Cibinong, Java. Those individuals that could not be identified to species were preserved in 70% ethanol and their taxonomic characteristics later examined in the laboratory. In the case of the Gobiidae and Eleotridae, representative samples were transported to Bristol University, where they were examined by one of us (P.J. Miller), who was able to identify each individual to species, or to its closest affinity or genus when the head papillae, a crucial diagnostic characteristic of that family, had become abraded. The gobioid fish species were identified using Harry (1948), Koumans (1953), Akihito (1967), Miller (1973), Akihito and Meguro (1975a,b, 1976), Wongrat (1977), Sakai and Nakamura (1979), Murdy and Hoese (1985), Akihito *et al.* (1988), Miller (1989), Miller *et al.* (1989), Watson (1991, 1992), Kottelat *et al.* (1993), Watson and Kottelat (1994), Larson (2001), Larson and Murdy (2001), Allen *et al.* (2002), Keith *et al*. (2005), Larson (2009), Hoese and Allen (2011), Keith *et al.* (2011a,b) and Maeda *et al.* (2011). Representatives of these taxa are lodged with the Natural History Museum, London. P.J. Miller has also retained some individuals for his own ongoing studies of gobioid systematics. Fifty eight gobies from Kabaena were lost in transit and are subsequently designated as Gobiid spp. Eleven specimens of a *Nomorhamphus* species were also brought back and lodged with the National Museum of Natural History, Smithsonian Institution, Washington, but these were all females and thus lacked the anal fin crucial for identifying the species in this genus (B. Collette, pers. comm.). This species is thus subsequently referred to as *Nomorhamphus* sp. Note that a preliminary list of the freshwater fish species of Buton was published by Tjakrawidjaja (2006), but that this used data collected from only six of the sites sampled during the present study and prior to the identification of several of the goby species.

STATISTICAL ANALYSES

All statistical analyses of the fish community data were undertaken using the routines in PRIMER v6 (Clarke and Gorley, 2006) and employing the square root of the percentage contribution of each species in each sample to avoid any group being excessively dominant (Lek *et al.*, 2011). As a one-way Analysis of Similarities (ANOSIM) test (Clarke, 1993), using a Bray-Curtis resemblance matrix derived from the percentage contributions of the various species in 2001 and 2002, demonstrated that the ichthyofaunal composition in those two years were not significantly different ($R = 0.012$; $P = 0.298$), the data for the two years were combined for subsequent analyses.

The Bray-Curtis resemblance matrix, derived from the above percentage contributions of the various species at the different sites, was subjected to hierarchical agglomerative clustering using group-average linkage (CLUSTER), in combination with the Similarity Profiles (SIMPROF) routine (Clarke *et al.*, 2008). The latter test enabled the groups of samples in which the species compositions of the fish faunas were not significantly different, but which were significantly different from other such groups, to be identified. The null hypothesis that the species compositions of the various samples were not significantly different was rejected if the significance level (P) associated with the test statistic (π) was < 0.05. The above Bray-Curtis resemblance matrix was also used to produce a non-metric Multi-Dimensional Scaling (nMDS) ordination plot.

Similarity Percentages (SIMPER; Clarke, 1993) was employed to elucidate which species typified the assemblages at each of the groups of sites identified by SIMPROF as discrete and which species contributed most to differences between the compositions of each pair of such groups. Focus was placed on those typifying and distinguishing species with the highest similarity/standard deviation ratio and dissimilarity/standard deviation ratio, respectively, and which were most abundant.

The Biota and Environment matching routine (BIOENV; Clarke and Ainsworth, 1993) was used to determine the combination of environmental variables that best explained the differences between the ichthyofaunal compositions of the clusters identified by SIMPROF. Prior to using this routine, Draftsman plots of the values recorded for each pair of the 18 environmental variables at each site were visually examined to assess whether the data for each variable were skewed and, if so, which type of transformation was required to ameliorate that effect, and also whether the data for any pair of variables were highly correlated. These plots demonstrated that altitude, the minimum width of the river and the percentage contributions of boulders, cobbles, pebbles, gravel, sand and silt all required a square root transformation, while water temperature required a fourth root transformation and the remaining ten variables no transformation. Note that only the minimum width of the river was included as it was highly correlated with maximum river width. The environmental data were then normalised so that all variables were on a common scale. The null hypothesis for the BIOENV test, that the pattern of rank orders of similarity between the faunal resemblance matrix and environmental data was not related, was rejected if the significance level (P) was < 0.05. The value for the test statistic (ρ) reflects the strength of the correlation between the composition of the fauna and the environmental data, with ρ values ranging from *c.* 0 (little correlation) to *c.* 1 (near perfect correlation).

Bubbles of varying size, representing the magnitude of each of the main environmental variables selected by BIOENV as related to ichthyofaunal composition, were superimposed separately on a nMDS ordination plot derived from a matrix constructed from the means of the percentage contributions of each species in each cluster. The means of the same ichthyofaunal data and the values for the corresponding six environmental variables selected by BIOENV (see above) were used to produce separate matrices that were then subjected to the RELATE procedure. The resultant ρ value complements that produced by BIOENV using data for individual samples, with the null hypothesis being the same as for the BIOENV procedure.

The presence or absence of the native and endemic species collected from the rivers of Buton and Kabaena were collated with comparable data recorded previously for freshwater locations elsewhere in Wallacea, *i.e.* the Malili Lakes system and Lake Poso in central mainland Sulawesi, and four lakes in northern Sulawesi and in rivers in northern Sulawesi, Flores and Timor (see Appendix I for the full list of references). The resultant composite data were used to produce a Bray-Curtis resemblance matrix for constructing a dendrogram and, employing hierarchical agglomerative clustering using group-average linkage, to elucidate the relationships between the fish faunas in the different regions and between rivers and lakes.

Note that care has been taken to distinguish between native and endemic species in the comparisons between the ichthyofaunas in the various rivers and lakes because this distinction is crucial when discussing the adaptive radiation of fishes in the fresh waters of Wallacea. In this study of the fish faunas of Sulawesi and Wallacea, Parenti (2011) is followed in using the term native for a species in an area when its natural distribution includes, but is not restricted to that area, whereas a species is considered endemic to an area when it is restricted to that area, *e.g.* a particular lake system, Sulawesi or Wallacea, with the identify of the area in question being precisely designated in the text. When referring to native and endemic species collectively, the term 'non-introduced' is employed for clarity.

RESULTS

QUANTITATIVE CHECKLIST OF SPECIES AND FAMILIES

A total of 2179 fish was caught between mid-July and mid-September of 2001 and 2002 by electrofishing at numerous sites in the rivers of the islands of Buton and Kabaena (Table I; Fig. 1c,d), on which the environmental characteristics of the sites ranged widely (Fig. 2). The total catch contained 51 taxa that could be allocated either to a given species (noting that, in five of those cases, this referred to those species with which it has the greatest affinity, *e.g. Eleotris aff. fusca-melanosoma*), and 13 species that were clearly discrete and could be assigned to a particular genus (Table I). There was a small number of unidentified gobies, designated as gobiid spp., whose genus could not be identified (see Materials and Methods). The number of definitive genera and families were 43 and 22, respectively (Tables

I, II). The vast majority of the individuals belonged either to identifiable species (75%) or to discrete species whose genus was readily identifiable (22%). Examples of the range of body form, coloration and adaptations exhibited by the fishes of Buton and Kabaena are illustrated in Fig. 3.

Eleotris aff. fusca-melanosoma was the most abundant species overall, contributing *c*. 18% numerically to the total catch from both islands, followed by *Anguilla celebesensis* with *c*. 12% (Table I). *Nomorhamphus* sp., *Nomorhamphus ebrardtii*, *Sicyopterus* sp., *Glossogobius aff. celebius-kokius* and *Ophieleotris aff. aporos* were also relatively abundant, with each being represented by more than 100 individuals and thereby comprising $\geq$5% of the total catch. The above seven species contained two species of each of the Eleotridae, Zenarchopteridae (formerly part of the Hemiramphidae, see Lovejoy *et al*., 2004) and Gobiidae and a single species of the Anguillidae.

The Gobiidae was the most diverse family, with 26 species from 12 genera, followed by the sister family Eleotridae, of which there were seven species that each belonged to a different genus (Table II). The numbers of the Gobiidae, Eleotridae and Zenarchopteridae each contributed between *c*. 22 and 27% to the total catch (Table II). The only other family to contribute more than 4% was the Anguillidae with just over 12%.

The contributions made by some species to the catches on Buton and Kabaena differed markedly and particularly so with the two species of zenarchopterid caught during the study (Table I). Thus, *Nomorhamphus* sp. ranked second in abundance and contributed *c*.16% to the total catch from Buton, but was not recorded from Kabaena, whereas *Nomorhamphus ebrardtii* ranked first in abundance and contributed as much as 33.5% to the samples from Kabaena and was not found on Buton. The most abundant species on Buton, *Eleotris aff. fusca-melanosoma*, contributed *c*. 24% to the catches from that island but only *c*. 4% to those from Kabaena. In contrast, the eel *Anguilla celebesensis* ranked third in abundance and made a similar contribution, *i.e.* 11-12%, on both islands (Table I). Among the other identified species, 45 were found only on Buton and five only on Kabaena, but none of these was abundant. *Nomorhamphus ebrardtii* was the only species definitively endemic to Sulawesi (Table I), recognising, however, that this is probably also true for the other *Nomorhamphus* species, which could not be assigned to a particular species (see Discussion). Forty six species were native to Sulawesi and seven were introduced (Table I). All but one of the introduced species were of commercial value and belonged to either the Clariidae, Channidae or Cichlidae.

SITES WITH SIMILAR SPECIES COMPOSITIONS

Cluster analysis, using the matrix constructed from the contributions of the different species to the catches obtained at each of the various sampling sites, allied with the use of the SIMPROF routine, identified seven clusters within which the compositions of the fish faunas were similar and significantly different (P <0.05) from those in all other clusters (Fig. 4). There were also two outliers, each from Buton and represented by a single species, one containing just the catfish *Clarias teijsmanni* and the other only the killifish *Aplocheilus panchax*. The data for these sites were not included in subsequent analyses.

Five of the seven clusters contained samples obtained entirely from sites on either Buton, *i.e.* B1, B2, B4 and B5, or Kabaena, *i.e.* K2 (Fig. 4). One of the two remaining and largest clusters (B3) comprised 24 samples, of which 22 were from Buton, while the other (K1) contained 16 samples, of which 13 were from Kabaena.

The main typifying species for the fish faunas comprising the Buton clusters B1 and B2 was *Nomorhamphus* sp., while *Eleotris aff. fusca-melanosoma* was an important typifying species for B3, B4 and B5 (Table III). The K2 cluster, which comprised samples solely from sites on Kabaena, was typified by another species of zenarchopterid, *Nomorhamphus* *ebrardtii*, and the introduced catfish *Clarias batrachus*. The eel *Anguilla celebesensis* typified the catches, not only of clusters B1 and B3, but also of K1 and K2, whereas *Sicyopterus* sp. typified the samples in both the B1 and K1 clusters (Table III).

Within the group of clusters designated B1 to B5, it was particularly evident that relatively greater and consistent contributions by *Nomorhamphus* sp. distinguished the samples from B1 from those from all others and also those of B2 from the samples in the B3, B4 and B5 clusters (Table III). In contrast, relatively greater and consistent contributions of *Eleotris aff. fusca-melanosoma* distinguished the samples in the B3 cluster from those in all other 'Buton' clusters and likewise *Glossogobius aff. celebius-kokius* distinguished the B5 cluster from all other 'Buton' clusters. Larger contributions of *Clarias batrachus* were crucial for distinguishing the samples comprising K2 from those of K1, whereas the reverse was true for *Sicyopterus* sp. (Table III). Indeed, the latter goby species and three other congenerics were all found in samples yielding the K1 cluster but not in those of K2. The most striking of the features that distinguished the 'Buton' from 'Kabaena' clusters was the presence of substantial numbers of *Nomorhamphus* sp. in the samples from sites contributing to the B1 and B2 clusters (with lesser numbers in B5) and the absence of this species in both of the Kabaena clusters, *i.e.* K1 and K2, whereas the other zenarchopterid, *Nomorhamphus ebrardtii,* was confined to the samples from K1 and K2 and was particularly abundant in those from the latter cluster for which it was a typifying species.

RELATIONSHIPS BETWEEN SPECIES COMPOSITIONS AND ENVIRONMENTAL VARIABLES

The points for the samples from the seven clusters on the ordination plot, derived from the percentage composition of each species in each sample and coded for the clusters selected by SIMPROF, group in a similar manner to that in the cluster analysis derived using the same data (*cf.* Figs 4,5). Thus, the samples representing the main Buton cluster (B3) and Kabaena cluster (K1) formed separate groups in the middle part of the ordination plot, with those for the other Buton clusters (B1, B2, B4 and B5) lying outside those for B3 and those for K2 lying below those for K1 (Fig. 5).

Longitude, distance from river mouth, the percentage contributions of both sand and silt to the substrate, altitude and water temperature were the combination of variables selected by BIOENV that best explain the differences among the compositions of the fish faunas of the samples comprising the seven clusters identified as distinct by SIMPROF ($\rho = 0.44$; $P = 0.01$). When the percentage contribution of each species in each sample for each cluster and the values for each of the six environmental variables selected by BIOENV (see above) were averaged and used to produce separate matrices that were then subjected to the RELATE procedure, the ρ value increased to 0.69 ($P = 0.02$).

When superimposed on the above ordination plot, the sizes of the bubbles representing longitudinal position were larger for the five clusters comprising samples that were obtained exclusively, or predominantly, from sites on Buton (B1-B5) than for those for the clusters comprising samples entirely or mainly from Kabaena, *i.e.* K1 and K2 (Fig. 6a). This emphasises that the compositions of the fish faunas from the two islands were related to a factor or factors associated with their geographical location. Variations in the magnitude of the bubbles in Fig. 6b demonstrate that the differences between the ichthyofaunal compositions of the B1 and B2 clusters and those of the B3, B4 and B5 clusters reflect the fact that the samples for the first two clusters come from sites located further from the river mouth. The bubble plots showed that the samples comprising the K1 and K2 clusters were obtained from sites whose distances from the river mouth were similar to each other and were far more similar to those yielding the B1 and B2 clusters than the B3-5 clusters.

While the mean percentage contributions of sand to the substrate from which the samples comprising the B3, B4 and B5 clusters were obtained were all moderate (5-9%), this variable ranged widely from as low as 2% at B1 to as high as 29% at B2. Although the percentage contribution of silt at the sites from which the samples contributing to B1 and B2 followed the opposite trend to that of sand, there was a far greater variation in the amount of silt at sites yielding the B3 to B5 clusters than was the case with sand (*c.f.* Fig. 6c,d), with values ranging from as low as 5% for B3 and B5 to as high as 95% at B4. In the case of Kabaena, the substrate at the sites contributing the samples for the K2 cluster was characterised by a greater percentage of sand, and more particularly silt, than those contributing to the samples in the K1 cluster (Fig. 6c,d).

The average altitude of the sites from which the samples for the B3, B4 and B5 clusters were obtained ranged only from 32 to 51 m, and were thus greater than those which yielded the B1 cluster, *i.e.* 23 m, and far lower than that for the B2 cluster, *i.e.* 123 m (Fig. 6e). The average altitudes from which the samples comprising the K1 cluster, *i.e.* 106 m, and K2 cluster, *i.e.*, 118 m, were similar to those of the B2 cluster. The average temperatures at the sites from which the samples representing each cluster were obtained varied markedly, with, among the Buton clusters, the 31°C for B5 being greater than the 25-27°C for the B2, B3 and B4 clusters and the 22°C for the B1 cluster (Fig. 6f). The average temperature at sites contributing samples to the K2 cluster (29°C) was greater than those for the K1 cluster (25°C).

COMPARISONS OF FRESHWATER ICHTHYOFAUNAS WITHIN WALLACEA

On the basis of cluster analysis, derived from the presence or absence of the various native or endemic fish species in the rivers and lakes of Sulawesi, Flores and Timor, the faunas in all of the rivers formed a broad cluster separate from those in all of the lakes

(Fig. 7). However, the extents of the similarity among the various riverine groups demonstrate that the faunas in the rivers did comprise essentially the three groups, *i.e.* 1) Buton and Kabaena, 2) northern Sulawesi and Flores, and 3) Timor, the last of which was the most distinct. The fish faunas of the two central lakes (Malili and Poso) and the northern lakes on mainland Sulawesi were joined at a very low level of similarity (Fig. 7).

The eleven native species found in the rivers of both Buton and Kabaena contain six that have not been recorded in the other rivers of Wallacea (Table I, Appendix I). Eight native species were recorded in the rivers of both northern Sulawesi and Flores, among which the goby *Sicyopterus longifilis* was not found elsewhere. The list of 49 species for Timor contained only 17 that were found in the rivers of at least one of the other regions (Appendix I). The 32 species not recorded in the other regions included two or more species of the Anguillidae, Mugilidae, Atherinidae, Ambassidae and Terapontidae.

The native or endemic fish species in the Malili Lakes system contained at least 17 species of Melanotaenidae, represented entirely by members of the Telmatherininae (Celebes rainbowfishes), four species of the Adrianichthyidae comprising members of the Oryziinae (ricefishes), four species of Zenarchopteridae (halfbeaks), all belonging to the subfamily Zenarchopterinae, and ten species of Gobiidae (Appendix I). All but one of the above species are apparently endemic to the Malili Lakes system. The fish fauna of Lake Poso also contained species of the Adrianichthyidae (ricefishes), four of which belong to *Adrianichthys* and two to *Oryzias* (Appendix I), noting that, since the major recent revision of ricefishes and their relatives, those two genera are now no longer considered equivalent to the subfamilies Adrianachthyinae and Oryziinae (Parenti, 2008). The remaining species, comprising two gobiids and one zenarchopterid, are likewise endemic to Lake Poso (Appendix I). The only native fish species found in both of these two large central lake systems is the wide-ranging *Aplocheilus panchax*.

The native fish fauna of the lakes in northern Sulawesi was depauperate, comprising only five species, which probably reflected the detrimental impact of introduced species, of which as many as 12 have been recorded in these systems (Haryono, 2004). While gobiids and eleotrids collectively represented between 56 and 73% of all native and endemic species recorded in the rivers of Buton, Kabaena, northern Sulawesi and Flores, the gobys constituted only 20 to 28% of all such species in the Malili Lakes system and Lake Poso and eleotrids were not recorded in either of these water bodies (Appendix II).

DISCUSSION

MAIN OVERALL FINDINGS

The quantitative checklist, developed for the fish species in the rivers of Buton and Kabaena following extensive sampling of a range of habitats in those islands, provides the first such comprehensive data for any area within the biogeographically important region of Wallacea. The results emphasize that, while the ichthyofaunas of the riverine environments in these nearby satellite islands off the mainland of Sulawesi house no primary native freshwater species, they are diverse, containing 64 species that were distributed among as many as 43 genera and 22 families. The Gobiidae was shown to be by far the most speciose family and to contain many species that undergo an amphidromous migration and, in conjunction with the closely-related Eleotridae, to comprise more than half the total catch of fish. In terms of abundance, the remainder of the fauna was dominated by the Zenarchopteridae and Anguillidae.

Interpretation of the relevance of the data collected for the fish faunas of Buton and Kabaena benefited greatly from the results obtained by subjecting those data to a sequence of contemporary multivariate statistical analyses. The use of the recently-developed SIMPROF routine (Clarke and Gorley, 2006; Clarke *et al.*, 2008) was particularly valuable as it identified the sites that formed groups within which the species compositions were similar, but differed significantly from those in all other such groups. The use of this routine revealed that five of the seven clusters represented the compositions in samples that came from sites that were all on Buton, while one of the other clusters represented samples from sites located predominantly on Buton and the other from those situated predominantly on Kabaena. Thus, while the distinction between the compositions of the ichthyofaunas on the two islands was pronounced, it was not absolute. These results, in conjunction with analyses of environmental data using BIOENV, emphasized that the species at sites within each cluster are associated with a particular suite of environmental characteristics and the use of SIMPER identified the main species consistently found in each of those ‘habitat types’. Such data will be crucial for developing management plans for conserving the native fish fauna and, in particular, any species that are endemic to Sulawesi. The subjection to cluster analysis of the data for Buton and Kabaena and for fish communities in inland waters throughout other parts of Wallacea, as recorded in previous studies, revealed that, at a broad level, the faunas in the rivers were distinct from those in the lake systems, in which the vast majority of the endemic species in the region are located.

The following sections of the discussion have focused on the main fish families on Buton and Kabaena and the features that have contributed to their success. The type(s) of environmental conditions in which their most abundant native species were consistently prevalent have been emphasised, noting that the particular suite of species that typify each ‘habitat type’ are recorded in full in the results and Table III. Finally, the questions of introduced species and the implications of the differences between the compositions of the fish faunas of the river and lake systems within Wallacea are considered.

GOBIIDAE

The success of the Gobiidae in the rivers on the islands of Buton and Kabaena is reflected in the following. 1) The members of this family contribute approximately half the number of native fish species in the rivers in each of these islands. 2) Their species contributed as much as approximately one fifth and one third of the individuals in the catches of ‘non-introduced’ fish species on Buton and Kabaena, respectively. 3) Gobies were widely distributed, being recorded in samples from sites represented within each of the seven main clusters identified by SIMPROF for Buton and Kabaena, and a goby species was a typifying species for the small suite of species that typified three of those main clusters (B1, B5 and K1 in Table III). The very high prevalence of gobiids on Buton and Kabeana parallels the situation with the ichthyofaunas of the rivers of northern mainland Sulawesi and Flores (Haryono *et al.*, 2002; Tjakrawidjaja, 2002; Haryono, 2004).

The high diversity and large numbers of the Gobiidae in the riverine faunas of Wallacea is a characteristic of the fish faunas of high island streams of the tropical Indo-Pacific in general (Ryan, 1991; Jenkins *et al.*, 2010; McDowall, 2010; Thuesen *et al.*, 2011). It is thus relevant that many goby species in this region exhibit amphidromy, *i.e.* they are swept out to sea as larvae but later return to rivers where they eventually become mature, and that such migrations are particularly prevalent among species living on small tropical and subtropical islands (Keith, 2003; McDowall, 2010; Keith and Lord, 2011). Furthermore, amphidromy is most common among the Sicydiinae (McDowall, 2010), whose species contributed *c.* 40% to the total number of goby species found on Buton and Kabaena, and is exhibited among the *Glossogobius* species by at least *G. aff. celebius-kokius* (Hoese and Allen, 2011; Keith and Lord, 2011), which is well represented on these islands. Such movements by these amphidromous gobiids into marine waters would have enabled these species to be dispersed across the marine divide and into the rivers of recently-emerged high islands of the Indo-Pacific. They would have then been able to colonise the range of riverine habitats on islands such as Buton and Kabaena, which emerged within the last five million years (Lohman *et al.*, 2011) and within which there are no native, primary freshwater species (Kottelat *et al.*, 1993).

The ability of gobies to colonise a variety of habitats would have been facilitated by their range in body size, behaviour, diet and morphological adaptations, such as the possession of a sucker-like pelvic fin (Fig. 3d), which allows them to maintain their position in areas of rapid flow and facilitates movement over or around structures such as waterfalls (*e.g.* Ryan, 1991; Keith, 2003; Blob *et al.*, 2007, 2008). Such obstacles to movements are numerous in the rivers of Buton and Kabeana (Fig. 2a,b). An example of an alternative adaptation for counteracting the effects of rapid flow is provided by another gobioid, *Rhyacichthys aspro*. This species possesses a flattened ventral body surface, pelvic fins that contribute to a suction device and large and broad pectoral fins that create a hydrofoil force with a downward component (Miller, 1973; Nelson, 2006; Fig. 3e).

The fact that the most abundant species of goby overall, *Sicypopterus* sp., was among the most important typifying species for the ichthyofaunal compositions of the sites in the B1 and K1 clusters emphasizes that this goby is consistently abundant at a group of sites on both Buton and Kabaena. It is therefore relevant that the sites in both clusters were located in relatively upstream areas in undisturbed forest where there was little sand or silt and the water was cool (Figs 2a,b; 5). The congener *S. zosterophorum* was also consistently found at the sites from which the samples representing the B1 cluster were obtained. In contrast, the second most abundant goby, *Glossogobius aff. celebius-kokius*, was the most important typifying species for the B5 cluster on Buton, which represented samples obtained from sites located at lower altitudes and much further downstream and in exposed areas where temperatures were particularly high (Fig. 5). The fact that the upstream and downstream locations occupied by the above abundant gobiid species differ would contribute to marked differences in community structure in different reaches of the river, as has been found in the community structure of Fijian rivers (Jenkins and Jupiter, 2011). Indeed, the fact that gobies were present at sites which contributed samples to the other four clusters emphasizes that gobies are distributed across a wide range of environmental niches in the rivers of Buton and Kabaena.

ELEOTRIDAE

Although the Eleotridae was represented overall on Buton and Kabaena by fewer species than the Gobiidae *i.e.* 7 *v.* 26, it made a similar large contribution to the overall catch of fish on those two islands, thereby accounting for the number of individuals of these two closely-related families collectively comprising approximately half of the fish caught. As with many gobiid species in Buton and Kabaena (see above), the species of eleotrid recorded on these islands are almost certainly all amphidromous (McDowall, 1988; Donaldson and Myers, 2002; Maeda and Tachihara, 2005; Maeda *et al.*, 2007). Thus, as with gobies, the sucessful colonisation of these islands by eleotrids was presumably achieved through the distribution of their larvae and young juveniles via the marine environment.

It is noteworthy, however, that, while the eleotrid *Eleotris aff. melanosoma-fusca* was a typifying species of the fish fauna at sites representing three of the seven clusters, all of which were on Buton (B3, B4, B5), a goby species was not likewise a typifying species for the first two of those clusters. This difference is attributable to the fact that the sites that yielded consistently high numbers of this eleotrid were located at relatively low altitudes and in the lower reaches of rivers (Fig. 2d), where there is a substantial amount of sand and/or silt (Fig. 5), and thus further downstream than the two clusters of sites at which the goby

Sicypopterus sp. was such an important typifying species (B1 and K1). The type of habitat in which *E. aff. melanosoma-fusca* is most abundant is consistent with this species being recorded as associated with soft substrata in tropical and sub-tropical rivers and brackish waters (Allen *et al.*, 2002; Maeda and Tachihara, 2004; Maeda *et al.*, 2007).

As another eleotrid, *Ophiocara porocephala*, was the main typifying species of the samples from the sites represented by the B4 cluster, it is typically found in downstream areas (as with *E. aff. melanosoma-fusca*), and, in this case, where the silt content is particularly high. This finding is consistent with the fact that, in the Angabanga river system in Papua New Guinea, *O. porocephala* was found only in muddy sites and that it was often abundant in estuaries within which it can complete its life cycle (Blaber *et al.*, 1989; Blaber and Milton, 1990; Hyslop, 1999).

The far poorer representation of the Eleotridae in Kabaena than Buton may have been due partly to the rivers on this island having, by necessity, being sampled mainly in their more inland regions some distance from the coast and thus further from their typical downstream habitats. This would also help explain why the eighth most abundant species, the flagtail *Kuhlia marginata*, which appears to be most abundant in the downstream regions of rivers elsewhere (Hyslop, 1999; Randall and Randall, 2001), was recorded only from Buton.

ZENARCHOPTERIDAE AND ANGUILLIDAE

Although the Zenarchopteridae was represented by only three species (among which only two were abundant) and two genera, its numbers still constituted over 21% of the total catch from Buton and Kabaena collectively and thus ranked as high as third in terms of overall abundance. Furthermore, one of these species, *i.e. N. ebrardtii*, was among the 56 species, which, on the basis of a collation of the results of previous publications (*e.g.* Kottelat *et al.*, 1993; Meisner, 2001; Collette, 2004), was listed by Parenti (2011) as endemic to the freshwaters of Sulawesi, and to which a recently-described species must now be added (Huylebrouck *et al.,* 2012). As all of the *Nomorhamphus* species recorded for Sulawesi are endemic to Sulawesi, it seems reasonable to assume that *Nomorhamphus* sp. is likewise almost certainly endemic to that region.

It was particularly striking that the catches of *Nomorhamphus* sp. and *N. ebrardtii* were so substantial that these two species ranked, respectively, third and fourth overall in terms of abundance, and yet the former was caught only on Buton and the latter only on Kabaena. It would thus appear that a small group of *Nomorhamphus* sp. found its way to Buton and, then in the absence of primary freshwater species, rapidly multiplied and that the same was true for *N. ebrardtii* on Kabaena.

The sites at which *Nomorhamphus* sp. was a typifying species were located in upstream areas in relatively undisturbed forest, where there was extensive overhanging vegetation and relatively cool water temperatures and only a small amount of silt (Figs 2b, 5). The large numbers of invertebrates deposited on the water surface from the overhanging vegetation would provide an abundant food source for this live-bearing zenarchopterid species (Kottelat *et al.*, 1993; Meisner, 2001). The same environmental characteristics are found at the sites on Kabaena (K1) that yielded the other *Nomorhamphus* species, *i.e. N. erbrardtii*.

It is highly relevant that, while the Anguillidae was almost exclusively represented by *Anguilla celebesenis,* this very abundant species was the only one present in every sample and typified the fauna of two of the Buton clusters and of both of those from Kabaena. This implies that the glass eel stage of this catadromous species exhibits no strong ‘preference’ to enter a given river or for later stages subsequently to colonise sites within a river that have particular environmental characteristics.

INTRODUCED FISH SPECIES

The detrimental impacts of introduced fish on the native fish species on the Sulawesian mainland, and particularly on those in the large central lake systems which contain such a diverse and endemic fauna, have been widely recognised (Whitten *et al.*, 1987; Kottelat *et al.*, 1993; Parenti, 2011; Herder *et al.*, 2012). All but *Rasbora* sp. of the seven introduced species recorded in the rivers of Buton and Kabaena (Table I) were stocked as a food source (Whitten *et al.*, 1987) and all except *Clarias batrachus* were found on only one of the islands. The latter clariid was the only introduced species that was even moderately abundant on either island and the only one to constitute a typifying species for a cluster, *i.e.* K2. This latter finding does indicate, however, that *C. batrachus* can have a serious influence on the composition of the native fish fauna in a river on the satellite islands of Sulawesi and is consistent with this species being among the eight freshwater fishes listed by Cambray (2003) as among on the one hundred world's worst invasive alien species. Furthermore, as the sample from a Buton riverine site, representing one of the two outliers in the dendrogram (Fig. 4), contained only *Clarias teijsmanni*, the introduction of this catfish would appear to have been responsible for the extinction of the local native fish community at that site. Although there are no large lakes on Buton, the sampling of one of its few small lakes (Lasalimu) on two occasions yielded 346 tilapia *Oreochromis niloticus*, a congener of another of the world's worst invasive alien species, and no other fish species (D. Bird pers. observ.). This emphasises that the native/endemic fish faunas of lakes in Sulawesi are particularly susceptible to elimination by certain introduced species, especially when, as with Lake Lasalimu, they are already partly degraded through anthropogenic effects such as eutrophication.

Buton and Kabaena contain none of the ancient, large and deep lake systems that are present in the central highlands of mainland Sulawesi and within which fish and other taxa have undergone extensive adaptive radiations (von Rintelen *et al.*, 2004; Herder *et al.*, 2006a; Schubart and Ng, 2008; von Rintelen *et al.*, 2010). It is thus relevant that *N. ebrardtii* on Kabaena, and almost certainly also *Nomorhamphus* sp. on Buton, were the only two fish species represented in the samples from the rivers on these islands that were endemic to Sulawesi overall. Although *Nomorhamphus ebrardtii* was not found on Buton, it has been recorded immediately to the north of Kabaena in the rivers of southern mainland Sulawesi and to the east of that region on the island of Kandari (Meisner, 2001). While the above two *Nomorhamphus* species are confined to rivers, five other *Nomorhamphus* species are restricted to the large central lakes and another zenarchopterid, *Tondanichthys kottelati*, is endemic to lakes in northern mainland Sulawesi (Haryono, 2004) (Appendix 1). Thus, the evolution of zenarchopterids in Sulawesi has pursued either a riverine or lacustrine route.

As pointed out earlier, cluster analysis demonstrated that the compositions of the fish faunas in the rivers of Buton, Kabaena, mainland Sulawesi, Flores and Timor differ. This difference is emphasised by the fact that the eleotrid *Belobranchus belobranchus* was the only cosmopolitan native fish species that was recorded in the rivers of each of the above regions (Table I, Appendix I). However, the analyses also revealed that the compositions of the fish faunas of these rivers as a whole differed from those in the large central lake systems of mainland Sulawesi. Thus, the riverine faunas within that region always contained many goby species (with those that undergo an amphidromous migration being particularly well represented) and few or no endemic species (see Appendix 1 and accompanying references). In contrast, the corresponding faunas in the two large and deep lake systems of central mainland Sulawesi, *i.e.* the Malili Lakes system and Lake Poso, contained relatively fewer goby species and very largely comprised endemic species (see Appendix 1 and accompanying references). Indeed, none of the gobies in the large ancient lakes belonged to the Sicydiinae, whose species undergo an amphidromous migration and are very well represented in the rivers of Buton and Kabaena.

The remarkable extent of endemicity in the lacustrine faunas is exemplified by the fact that 33 of the 36 'non-introduced' species in the Malili Lakes were endemic to that system and nine of the ten 'non-introduced' species in Lake Poso were endemic to that lake (Appendix I). The majority of these species belong to a restricted number of families or subfamilies, *i.e.* the Telmatherininae (Celebes rainbowfishes), Adrianichthyidae (ricefishes), Zenarchopterinae (halfbeaks) or Gobiidae. Remarkably, *Aplocheilus panchax* was the only species common to both of those lake systems. The possession by the ancient Malili Lake system of a greater number of endemic species than Lake Poso is related to the fact that, unlike the latter lacustrine environment, the former system contains a series of hydrologically-interconnected lakes, each with its own unique environment and within which separate radiations have occurred and between which dispersal is limited (Vaillant *et al.*, 2011). The question of the origin and mechanism and time of arrival of the ancestors of the groups that have undergone extensive radiations in these lake systems is being explored in a series of ongoing molecular and paleogeographic studies (Sparks and Smith, 2004; Herder *et al.*, 2006a; Roy *et al.*, 2007; Lohman *et al.*, 2011; Stelbrink *et al.*, 2012).

From the above it follows that the remarkable endemicity of the freshwater fish fauna of Wallacea very largely reflects adaptive radiations that took place in the deep lakes of central Sulawesi. In contrast, the corresponding ichthyofaunas in the riverine environments of this biodiversity hotspot contain few endemic species and comprise predominantly native species which, in many cases, undergo an amphidromous migration.

Acknowledgements

Our gratitude is expressed to numerous students who helped with sampling and to Operation Wallacea, and particularly the Director Dr Tim Coles, for providing financial and logistical support. Funds for this project were also kindly provided by the British Ecological Society. Bruce Collette kindly examined some *Nomorhamphus* individuals. Two anonymous referees provided several helpful comments and criticisms which have improved the text.

References

Akihito, P. (1967). On four species of the gobiid fishes of the genus *Eleotris* found in Japan. *Japanese Journal of Ichthyology* **14,** 135-166.

Akihito, P. & Meguro, K. 1975a. First record of *Glossogobius celebius* from Japan. *Japanese Journal of Ichthyology* **21,** 227-230.

Akihito, P. & Meguro K. 1975b. Description of a new species of gobiid fish, *Glossogobius aureus*, with notes on related species of the genus. *Japanese Journal of Ichthyology* **22,** 127-142.

Akihito, P. & Meguro, K. 1976. *Glossogobius sparsipapillus*, a new species of goby from Vietnam. *Japanese Journal of Ichthyology* **23,** 9-11.

Akihito, P., Hayashi, M. & Yoshino, T. (1988). Suborder Gobioidei. In *The Fishes of the Japanese Archipelago* (Masuda, K., Amaoka, C., Araga, C., Uyeno, T., Yoshino, T., eds), 2nd ed., pp. 236-289, [English version]. Tokyo: Tokai University Press.

Allen, G. R., Midgley, S. H. & Allen, M. (2002). *Field guide to the freshwater fishes of Australia*. Perth, Western Australia: Western Australian Museum.

Blaber, S. J. M., Brewer, D. T. & Salinl, J. P. (1989). Species composition and biomass of fishes in different habitats of a tropical northern Australian estuary: their occurence in the adjoining sea and estuarine dependence. *Estuarine, Coastal and Shelf Science* **29**, 509-531.

Blaber, S. J. M. & Milton, D. A. (1990). Species composition, community structure and zoogeography of fishes of mangrove estuaries in the Solomon Islands. *Marine Biology* **105**, 259-267.

Blob, R. W., Wright, K. M., Becker, M., Maie, T., Iverson, T. J., Julius, M. L. & Schoenfuss, H. L. (2007). Ontogenetic change in novel functions: waterfall climbing in adult Hawaiian gobiid fishes. *Journal of Zoology* **273**, 200-209. DOI: 10.1111/j.1469-7998.2007.00315.x.

Blob, R. W., Bridges, W. C., Ptacek, M. B., Maie, T., Cediel, R. A., Bertolas, M. M., Julius, M. L. & Schoenfuss, H. L. (2008). Morphological selection in an extreme flow environment: body shape and waterfall-climbing success in the Hawaiian stream fish *Sicyopterus stimpsoni. Integrative & Comparative Biology* **48**, 734-749. DOI:10.1093/icb/icn086.

Cambray, J. A. (2003). Impact on indigenous species biodiversity caused by the globalisation of alien recreational freshwater fisheries. *Hydrobiologia* **500**, 217-230. DOI: 10.1023/A:1024648719995.

Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* **18**, 117-143. DOI: 10.1111/j.1442-9993.1993.tb00438.x.

Clarke, K. R. & Ainsworth, M. (1993). A method of linking multivariate community structure to environmental variables. *Marine Ecology Progress Series* **92**, 205-219.

Clarke, K. R. & Gorley, R. N. (2006). *PRIMER v6: User Manual/Tutorial*. Plymouth: PRIMER-E.

Clarke, K. R., Somerfield, P. J. & Gorley, R. N. (2008). Testing of null hypotheses in exploratory community analyses: Similarity profiles and biota-environment linkage. *Journal of Experimental Marine Biology and Ecology* **366**, 56-69. DOI: 10.1016/j-jembe.2008.07.009.

Collette, B. B. (1995). *Tondanichthys kottelati*, a new genus and species of freshwater halfbeak (Teleostei: Hemiramphidae) from Sulawesi. *Ichthyological Exploration of Freshwaters* **6**, 171-174.

Collette, B. B. (2004). Family Hemiramphidae Gill 1859 - halfbeaks. *California Acadamy of Sciences Annotated Checklist of Fishes* **22,** 1-35.

Donaldson, T. J. & Myers, R. F. (2002). Insular freshwater fish faunas of Micronesia: patterns of species richness and similarity. *Environmental Biology of Fishes* **65**, 139-149. DOI: 10.1023/A:1020050931158.

Hadiaty, R. K. & Wirjoatmodjo, S. (2002). Studi pendahuluan biodiversitas dan distribusi ikan di danau Matano, Sulawesi selatan. *Jurnal Iktiologi Indonesia* **2**, 23-29.

Hadiaty, R. K., Wirjoatmodjo, S. & Sulistiono, d. (2004). Koleksi ikan di danau mahalona, Lanto dan Masapi, Sulawesi selatan. *Jurnal Iktiologi Indonesia* **4**, 31-42.

Harry, R. R. (1948). The gobies of the Indo-Malayan eleotrid genus *Bunaka*. *Proceedings of the California Zoological Club* **1,** 13-18.

Haryono (2004). Komunitas ikan di perairan danau wilayah Sulawesi utara dan Gorontalo. *Biota* **9**, 54-62.

Haryono, A. H., Tjakrawidjaja, D. & Riyanto, A. (2002). Iktiofauna di perairan sekitar gunung kabela taman nasional Bogani Nani wartabone Sulawesi utara. *Jurnal Iktiologi Indonesia* **2**, 31-40.

Herder, F. & Chapuis, S. (2010). *Oryzias hadiatyae*, a new species of ricefish (Atherinomorpha: Beloniformes: Adrianichthyidae) endemic to Lake Masapi, central Sulawesi, Indonesia. *The Raffles Bulletin of Zoology* **58**, 269-280.

Herder, F., Nolte, A. W., Pfaender, J., Schwarzer, J., Hadiaty, R. K. & Schliewen, U. K. (2006a). Adaptive radiation and hybridization in Wallace's dreamponds: evidence from sailfin silversides in the Malili Lakes of Sulawesi. *Proceedings of the Royal Society B: Biological Sciences* **273**, 2209-2217. DOI: 10.1098/rspb.2006.3558.

Herder, F., Schwarzer, J., Pfaender, J., Hadiaty, R. K. & Schliewen, U. K. (2006b). Preliminary checklist of sailfin silversides (Teleostei: Telmatherinidae) in the Malili Lakes of Sulawesi (Indonesia), with a synopsis of systematics and threats. *Verhandlungen der Gesellschaft für Ichthyologie* **5**, 139-163.

Herder, F., Schliewen, U. K., Geiger, M. F., Hadiaty, R. K., Gray, S. M., McKinnon, J. S., Walter, R. P. & Pfaender, J. (2012). Alien invasion in Wallace’s dreamponds: records of the hybridogenic “flowerhorn” cichlid in Lake Matano, with an annotated checklist of fish species introduced to the Malili Lakes system in Sulawesi. *Aquatic Invasions* **7**, 521-535. DOI: 10.3391/ai.2012.7.4.009.

Hoese, D. & Allen, G. R. (2011). A review of the amphidromous species of the *Glossogobius celebius* complex, with the description of three new species. *Cybium* **35**, 269-284.

Huylebrouck, J., Hadiaty, R. K. & Herder, F. (2012). *Nomorhamphus rex,* a new species of viviparous halfbeak (Atherinomorpha: Beloniformes: Zenarchopteridae) endemic to Sulawesi selatan, Indonesia. *The Raffles Bulletin of Zoology* **60**, 477-485.

Hyslop, E. J. (1999). Longitudinal variation in fish species composition in the Angabanga river, Papua New Guinea with observations on the trophic status of certain fish species. *Ecology of Freshwater Fish* **8**, 102-107. DOI: 10.1111/j.1600-0633.1999.tb00060.x.

Jenkins, A. P., Jupiter, S. D., Qauqau, I. & Atherton, J. (2010). The importance of ecosystem-based management for conserving aquatic migratory pathways on tropical high islands: a case study from Fiji. *Aquatic Conservation: Marine and Freshwater Ecosystems* **20**, 224-238. DOI: 10.1002/aqc.1086.

Jenkins, A. P., Jupiter, S. D. (2011). Spatial and seasonal patterns in freshwater ichthyofaunal communities of a tropical high island in Fiji. *Environmental Biology of Fishes* **91,** 261-274. DOI 10.1007/s10641-011-9776-4.

Keith, P. (2003). Biology and ecology of amphidromous Gobiidae of the Indo-Pacific and the Caribbean regions. *Journal of Fish Biology* **63**, 831-847. DOI: 10.1046/j.1095-8649.2003.00197.x.

Keith, P., Hoareau, T., & Bosc, P. (2005). The genus Cotylopus (Teleostei: Gobioidei) endemic to the rivers of islands of the Indian Ocean with description of new species from Mayotte (Comoros). *Journal of Natural History* **39,** 1395-1405.

Keith, P. & Lord, C. (2011). Tropical Freshwater Gobies. In *The Biology of Gobies* (Kapoor, B. G. ed.), pp. 243-277. Enfield: Science Publishers. DOI: 10.1201/b11397-18.

Keith, P., Allen, G., Lord, C. & Hadiaty, R. (2011a). Five new species of *Sicyopterus* (Gobioidei: Sicydiinae) from Papua New Guinea and Papua. *Cybium* **35,** 299-318.

Keith, P., Lord, C., Lorion, J., Watanabe, S., Tsukamoto, K., Couloux, A. & Dettai, A. (2011b). Phylogeny and biogeography of Sicydiinae (Teleostei: Gobiidae) inferred from mitochondrial and nuclear genes. *Marine Biology* **158,** 311-326. DOI: 10.1007/s00227-010-1560-z.

Kottelat, M. (1990a). Synopsis of the endangered buntingi (Osteichthyes: Adrianichthyidae and Oryziidae) of Lake Poso, central Sulawesi, Indonesia, with a new reproductive guild and descriptions of three new species. *Ichthyological Exploration of Freshwaters* **1**, 49-67.

Kottelat, M. (1990b). The ricefishes (Oryziidae) of the Malili lakes, Sulawesi, Indonesia, with a description of a new species. *Ichthyological Exploration of Freshwaters* **1**, 151-166.

Kottelat, M. (1990c). Sailfin silversides (Pisces: Telmatherinidae) of Lakes Towuti, Mahalona and Wawantoa (Sulwesi, Indonesia) with descriptions of two new genera and two new species. *Ichthyological Exploration of Freshwaters* **1**, 227-246.

Kottelat, M. (1991). Sailfin silversides (Pisces: Telmatherinidae) of Lake Matano, Sulawesi, Indonesia, with a description of six new species. *Ichthyological Exploration of Freshwaters* **1**, 321-344.

Kottelat, M., Whitten, A. J., Kartikasari, S. N. & Wirjoatmodjo, S. (1993). *Freshwater fishes of western Indonesia and Sulawesi*. Jakarta: Periplus Editions.

Koumans, F. P. (1953). Gobioidea. In *The Fishes of the Indo-Australian Archipelago* (Weber, M. & De Beaufort, L. F., eds), 10, 423 pp. Leiden: E.J. Brill Limited.

Larson, H. K. (2001). A revision of the gobiid fish genus *Mugilogobius* (Teleostei: Gobioidei), and its systematic placement. *Records of the Australian Museum Supplement* **62**.

Larson, H. K. & Murdy, E. O. (2001). Families Eleotridae, Gobiidae. In: *The living marine resources of the western central Pacific* volume 6. FAO species identification guide for fisheries purposes (Carpenter, K. E. & Niem, V. H. eds), pp 3574-3603. Rome, Food and Agriculture Organisation of the United Nations.

Larson, H. K. & Pidgeon, B. (2004). New records of freshwater fishes from East Timor. *The Beagle, Records of the Museums and Art Galleries of the Northem Territ,ory* **20,** 195-198.

Larson, H. K. (2009). Review of the gobiid fish genera *Eugnathogobius* and *Pesudogobiopsis* (Gobioidei: Gobiidae: Gobionellinae), with descriptions of three new species. *The Raffles Bulletin of Zoology* **57,** 127-181.

Lek, E., Fairclough, D. V., Platell, M. E., Clarke, K. R., Tweedley, J. R. & Potter, I. C. (2011). To what extent are the dietary compositions of three abundant, co-occurring labrid species different and related to latitude, habitat, body size and season? *Journal of Fish Biology* **78**, 1913-1943. DOI: 10.1111/j.1095-8649.2011.02961.x.

Lohman, D. J., de Bruyn, M., Page, T., von Rintelen, K., Hall, R., Ng, P. K. L., Shih, H.-T., Carvalho, G. R. & von Rintelen, T. (2011). Biogeography of the Indo-Australian Archipelago. *Annual Review of Ecology, Evolution, and Systematics* **42**, 205-226. DOI: 10.1146/annurev-ecolsys-102710-145001.

Lovejoy, N. R., Iranpour, M. & Collette, B. B. (2004). Phylogeny and jaw ontogeny of beloniform fishes. *Integrative and Comparative Biology* **44**, 366-377. DOI: 10.1093/icb/44.5.366.

Maeda, K. & Tachihara, K. (2004). Instream distributions and feeding habits of two species of sleeper, *Eleotris acanthopoma* and *Eleotris fusca*, in the Teima River, Okinawa Island. *Ichthyological Research* **51**, 233-240. DOI: 10.1007/s10228-004-0224-8.

Maeda, K. & Tachihara, K. (2005). Recruitment of amphidromous sleepers *Eleotris acanthopoma*, *Eleotris melanosoma*, and *Eleotris fusca* into the Teima River, Okinawa Island. *Ichthyological Research* **52**, 325-335. DOI: 10.1007/s10228-005-0289-z.

Maeda, K., Yamasaki, N. & Tachihara, K. (2007). Size and age at recruitment and spawning season of sleeper, genus *Eleotris* (Teleostei: Eleotridae) on Okinawa Island, southern Japan. *The Raffles Bulletin of Zoology* **Supplement 14**, 199-207.

Maeda, K., Yamasaki, N. & Tachihara, K. (2011). A redescription of *Stiphodon pulchellus* (Herre, 1927) (Gobiidae: Sicydiinae). *Cybium* **35,** 319-328.

McDowall, R. M. (1988). *Diadromy in fishes: migration between freshwater and marine environments*. London: Croom Helm.

McDowall, R. M. (2010). Why be amphidromous: expatrial dispersal and the place of source and sink population dynamics? *Reviews in Fish Biology and Fisheries* **20**, 87-100. DOI: 10.1007/s11160-009-9125-2.

Meisner, A. D. (2001). Phylogenetic systematics of the viviparous halfbeak genera Dermogenys and Nomorhamphus (Teleostei: Hemiramphidae: Zenarchopterinae). *Zoological Journal of the Linnean Society* **133**, 199-283. DOI: 10.1006/zjls.2000.0281.

Michaux, B. (2010). Biogeology of Wallacea: geotectonic models, areas of endemism, and natural biogeographical units. *Biological Journal of the Linnean Society* **101**, 193-212. DOI: 10.1111/j.1095-8312.2010.01473.x.

Miller, P. J. (1973). The osteology and adaptive features of *Rhyacichthys aspro* (Teleostei: Gobioidei) and the classification of gobioid fishes. *Journal of Zoology, London* **171,** 397-434. DOI: 10.1111/j.1469-7998.1973.tb05347.x.

Miller, P. J. (1989). The classification of bumble-bee gobies (*Brachygobius* and associated genera) (Teleostei: Gobiidae). *Cybium* **13,** 375-383.

Miller, P. J., Wright, J. & Wongrat, P. (1989). An Indo-Pacific goby (Teleostei: Gobioidei) from West Africa, with systematic notes on *Butis* and related eleotridine genera. *Journal of natural History* **23,** 311-324.

Murdy, W. O. & Hoese, D. F. (1985). Revision of the gobiid fish genus *Istigobius*. *Indo-Pacific Fishes* **4,** 1-41.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B. & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature* **403**, 853-858. DOI: 10.1038/35002501.

Nelson, J. S. (2006). *Fishes of the world.* New Jersey: John Wiley.

Nilawati, J. & Tantu, F. Y. (2008). *Telmatherina albolabiosus,* a new species of sailfin silversides (Atheriniformes: Telmatherinidae) from Lake Matano, South Sulawesi. *Wallacea, Journal of Biodiversity* **1**, 20-26.

Parenti, L. R. (2008). A phylogenetic analysis and taxonomic revision of ricefishes, *Oryzias* and relatives (Beloniformes, Adrianichthyidae). *Zoological Journal of the Linnean Society* **154,** 494-610. DOI: 10.1111/j.1096-3642.2008.00417.x.

Parenti, L. R. (2011). Endemism and Conservation of the Native Freshwater Fish Fauna of Sulawesi, Indonesia. In *Prosiding Seminar Nasional Ikan VI & Kongres MasyarakatIktiologi Indonesia III (Proceedings of the VIth National Seminar and 3rd Congress of the Indonesian Society of Ichthyologists* (Simanjuntak, ed.), pp. 1-10. Cibinong: Masyarakat Iktiologi Indonesia (Indonesian Society of Ichthyologists).

Parenti, L. R. & Soeroto, B. (2004). *Adrianichthys roseni*, and *Oryzias nebulosus*, two new ricefishes (Atherinomorpha: Beloniformes: Adrianichthyidae) from Lake Poso, Sulawesi, Indonesia. *Ichthyological Research* **51**, 10-19.

Randall, J. E. & Randall, H. A. (2001). Review of the fishes of the genus *Kuhlia* (Perciformes: Kuhliidae) of the Central Pacific. *Pacific Science* **55**, 227-256.

Roy, D., Paterson, G., Hamilton, P. B., Heath, D. D. & Haffner, G. D. (2007). Resource-based adaptive divergence in the freshwater fish Telmatherina from Lake Matano, Indonesia. *Molecular Ecology* **16**, 35-48. DOI: 10.1111/j.1365-294X.2006.03106.x.

Ryan, P. A. (1991). The success of the Gobiidae in tropical Pacific insular streams. *New Zealand Journal of Zoology* **18**, 25-30.

Sakai, H. & Nakamura, M. (1979). Two new species of freshwater gobies (Gobiidae: Sicydiaphiinae) from Ishigaki Island, Japan. *Japanese Journal of Ichthyology* **26,** 43-54.

Schubart, C. D. & Ng, P. K. L. (2008). A new molluscivore crab from Lake Poso confirms multiple colonization of ancient lakes in Sulawesi by freshwater crabs (Decapoda: Brachyura). *Zoological Journal of the Linnean Society* **154**, 211-221. DOI: 10.1111/j.1096-3642.2008.00441.x.

Soeroto, B. & Tungka, F. (1991). Fish fauna, fisheries and Adrianichthyoidei in Lake Poso. In *Phylogeny and species differentiation of Adrianichthyoidei in Indonesia*, pp. 12-14: Study Report. Monobusho International Scientific Research Program.

Soeroto, B. & Tungka, F. (1996). The inland fishes and the distribution of Adrianichthyoidea of Sulawesi Island, with species comments on the endangered species in Lake Poso. In *Proceedings of the first international conference on eastern Indonesian-Australian vertebrate fauna* (Kichener, D. J. & Suyanto, A., eds.), pp. 1-5. Manado, Indonesia, November 22-26, 1994: Western Australian Museum for Lembaga Ilmu Pengetahuan Indonesia.

Sparks, J. S. & Smith, W. L. (2004). Phylogeny and biogeography of the Malagasy and Australasian rainbowfishes (Teleostei: Melanotaenioidei): Gondwanan vicariance and evolution in freshwater. *Molecular Phylogenetics and Evolution* **33**, 719-734. DOI: 10.1016/j.ympev.2004.07.002.

Stelbrink, B., Albrecht, C., Hall, R. & von Rintelen, T. (2012). The biogeography of Sulawesi revisited: Is there evidence for a vicariant origin of taxa on Wallace's "anomalous island"? *Evolution* **66**, 2252-2271. DOI: 10.1111/j.1558-5646.2012.01588.x.

Thuesen, P. A., Ebner, B. C., Larson, H., Keith, P., Silcock, R. M., Prince, J. & Russell, D. J. (2011). Amphidromy links a newly documented fish community of continental Australian streams, to oceanic islands of the West Pacific. *PLoS ONE* **6**, e26685. DOI: 10.1371/journal.pone.0026685.

Tjakrawidjaja, A. H. (2002). Jenis ikan air tawar dari Manggarai, Flores, dengan variasi aspek limnologinya. *Jurnal Iktiologi Indonesia* **2**, 15-22.

Tjakrawidjaja, A. H. (2006). Fauna ikan air tawar di pulau Buton provinsi Sulawesi tenggara. *Jurnal Iktiologi Indonesia* **6**, 79-84.

Vaillant, J. J., Haffner, G. D. & Cristescu, M. E. (2011). The ancient laes of Indonesia: towards intergrated research on speciation. *Integrative and Comparative Biology* **51,** 634-643. DOI: 10.1093/icb/icr101.

von Rintelen, T., Wilson, A. B., Meyer, A. & Glaubrecht, M. (2004). Escalation and trophic specialization drive adaptive radiation of freshwater gastropods in ancient lakes on Sulawesi, Indonesia. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **271**, 2541-2549. DOI: 10.1098/rspb.2004.2842.

von Rintelen, K., Glaubrecht, M., Schubart, C. D., Wessel, A. & Von Rintelen, T. (2010). Adaptive radiation and ecological diversification of Sulawesi's ancient lake shrimps. *Evolution* **64**, 3287-3299. DOI: 10.1111/j.1558-5646.2010.01043.x.

Wallace, A. R. (1863). On the physical geography of the Malay archipelago. *Journal of the Royal Geographical Society* **33**, 217-234.

Watson, R. E. (1991). A provisional review of the genus *Stenogobius* with descriptions of a new subgenus and thirteen new species. (Pisces: Teleostei: Gobiidae). *Records of the Western Australian Museum* **15,** 627-710.

Watson, R. E. (1992). A revision of the gobiid fish genus *Awaous* from insular streams of the Pacific plate. *Ichthyological Exploration of Freshwaters* **3,** 161-176.

Watson, R. E. & Kottelat, M. (1994). *Lentipes whittenorum* and *Sicyopus auxilimentus*, two new species of freshwater gobies from the western Pacific (Teleostei: Gobiidae: Sicydiinae). *Ichthyological Exploration of Freshwaters* **5,** 351-364.

Wentworth, C. K. (1922). A scale of grade and class terms for clastic sediments. *Journal of Geology* **30**, 377-382.

Whitten, A. J., Mustafa, M. & Henderson, G. S. (1987). *The ecology of Sulawesi*. Yogyakarta: Gadjah Mada University Press.

Wongrat, P. (1977). Systematics, Phylogeny and comparative anatomy of Eleotrine Gobies. Ph.D. Thesis, University of Bristol.

Electronic references

Conservation International (2012). Wallacea. Available from http://www.conservation.org/where/priority_areas/hotspots/asia-pacific/wallacea/Pages/biodiversity.aspx (last accessed 16 January 2013).

Table 1

Table I. List of fish species and their families recorded at sites in rivers on the islands of Buton and Kabaena during 2001 and 2002, together with their total numbers in the samples (N), percentage contributions to the total catch (%), rankings by abundance (R) and the means and ranges of their standard lengths. The "origin" of each fully identified species, *i.e.* if it is endemic, native or introduced to Sulawesi, is recorded, as are the numbers of each species and percentage contributions collected on Buton (#B and %B) and Kabaena (#K and %K). N.B. 58 unidentified gobies are not included in the rankings (see Material and Methods).

Species	Family	Origin	N	%	R	#B	%B	#K	%K	Mean (mm)	Range (mm)
Eleotris aff. fusca-melanosoma	Eleotridae	Native	395	18.1	1	370	24.3	25	3.8	71	17-232
Anguilla celebesensis	Anguillidae	Native	267	12.3	2	182	12.0	85	13.0	233	46-1080
Nomorhamphus sp.	Zenarchopteridae	Endemic?	249	11.4	3	249	16.4			39	14-90
Nomorhamphus ebrardtii	Zenarchopteridae	Endemic	221	10.1	4			221	33.5	43	14-85
Sicyopterus sp.	Gobiidae		145	6.7	5	38	2.5	107	16.2	53	24-93
Glossogobius aff. celebius-kokius	Gobiidae	Native	124	5.7	6	102	6.7	22	3.3	66	14-222
Ophieleotris aff. aporos	Eleotridae	Native	108	5.0	7	108	7.1			88	25-207
Kuhlia marginata	Kuhliidae	Native	67	3.1	8	67	4.4			45	20-136
Gobiid spp.	Gobiidae		58	2.7				58	8.8	68	25-260
Clarias batrachus	Claridae	Introduced	57	2.6	9	3	0.2	54	8.2	127	44-283
Ophiocara porocephala	Eleotridae	Native	34	1.6	10	29	1.9	5	0.8	78	34-159
Awaous aff. grammepomus-ocellatus	Gobiidae	Native	34	1.6	10	34	2.2			112	46-200
Rhyacichthys aspro	Rhyacichthyidae	Native	33	1.5	12	33	2.2			91	18-188
Butis amboinensis	Eleotridae	Native	32	1.5	13	32	2.1			62	28-97
Sicyopterus micrurus	Gobiidae	Native	32	1.5	13	22	1.5	10	1.5	58	15-94
Ambassis miops	Ambassidae	Native	26	1.2	15	26	1.7			26	10-61
Sicyopterus macrostetholepis	Gobiidae	Native	26	1.2	15	21	1.4	5	0.8	44	28-62
Clarias teijsmanni	Claridae	Introduced	25	1.2	17	25	1.6			110	81-162
Oreochromis mossambicus	Cichlidae	Introduced	24	1.1	18			24	3.6	45	19-109
Redigobius sp.	Gobiidae	Native	22	1.0	19	20	1.3	2	0.3	23	17-28
Stiphodon elegans	Gobiidae	Native	21	1.0	20	8	0.5	13	2.0	30	16-60
Microphis sp.	Syngnathidae		18	0.8	21	17	1.1	1	0.2	126	106-155

Table I continued

Species	**Family**	**Origin**	**N**	**%**	**R**	**#B**	**%B**	**#K**	**%K**	**Mean (mm)**	**Range (mm)**
Lentipes sp.	Gobiidae		17	0.8	22			17	2.6	-	-
Sicyopus zosterophorum	Gobiidae	Native	12	0.6	23	12	0.8			43	33-49
Aplocheilus panchax	Aplocheilidae	Native	11	0.5	24	11	0.7			35	30-43
Belobranchus belobranchus	Eleotridae	Native	9	0.4	25	6	0.4	3	0.5	84	57-102
Mugil sp.	Mugilidae		9	0.4	25	9	0.6			86	69-121
Glossogobius aff. obscurus-brunneus	Gobiidae	Native	8	0.4	27	8	0.5			115	55-163
Redigobius bikolanus	Gobiidae	Native	8	0.4	27	8	0.5			28	13-49
Schismatogobius bruynisi	Gobiidae	Native	8	0.4	27	8	0.5			34	30-36
Rasbora sp.	Cyprinidae	Introduced	7	0.3	30	7	0.5			21	12-29
Oreochromis niloticus	Cichlidae	Introduced	5	0.2	31	5	0.3			57	39-71
Bunaka gyrinoides	Eleotridae	Native	5	0.2	31	5	0.3			96	73-134
Lamnostoma mindora	Ophichthidae	Native	5	0.2	31	5	0.3			368	246-474
Caranx papuensis	Carangidae	Native	4	0.2	34	4	0.3			93	84-112
Scatophagus argus	Scatophagidae	Native	4	0.2	34	4	0.3			75	62-94
Anabas testudineus	Anabantidae	Introduced	3	0.1	36			3	0.5	93	85-103
Channa striata	Channidae	Introduced	3	0.1	36			3	0.5	263	125-315
Periophthalmus argentilineatus	Gobiidae	Native	3	0.1	36	3	0.2			52	44-59
Microphis leiaspis	Syngnathidae	Native	3	0.1	36	3	0.2			132	109-149
Tetraroge niger	Tetrarogidae	Native	3	0.1	36	3	0.2			97	54-190
Tetraroge sp.	Tetrarogidae		3	0.1	36	3	0.2			29	29
Anguilla bicolor	Anguillidae	Native	2	0.1	42	2	0.1			186	147-225
Glossogobius bicirrhosus	Gobiidae	Native	2	0.1	42	2	0.1			59	52-65
Hypseleotris sp.	Eleotridae	Native	2	0.1	42	2	0.1			-	-
Periophthalmus minutus	Gobiidae	Native	2	0.1	42	2	0.1			69	65-72
Stenogobius ophthalmoporus	Gobiidae	Native	2	0.1	42	2	0.1			66	60-72
Stiphodon semoni	Gobiidae	Native	2	0.1	42	2	0.1			-	-
Zenarchopterus gilli	Zenarchopteridae	Native	2	0.1	42	2	0.1			154	152-156
Muraenidae sp.	Muraenidae		2	0.1	42	2	0.1			147	73-220
Meiacanthus anema	Blenniidae	Native	1	<0.1	50			1	0.2	42	42
Glossogobius concavifrons	Gobiidae	Native	1	<0.1	50	1	0.1			35	35
Hypogymnogobius xanthomelus	Gobiidae	Native	1	<0.1	50	1	0.1			-	-

Table I continued

Species	Family	Origin	N	%	R	#B	%B	#K	%K	Mean (mm)	Range (mm)
Pseudogobiopsis oligactis	Gobiidae	Native	1	<0.1	50	1	0.1			-	-
Pseudogobiopsis sp.	Gobiidae		1	<0.1	50	1	0.1			-	-
Sicyopterus gymnauchen	Gobiidae	Native	1	<0.1	50	1	0.1			40	40
Sicyopterus microcephalus	Gobiidae	Native	1	<0.1	50	1	0.1			61	61
Sicyopterus ouwensi	Gobiidae	Native	1	<0.1	50	1	0.1			-	-
Stenogobius sp.	Gobiidae		1	<0.1	50	1	0.1			26	26
Kuhlia rupestris	Kuhliidae	Native	1	<0.1	50	1	0.1			-	-
Moringua javanica	Moringuidae	Native	1	<0.1	50	1	0.1			289	289
Gymnothorax tile	Muraenidae	Native	1	<0.1	50	1	0.1			329	329
Thyrsoidea macrurus	Muraenidae	Native	1	<0.1	50	1	0.1			277	277
Doryicthys sp.	Syngnathidae		1	<0.1	50	1	0.1			74	74
Microphis mento	Syngnathidae	Native	1	<0.1	50	1	0.1			145	145
No of individuals			**2,179**			**1,520**		**659**			
No of species			**64**			**58**		**18**			
No of genera			**43**			**38**		**16**			
No of samples			**63**			**45**		**18**			

Table 2

Table II. List of fish families recorded at sites on the islands of Buton and Kabaena, together with their total numbers in the samples (N), percentage contributions to the total catch (%), rankings by abundance (R) and the numbers of their species and genera. The numbers and percentage contributions of each family to the samples collected from Buton (#B and %B) and Kabaena (#K and %K) are also provided.

Family	**N**	**%**	**R**	**# B**	**% B**	**# K**	**% K**	**Species**	**Genera**
Eleotridae	585	26.8	1	552	36.3	33	5.0	7	7
Gobiidae	534	24.5	2	300	19.7	234	35.5	26	12
Zenarchopteridae	472	21.7	3	251	16.5	221	33.5	3	3
Anguillidae	269	12.4	4	184	12.1	85	12.9	2	1
Clariidae	82	3.8	5	28	1.8	54	8.2	2	1
Kuhliidae	68	3.1	6	68	4.5			2	1
Rhyacichthyidae	33	1.5	7	33	2.2			1	1
Cichlidae	29	1.3	8	5	0.3	24	3.6	2	1
Ambassidae	26	1.2	9	26	1.7			1	1
Syngnathidae	23	1.1	10	22	1.5	1	0.1	4	2
Aplocheilidae	11	0.5	11	11	0.7			1	1
Mugilidae	9	0.4	12	9	0.6			1	1
Cyprinidae	7	0.3	13	7	0.5			1	1
Tetrarogidae	6	0.3	14	6	0.4			2	1
Ophichthidae	5	0.2	15	5	0.3			1	1
Carangidae	4	0.2	18	4	0.3			1	1
Muraenidae	4	0.2	18	4	0.3			3	3
Scatophagidae	4	0.2	18	4	0.3			1	1
Anabantidae	3	0.1	20			3	0.5	1	1
Channidae	3	0.1	20			3	0.5	1	1
Blenniidae	1	<0.1	22			1	0.2	1	1
Moringuidae	1	<0.1	22	1	0.1			1	1
No of individuals	**2,179**			**1,520**		**659**			
No of species	**64**			**58**		**18**			
No of genera	**43**			**38**		**16**			
No of families	**22**			**19**		**10**			
No of samples	**63**			**45**		**18**			

Table 3

Table III. List of species shown by SIMPER analysis to be most important in typifying the species composition of each of the seven clusters of fish samples (shaded boxes), which had been identified by SIMPROF analysis as distinct, and the species that distinguished between the composition of the fish fauna in each cluster from that in each other cluster (non-shaded boxes). *, indicates the percentage contribution of a species is consistently greater for the cluster in the vertical column than in the horizontal row.

	B1	**B2**	**B3**	**B4**	**B5**	**K1**	**K2**
B1	*Nomorhamphus* sp. *Sicyopterus* sp. *S. zosterophorum* *A. celebesensis*						
B2	*Sicyopterus* sp. * *S. zosterophorum* * *Nomorhamphus* sp. * *A. celebesensis* *	*Nomorhamphus* sp.					
B3	*Nomorhamphus* sp. * *E. aff. fusca-melanosoma* *Sicyopterus* sp. * *S. zosterophorum* *	*Nomorhamphus* sp. * *E. aff. fusca-melanosoma* *A. celebesensis* *O. aff. aporos*	*E. aff. fusca-melanosoma* *A. celebesensis* *O. aff. aporos*				
B4	*O. porocephala* *Nomorhamphus* sp. * *Sicyopterus* sp. *	*Nomorhamphus* sp. * *O. porocephala* *E. aff. fusca-melanosoma*	*O. porocephala* *E. aff. fusca-melanosoma* * *Anguilla celebesensis*	*O. porocephala* *E. aff. fusca-melanosoma*			
B5	*Nomorhamphus* sp. * *G. aff. celebius-kokius* *Sicyopterus* sp. *	*Nomorhamphus* sp. * *G. aff. celebius-kokius*	*E. aff. fusca-melanosoma* * *G. aff. celebius-kokius*	*O. porocephala* * *G. aff. celebius-kokius*	*G. aff. celebius-kokius* *Redigobius* sp. *B. amboinensis* *E. aff. fusca-melanosoma*		
K1	*Nomorhamphus* sp. * *S. zosterophorum* *	*Nomorhamphus* sp. * *Sicyopterus* sp. *A. celebesensis*	*E. aff. fusca-melanosoma* * *Sicyopterus* sp.	*O. porocephala* * *A. celebesensis*	*G. aff. celebius-kokius* * *A. celebesensis* *Sicyopterus* sp.	*A. celebesensis* *Sicyopterus* sp.	
K2	*Nomorhamphus* sp. * *C. batrachus* *Sicyopterus* sp. * *N. ebrardti* *S. zosterophorum* *	*Nomorhamphus* sp. * *C. batrachus* *N. ebrardti*	*E. aff. fusca-melanosoma* * *C. batrachus* *N. ebrardti*	*O. porocephala* * *C. batrachus* *N. ebrardti* *E. aff. fusca-melanosoma* *	*C. batrachus* *G. aff. celebius-kokius* * *N. ebrardti*	*C. batrachus* *N. ebrardti* *Sicyopterus* sp. * *A. celebesensis* *	*C. batrachus* *N. ebrardtii* *A. celebesensis*

List of Figures

Figure 1. Maps showing the following. (a) Wallacea, *i.e.* the area between Wallace's Line and Lydekker's Line in south east Asia, with the countries in capitals and regions in lower case and Indonesia in darker grey. (b) Mainland Sulawesi and the satellite islands of Buton and Kabaena, with the areas labelled ■ when there were data on the freshwater fish faunas. (c) Buton and (d) Kabaena. Note that the ● which denotes the location of sites sometimes covered two relatively nearby sites.

Figure 2. Examples of sampling sites. (a) Upper reaches of a river on Buton, with sections containing large boulders and rocks, associated with waterfalls that were interspersed with calmer sections, (b) upper reaches of a river in Buton, with deep pools and overhanging vegetation, (c) a deforested and exposed region of a river on Buton in which water temperatures were elevated and (d) wide, slower-flowing, lower reaches of a river on Buton where the substrata comprised mainly sand and/or gravel.

Figure 3. Examples of the diversity of riverine fish species caught during the present study. (a) A female *Nomorhampus* sp. (Zenarchopteridae). The reduced upper jaw is an adaptation for catching prey that falls on the water surface from overhanging vegetation in relatively undisturbed forests. (b) and (c) *Ophieleotris aff. aporos* and *Ophiocara porocephala* (Eleotridae), which tend to occupy the deeper, slower-flowing sections of rivers. (d) *Awaous aff. grammepomus-ocellatus* (Gobiidae), showing the fused pelvic fins, which form the sucker used by many species of goby for anchoring to the substratum. (e) *Rhyacichthys aspro* (Rhyacichthyidae). The greatly-enlarged pelvic fins and dorso-ventrallly flattened body are adaptations that enable this benthic species to live in fast-flowing water.

Each fish was photographed live under light anaesthesia in benzocaine. Scale bar represents 1cm.

Figure 4. Dendrogram derived from CLUSTER analysis using the percentage contributions of the various fish species to each sample collected from 63 sites in Buton and Kabaena in 2001 and 2002. The clusters under each thick vertical line represent samples from sites at which, at the species level, the faunal compositions were shown by SIMPROF not to be significantly different from each other ($P < 0.05$), but to be significantly different from those in all other groups of samples ($P > 0.05$).

Figure 5. Non-metric Multidimensional Scaling 21 ordination plots of the Bray-Curtis matrix constructed from the percentage contributions of each fish species to the samples collected from each of the 63 sites sampled in Buton and Kabaena. Points coded according to the cluster to which sample belongs: B1 (▲), B2 (△), B3 (▲), B4 (▽), B5 (▼), K1 (■) and K2 (■). *k* refers to a Kabaena site in a Buton cluster (B3) and *b* to a Buton site in a Kabaena cluster (K1).

Figure 6. The non-metric Multidimensional Scaling ordination plot of the Bray-Curtis matrix constructed from the mean percentage contributions of each fish species to the seven clusters identified by SIMPROF is repeated in (a) to (f). Circles (bubbles) of varying size, representing the magnitudes of the effects of (a) longitude, (b) distance to the river mouth, the percentage contribution of (c) sand and (d) silt at each site, (e) altitude and (f) water temperature have been superimposed on the ordination plot shown in (a). The variables in (a) to (e) were those selected by BIOENV as having the greatest relationship with ichthyofaunal composition.

Figure 7. Cluster dendrogram derived from a Bray-Curtis similarity matrix constructed from the presence or absence of fish species in the freshwaters of different locations in Wallacea. B, Buton; K, Kabaena, NR, North Sulawesi; F, Flores; T, East and West Timor; M, Malili Lakes system; P, Lake Poso; NL, North Sulawesian Lakes. Sampling sites in the first five locations were all in rivers.

Figure 1

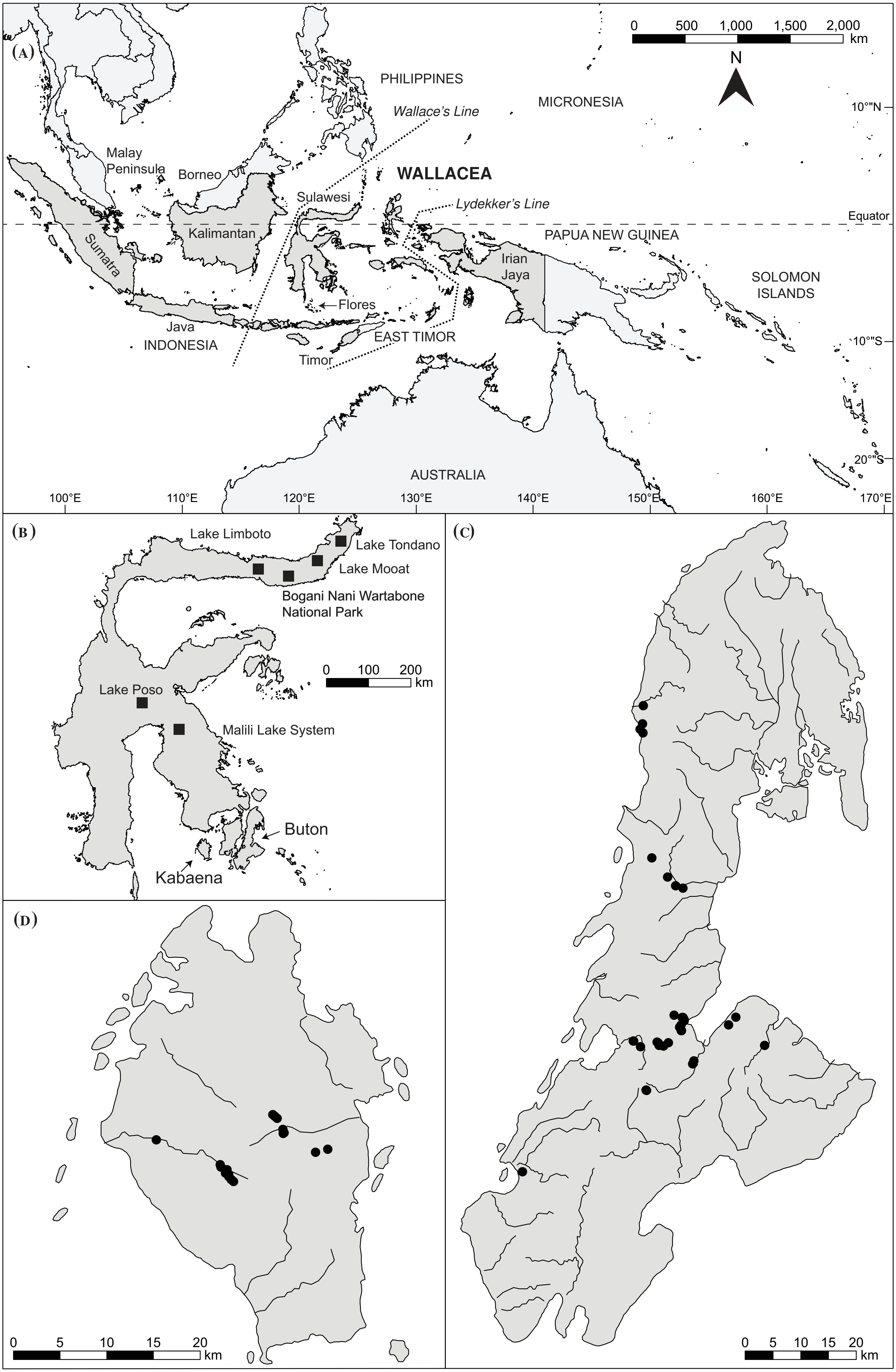

(A)
0
500
1,000
1,500
2,000
km
N
PHILIPPINES
MICRONESIA
Wallace's Line
10°"N
Malay
Peninsula
Borneo
WALLACEA
Sulawesi
Lydekker's Line
Equator
Kalimantan
PAPUA NEW GUINEA
Sumatra
Irian
Jaya
SOLOMON
ISLANDS
Flores
Java
EAST TIMOR
INDONESIA
10°"S
Timor
20°"S
AUSTRALIA
100°E
110°E
120°E
130°E
140°E
150°E
160°E
170°E
(B)
Lake Limboto
Lake Tondano
Lake Mooat
Bogani Nani Wartabone
National Park
0
100
200
km
Lake Poso
Malili Lake System
Buton
Kabaena
(C)
(D)
0
5
10
15
20
km
0
5
10
15
20
km

Figure 2

Figure 3

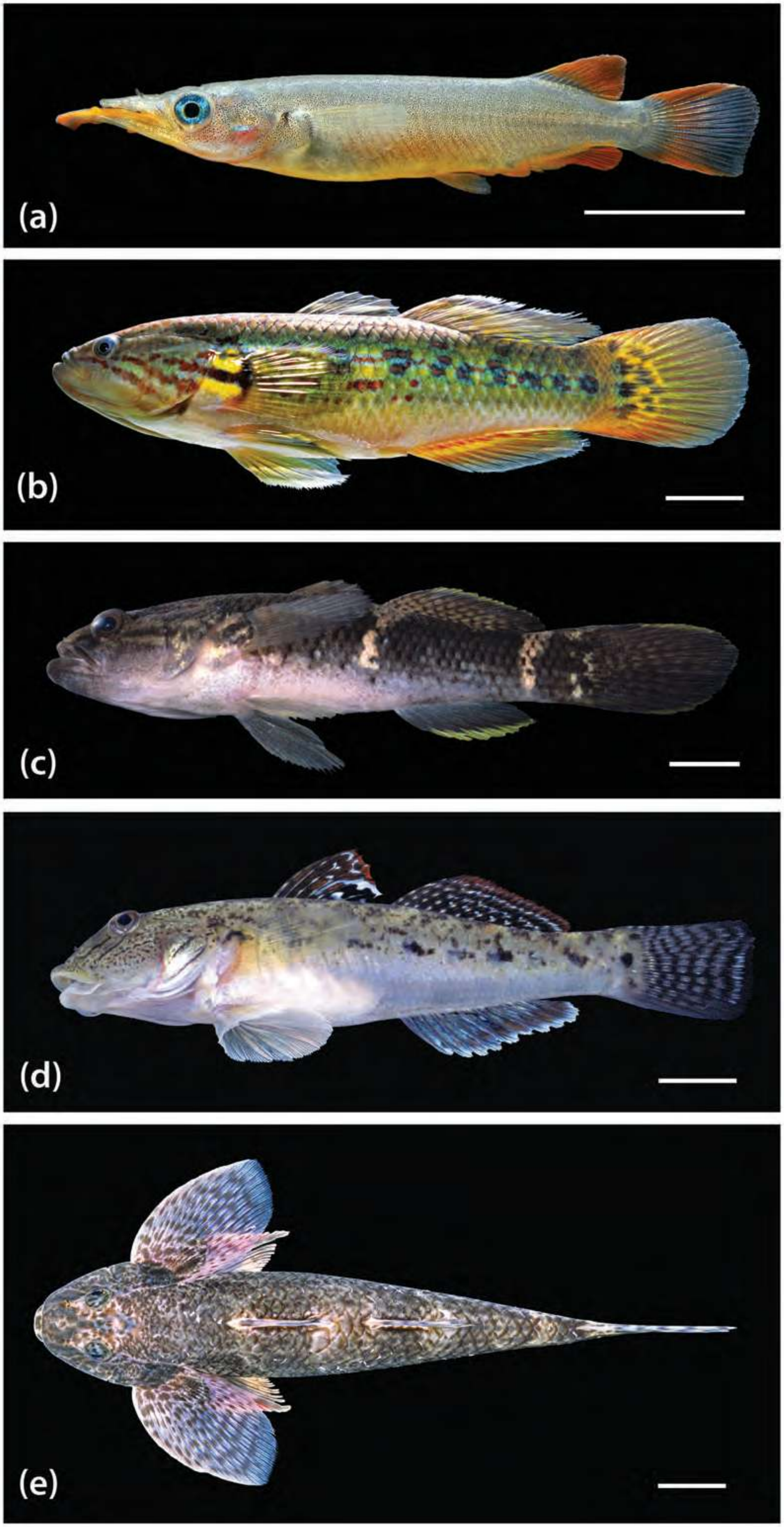


Figure 4

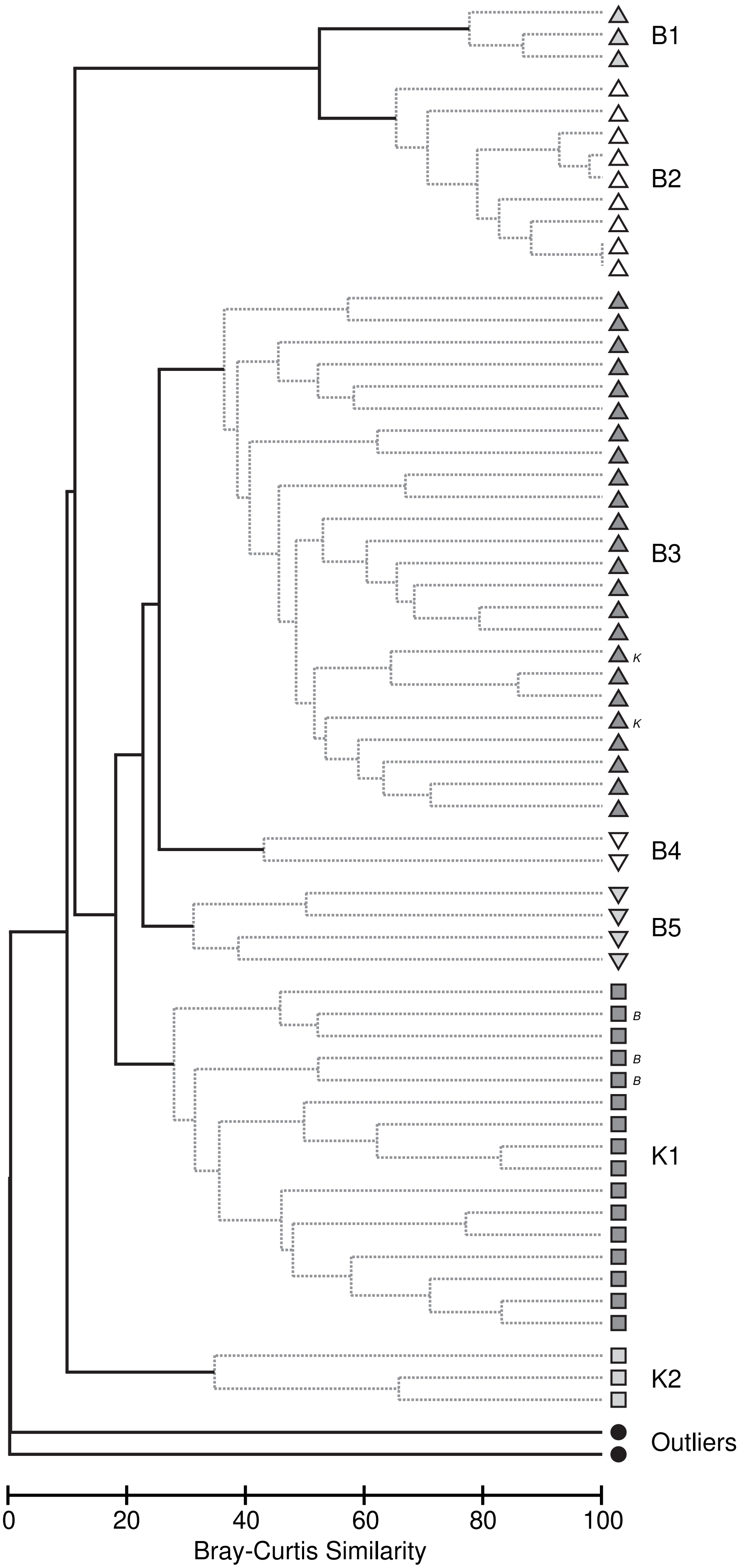
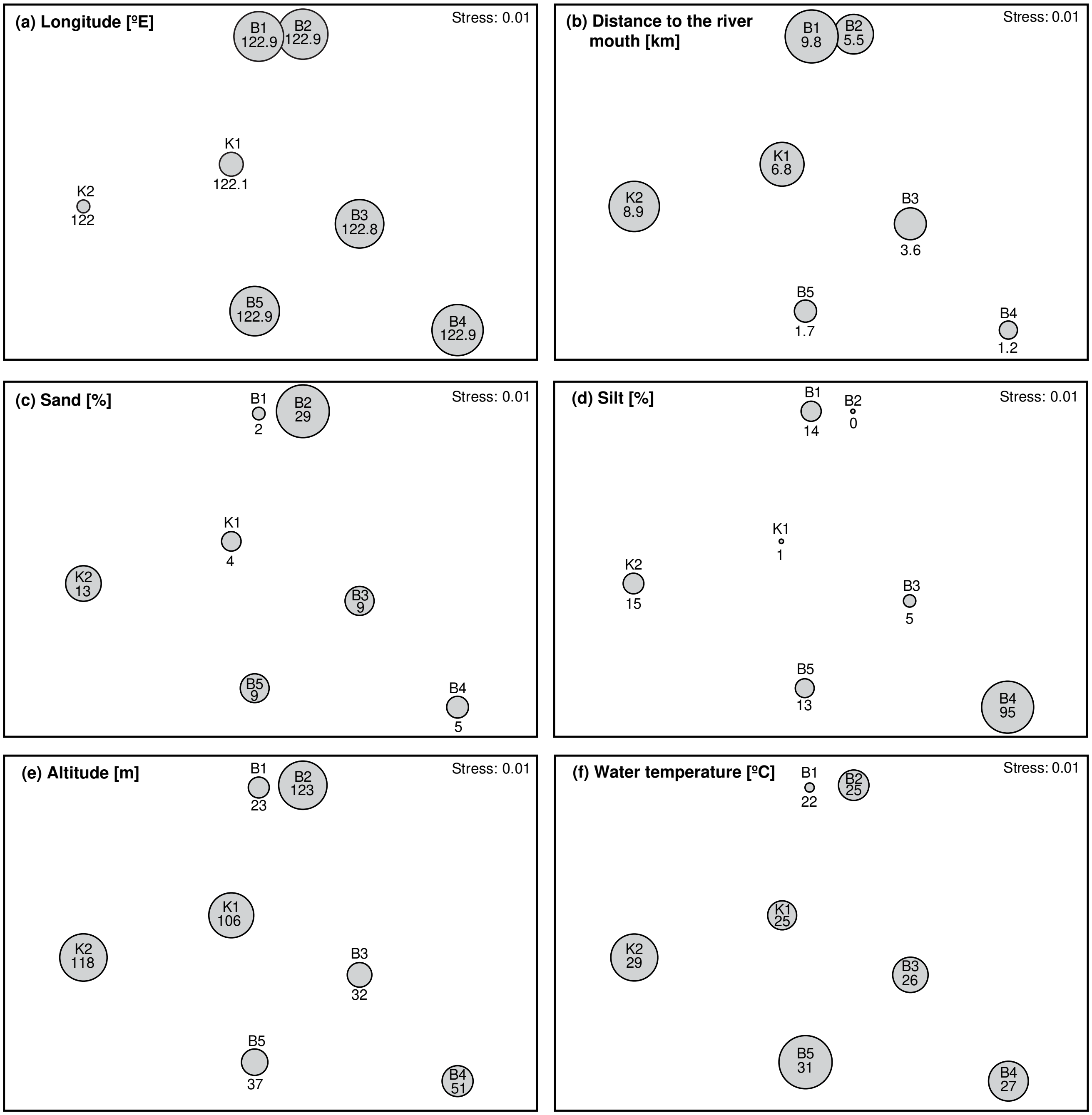

B1
B2
B3
K
K
B4
B5
B
B
B
K1
K2
Outliers
0
20
40
60
80
100
Bray-Curtis Similarity

Figure 5



(a) Longitude [ºE]
Stress: 0.01
B1 122.9
B2 122.9
K1 122.1
K2 122
B3 122.8
B5 122.9
B4 122.9
(b) Distance to the river mouth [km]
Stress: 0.01
B1 9.8
B2 5.5
K1 6.8
K2 8.9
B3 3.6
B5 1.7
B4 1.2
(c) Sand [%]
Stress: 0.01
B1 2
B2 29
K1 4
K2 13
B3 9
B5 9
B4 5
(d) Silt [%]
Stress: 0.01
B1 14
B2 0
K1 1
K2 15
B3 5
B5 13
B4 95
(e) Altitude [m]
Stress: 0.01
B1 23
B2 123
K1 106
K2 118
B3 32
B5 37
B4 51
(f) Water temperature [ºC]
Stress: 0.01
B1 22
B2 25
K1 25
K2 29
B3 26
B5 31
B4 27

Figure 6

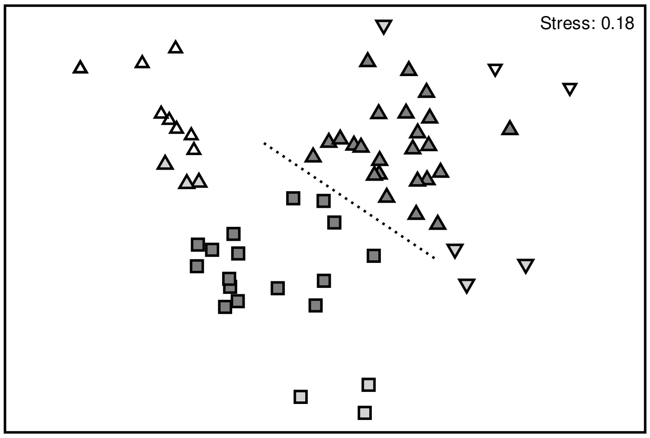
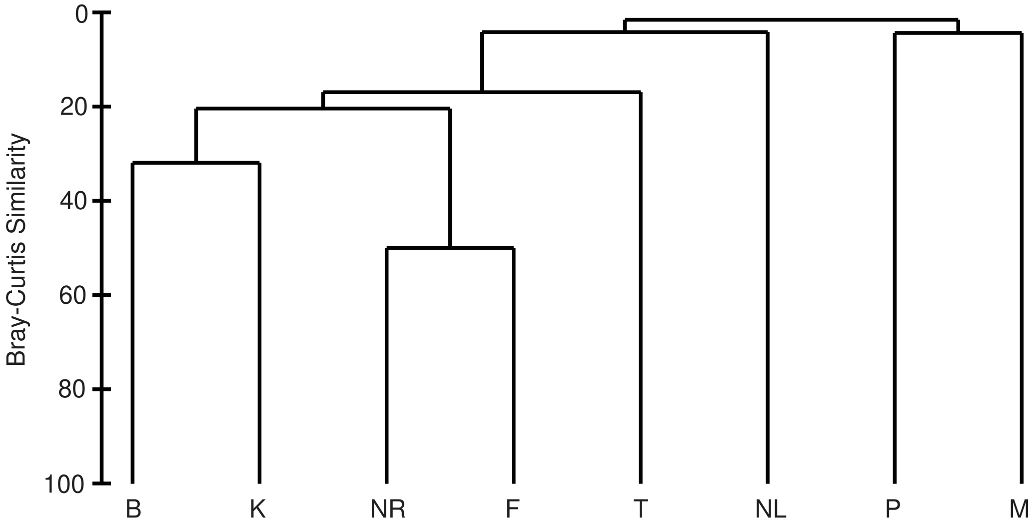


Figure 7



Appendix I. List of "non-introduced" species recorded in the freshwaters of Wallacea. B, Buton (present study); K, Kabaena (present study); NR, North Sulawesi (Haryono *et al.*, 2002); F, Flores (Tjakrawidjaja, 2002); T, East and West Timor (Larson and Pidgeon, 2004); M, Malili Lakes system (Soeroto and Tungka, 1996; Larson, 2001; Hadiaty and Wirjoatmodjo, 2002; Hadiaty *et al.*, 2004; Nilawati and Tantu, 2008; Herder and Chapuis, 2010); P, Lake Poso (Soeroto and Tungka, 1991; 1996; Parenti and Soeroto, 2004) and NL, North Sulawesian Lakes (Collette, 1995; Haryono, 2004). Sampling sites in the first five locations were all in rivers. *, denotes species listed as endemic to Sulawesi by Parenti (2011).

Species	B	K	NR	F	T	M	P	NL
Megalopidae								
Megalops cyprinoides					+			
Anguillidae								
Anguilla australis					+			
Anguilla celebesensis	+	+			+			+
Anguilla bicolor	+							
Anguilla marmorata			+	+	+			
Anguilla reinhardtii					+			
Moringuidae								
Moringua javanica	+							
Muraenidae								
Gymnothorax tile	+							
Thyrsoieda macrurus	+							
Muraenidae sp.	+							
Ophichthidae								
Lamnostoma mindora	+							
Mugilidae								
Cestraeus goldiei					+			
Crenimugil sp.			+					
Liza subviridis					+			
Valamugil seheli					+			
Valamugil sp.								+
Mugil sp.	+							
Melanotaeniidae								
Telmatherina abendanoni *						+		
Telmatherina albolabiosus *						+		
Telmatherina antoniae *						+		
Telmatherina bonti *						+		
Melanotaeniidae cont.								
Telmatherina celebensis *						+		
Telmatherina obscura *						+		
Telmatherina opudi *						+		
Telmatherina prognatha *						+		
Telmatherina sarasinorum *						+		
Telmatherina wahjui *						+		
Telmatherina sp.						+		
Tominanga aurea *						+		
*Tominanga sanguicauda**						+		
Paratherina cyanea *						+		
Paratherina labiosa *						+		
Paratherina striata *						+		
Paratherina wolterecki *						+		
Atherinidae								
Atherinomorus lacunosus					+			
Craterocephalus sp.					+			
Hypoatherina sp.			+					
Adrianichthyidae								
Adrianichthys kruyti *							+	
Adrianichthys oophorus *							+	
Adrianichthys poptae *							+	
Adrianichthys roseni *							+	
Oryzias hadiatyae *						+		
Oryzias celebensis					+			
Oryzias marmoratus *						+		
Oryzias matanensis *						+		
Oryzias nigrimas *							+	

Appendix I continued

Species	B	K	NR	F	T	M	P	NL
Adrianichthyidae cont.								
Oryzias orthognatnus *							+	
Oryzias profundicola *						+		
Oryzias timorensis					+			
Synbranchidae								
Monopterus albus			+					
Zenarchopteridae								
Nomorhamphus celebensis *							+	
Nomorhamphus ebrardtii *		+						
Nomorhamphus kolonodalensis *						+		
Nomorhamphus magarrhamphus *						+		
Nomorhamphus towoetii *						+		
Nomorhamphus weberi *						+		
Nomorhamphus sp.	+							
Zenarchopterus gilli	+							
Tondanichthys kottelati *								+
Aplocheilidae								
Aplocheilus panchax	+		+			+	+	
Syngnathidae								
Doryicthys sp.	+							
Microphis argulus				+				
Microphis leiaspis	+							
Microphis mento	+							
Microphis retzii					+			
Microphis sp.	+	+						
Carangidae								
Caranx papuensis	+							
Caranx sexfasciatus					+			
Scorpaenidae								
Tetraroge barbata				+				
Tetraroge niger	+							
Tetroge sp.	+							
Ambassidae								
Ambassis buruensis					+			
Ambassis dussumieri					+			
Ambassis macracanthus					+			
Ambassis miops	+				+			
Ambassis urotaenia					+			

Species	B	K	NR	F	T	M	P	NL
Serranidae								
Epinephelus malabaricus					+			
Lutjanidae								
Lutjanus argentimaculatus					+			+
Lutjanus fuscescens					+			
Gerreidae								
Gerres filamentosus					+			
Toxotidae								
Toxotes jaculatrix					+			
Terapontidae								
Mesopristes argenteus					+			
Mesopristes cancellatus					+			
Terapon jarbua					+			
Kuhlidae								
Kuhlia marginata	+		+		+			
Kuhlia rupestris	+				+			
Blenniidae								
Meiacanthus anema		+						
Rhyacichthyidae								
Rhyacichthys aspro	+		+	+				
Eleotridae								
Belobranchus belobranchus	+	+	+	+	+			
Bunaka gyrinoides	+				+			
Butis amboinensis	+							
Eleotris fucsa					+			
Eleotris aff. fusca-melanosoma	+	+						
Eleotris melanosoma					+			
Giurus margaritacea					+			
Ophieleotris aporos								+
Ophieleotris aff. aporos	+							
Ophiocara porocephala	+	+	+		+			
Gobiidae								
Awaous aff. grammepomus-ocellatus	+							
Awaous melanocephalus			+		+			
Glossogobius aureus								+
Glossogobius bicirrhosus	+							
Glossogobius celebius					+			
Glossogobius aff. celebius-kokius	+	+						

Appendix I continued

Species	**B**	**K**	**NR**	**F**	**T**	**M**	**P**	**NL**
Gobiidae cont.								
Glossogobius concavifrons	+							
Glossogobius flavipinnis *						+		
Glossogobius intermedius *						+		
Glossogobius matanensis *						+		
Glossogobius aff. obscurus-brunneus	+							
Hypseleotris sp.	+							
Hypogymnogobius xanthomelus	+							
Istigobius ornatus				+				
Lentipes sp.1		+						
Lentipes sp.2					+			
Mugilogobius adeia *						+		
Mugilogobius amadi *							+	
Mugilogobius cavifrons					+	+		
Mugilogobius latifrons *						+		
Mugilogobius lepidotus *						+		
Mugilogobius rexi *						+		
Mugilogobius sarasinorum *							+	
Mugilogobius sp.						+		
Periophthalmus argentilineatus	+				+			
Periophthalmus minutus	+							
Pseudapocryptes borneensis					+			
Pseudogobiopsis oligactis	+							
Pseudogobiopsis sp.	+							
Redigobius bikolanus	+				+			
Redigobius penango *						+		
Redigobius sp.	+	+						

Species	**B**	**K**	**NR**	**F**	**T**	**M**	**P**	**NL**
Gobiidae cont.								
Schismatogobius bruynisi	+		+					
Sicyopterus cyanocephalus			+	+	+			
Sicyopterus gymnauchen	+							
Sicyopterus hageni				+	+			
Sicyopterus longifilis			+	+				
Sicyopterus macrostetholepis	+	+	+	+				
Sicyopterus microcephalus	+							
Sicyopterus micrurus	+	+		+	+			
Sicyopterus ouwensi	+		+	+				
Sicyopterus parvei				+				
Sicyopterus wichmanni					+			
Sicyopterus zosterophorum	+							
Sicyopterus sp.1	+	+						
Sicyopterus sp.2			+					
Sicyopus sp.			+					
Stenogobius opthalmoporus	+							
Stenogobius sp.	+							
Stiphodon aff. atratus					+			
Stiphodon elegans	+	+						
Stiphodon semoni	+		+	+				
Gobiidae sp.		+						
Scatophagidae								
Scatophaguss argus	+				+			
Acanthuridae								
Acanthurus nigrofuscus					+			
Number of species	**54**	**15**	**18**	**14**	**49**	**36**	**10**	**6**

Note that fourteen other species, all of which are endemic to Sulawesi, have not been included in the table as no data were available on the fish communities to which they belonged. These species are as follows; the melanotaeniid, *Marosatherina ladigesi*, the phallostethid, *Neostethus djajaorum*, the adrianichthyids, *Oryzias bonneorum*, *Oryzias nebulosus, Oryzias sarasinorum* and *Oryzias woworae*, the zenarchopterids, *Dermogenys orientalis*, *Dermogenys vogti*, *Nomorhamphus brembachi*, *Nomorhamphus hageni*, *Nomorhamphus liemi* and *Nomorhamphus rex*, the terapontid, *Lagusia micraacanthus* and the eleotrid, *Bostrychus microphthalmus* (See review by Parenti, 2011 and subsequent addition by Huylebrouck *et al.*, 2012).

Appendix II. List of fish families recorded in the fresh waters of Wallacea, together with their total numbers of species and the percentage contributions by those species to the total number of species (%). W is the total for Wallacea. *, denotes additional endemic species (see Appendix I) found in regions of Wallacea not included in this study. Most speciose families, *i.e.* contributed ≥ 10% to the total number of species in a region, are highlighted in grey.

	B	%B	K	%K	NR	%NR	F	%F	T	%T	M	%M	P	%P	NL	%NL	W	%W
Megalopidae									1	2.0							**1**	**0.6**
Anguillidae	2	3.7	1	6.7	1	5.6	1	7.1	4	8.2					1	16.7	**5**	**3.0**
Moringuidae	1	1.9															**1**	**0.6**
Muraenidae	3	5.6															**3**	**1.8**
Ophichthidae	1	1.9															**1**	**0.6**
Mugilidae	1	1.9			1	5.6			3	6.1					1	16.7	**6**	**3.6**
Melanotaeniidae											17	47.2					**18**	**10.8**
Phallostethidae																	**1**	**0.6**
Atherinidae					1	5.6			2	4.1							**3**	**1.8**
Adrianichthyidae									2	4.1	4	11.1	6	60.0			**16**	**9.6**
Synbranchidae					1	5.6											**1**	**0.6**
Zenarchopteridae	2	3.7	1	6.7							4	11.1	1	10.0	1	16.7	**15**	**9.0**
Aplocheilidae	1	1.9			1	5.6					1	2.8	1	10.0			**1**	**0.6**
Syngnathidae	4	7.4	1	6.7			1	7.1	1	2.0							**6**	**3.6**
Carangidae	1	1.9							1	2.0							**2**	**1.2**
Scorpaenidae	2	3.7					1	7.1									**3**	**1.8**
Ambassidae	1	1.9							5	10.2							**5**	**3.0**
Serranidae									1	2.0							**1**	**0.6**
Lutjanidae									2	4.1					1	16.7	**2**	**1.2**
Gerreidae									1	2.0							**1**	**0.6**
Toxotidae									1	2.0							**1**	**0.6**
Terapontidae									3	6.1							**4**	**2.4**
Kuhlidae	2	3.7			1	5.6			2	4.1							**2**	**1.2**
Blenniidae			1	6.7													**1**	**0.6**
Rhyacichthyidae	1	1.9			1	5.6	1	7.1									**1**	**0.6**
Eleotridae	6	11.1	3	20.0	2	11.1	1	7.1	6	12.2					1	16.7	**11**	**6.6**
Gobiidae	25	46.3	8	53.3	9	50.0	9	64.3	12	24.5	10	27.8	2	20.0	1	16.7	**53**	**31.9**
Scatophagidae	1	1.9							1	2.0							**1**	**0.6**
Acanthuridae									1	2.0							**1**	**0.6**
Number of species	**54**		**15**		**18**		**14**		**49**		**36**		**10**		**6**		**166**	
Number of families	**16**		**6**		**9**		**6**		**18**		**5**		**4**		**6**		**29**	