DIVERSITY OF FRESHWATER FISHES FROM EASTERN SABAH: ANNOTATED CHECKLIST FOR DANUM VALLEY AND A CONSIDERATION OF INTER- AND INTRA-CATCHMENT VARIABILITY

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ABSTRACT. - Intensive collection of freshwater fishes over a period of two years and a review of old records revealed that a total of 47 species in 12 families are currently known from the catchment of the upper Segama River near Danum Valley Field Centre, eastern Sabah, an increase of 10 species over previous checklists. Notes on occurrence, ecology and taxonomy are given. Additional collections were made from headwater streams in the catchment of the Kuamut River and from the lower Segama river to assess the contribution of inter- and intra-catchment variability to total biodiversity of the region. An additional 13 species in six families were found during a week-long survey of the lower Segama area, while an additional 5 species and two families were collected from headwaters of the Kuamut River in five collections over 18 months. Quantitative analysis of data from hillstreams from the Segama and Kuamut rivers showed substantial differences in fish communities over short geographical distances, whereas similar qualitative differences were found longitudinally along the Segama River. Full assessment of biodiversity must take such patterns into account.

KEYWORDS. - Freshwater fishes, fish communities, biodiversity, Sabah.

INTRODUCTION

Adequate description of freshwater fish communities for biodiversity purposes requires accurate taxonomy and quantitative measures of abundance (Kottelat et al., 1993; Kottelat & Whitten, 1996a). Environmental monitoring also requires that the distribution of species and their relative abundance are quantified (Kottelat & Whitten, 1996a). On the island of Borneo, the fish communities in the Malaysian state of Sabah have been sampled qualitatively and described over a number of years (Inger, 1955; Inger & Chin, 1962, with supplementary...
chapter by Chin, 1990; Lim & Wong, 1994; Chin & Samat, 1995). However, there have been few quantitative studies of communities (but see Samat, 1993) and coverage of the fish fauna of the state remains somewhat patchy, concentrated in readily accessible areas, such as Danum Valley Field Centre (DVFC) or Mount Kinabalu (e.g. Chin & Samat, 1995; Samat, 1990 respectively). Furthermore, most work in a specific area to date has involved short-term collection over a period of only a few days, procedures that can miss rare or seasonally abundant species (Magurran, 1988). Species accumulation curves for almost all taxa in tropical areas show extremely long tails, with new species being recorded for long periods after collection starts. During an on-going, long-term ecological study of the fishes in the DVFC area (Martin-Smith, unpublished data) such rare species could be collected opportunistically to establish a fuller picture of total species richness and diversity.

The contribution of longitudinal (within-river) and horizontal (between-river) species replacements or additions also needs to be assessed in providing biodiversity estimates for a region. Longitudinal gradients in fish communities are commonly found in rivers, both temperate and tropical, as the physical characteristics of the river change (Balon & Stewart, 1983). However, data are often not available for the upper reaches of tropical rivers due to problems with accessibility to small streams at the head of the catchment (Inger & Chin 1962; Kottelat et al. 1993). These headwater streams often harbour endemic species specialised for life in the fast-flowing, highly oxygenated water (Roberts, 1989). In Borneo, endemic hillstream loaches of the family Balitoridae are abundant and diverse in headwater streams (Chin, 1990). Horizontal variation in fish communities may be equally important in determining overall biodiversity for a region, especially if species replacements occur between drainages (Kottelat & Whitten, 1996a). However, data on species richness and abundance for adjacent areas are very scarce, especially in the tropics.

The objectives of this present work were twofold - firstly to provide a full species list for one intensively studied area (around DVFC) and secondly to compare communities from this area with those further downstream and those in equivalent habitats in a different watershed. The first objective addressed the problem of species accumulation over a long period of time, since intensive sampling using a variety of methods was undertaken over a period of two years, while the second objective investigated longitudinal and horizontal patterns in fish communities. Together, these methods provided a baseline for ichthyological biodiversity in the area.

The Segama and the Kinabatangan are the two largest rivers on the east coast of Sabah. Along with the Labuk, these rivers have been considered to form a distinct biogeographic zone, the Labuk-Segama watershed (Inger & Chin, 1962). The separation of the Segama and Kinabatangan catchments occurs about 30 km west of DVFC between streams running approximately east into the Segama and those running south or west into the Kuamut River, a major tributary of the Kinabatangan. The headwater streams of the two rivers are extremely close, less than 15 km separates streams draining into the Segama from those draining into the Kuamut (e.g. Sg. Bilong at km 83 and Sg. Malua at km 95 on main line west road). Accessibility to the streams of this area has been greatly improved by construction of logging roads within the last five years. Thus it has been possible to sample quantitatively from streams in both areas. In addition an opportunity arose for collection of material from the lower reaches of the Segama River during a short field trip. Although this collection was qualitative, these data allowed the opportunity to compare communities along a longitudinal gradient.
Study sites and sampling procedure. - Qualitative and quantitative samples of fish were taken from twenty streams and rivers in the upper Segama catchment and six streams in the upper Kuamut catchment during the period May 1995-May 1997 (see Fig. 1 Insets A and C for locations).

For quantitative samples, sampling was stratified by habitat type, three categories being recognised: riffle, run and pool. Sampling effort was undertaken proportionately to the occurrence of each habitat type at each site; some sites had few or no representatives of one or other habitat type. Fishes were collected using multiple-pass electrofishing. Each station was isolated with 5 mm minnow seines at the top and bottom of the section. Two or three passes were made in a downstream direction, all fishes that were stunned being collected. Fishes were held separately in buckets of water. All fish were identified to species and their standard length measured before being returned to the water, except for voucher specimens which were preserved in 10% formalin. The length of the section and the width every 3 m was measured. For comparison between Kuamut and Segama headwater streams, a subset of three and five streams respectively were chosen for data analysis. Details of these locations are given in Table 1.

For qualitative samples around DVFC and in the upper Kuamut catchment fish were caught using cast net (25 mm stretched mesh), scoop net or kick net. Details of the three additional sampling locations in the Kuamut headwaters are also given in Table 1.

Qualitative samples in the lower Segama River were taken between Kg. Tidong and Kg. Bukit Belacong (Fig.1 Inset B). Twenty two samples were taken between 12th and 17th June 1996 using cast net (25 mm stretched mesh), hook-and-line (bailed with fruit or small fish) or gill net (50 or 75 mm stretched mesh). Details of these locations and the methods used are given in Table 2.

Taxonomic procedure. - Voucher specimens of all species were lodged at DVFC. All preserved specimens were initially fixed in 10 % formalin solution for one to two weeks and transferred to 75 % ethyl alcohol for long term storage. Specimens examined are deposited in the Danum Valley Field Centre (DVFC), Lahad Datu district, Sabah; the Natural History Museum (BMNH), London; and the Zoological Reference Collection (ZRC), National University of Singapore. Identification details follow Kottelat et al. (1993) and Kottelat & Whitten (1996b). Standard length (SL) was measured from the tip of the upper jaw to the caudal peduncle, total length (TL) from the tip of the snout to the end of the upper caudal lobe. Certain species are based only on literature records.

Data analyses. - For quantitative samples, population estimates were generated using the Zippin maximum likelihood procedure (Zippin, 1958). Since numbers for many species at each station were small, Zippin estimates were generated from the total number of individuals of all species for each pass. A conversion factor (Zippin estimate divided by total number of fish caught) was then applied to the numbers of each individual species caught. Abundance was standardised by surface area, calculated from station dimensions. These standardised data were used in all analyses detailed below.

Species diversity was calculated for each site using the Shannon species diversity index ($H'$): $H' = Sp. ln(p_i)$, where $p_i$ is the proportion of individuals of species $i$ in each sample
Fig. 1. Map indicating sampling locations. Inset A: Kuamut headwater streams. Inset B: Course of Segama River. Inset C: Segama headwater streams. Sampling locations are indicated by *, quantitative samples for parametric analysis by *Q. Abbreviations: DVFC=Danum Valley Field Centre, BRL=Borneo Rainforest Lodge.
Table 1. Sampling locations in headwater streams of Segama and Kuamut rivers.

<table>
<thead>
<tr>
<th>Location Code &amp; stream name if known</th>
<th>Location</th>
<th>Description of Site</th>
<th>Type of sampling</th>
<th>No. Riffles Sampled</th>
<th>No. Runs Sampled</th>
<th>No. Pools Sampled</th>
</tr>
</thead>
<tbody>
<tr>
<td>CSR (unnamed stream)</td>
<td>4°59'20&quot;N 117°54'00&quot;E</td>
<td>Small hillstream, moderate gradient, some riffles and small cascades with small pools, substrate rocks, gravel and sand.</td>
<td>Quant.</td>
<td>10</td>
<td>3</td>
<td>8</td>
</tr>
<tr>
<td>PTA (Sg. Palum Tambun)</td>
<td>4°57'40&quot;N 117°48'20&quot;E</td>
<td>Large hillstream, moderate gradient, some riffles and abundant pools, substrate rocks, sand and some mud.</td>
<td>Quant.</td>
<td>10</td>
<td>3</td>
<td>10</td>
</tr>
<tr>
<td>SBE (Sg. Sapat Bebandir)</td>
<td>5°01'50&quot;N 117°44'50&quot;E</td>
<td>Moderate size hillstream, moderate gradient, abundant riffles with some deep pools, substrate rock, gravel and sand.</td>
<td>Quant.</td>
<td>10</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>SKA (Sg. Sapat Kalisun)</td>
<td>4°58'30&quot;N 117°48'40&quot;E</td>
<td>Small hillstream, moderate gradient, some riffles and abundant runs, substrate rock, gravel and some sand.</td>
<td>Quant.</td>
<td>10</td>
<td>2</td>
<td>8</td>
</tr>
<tr>
<td>WAT (unnamed stream)</td>
<td>4°56'00&quot;N 117°50'00&quot;E</td>
<td>Moderate size hillstream, moderate gradient, abundant riffles with few pools, substrate bedrock and sand.</td>
<td>Quant.</td>
<td>9</td>
<td>5</td>
<td>3</td>
</tr>
<tr>
<td>Lob (unnamed stream)</td>
<td>5°01'05&quot;N 117°32'40&quot;E</td>
<td>Large hillstream, steep gradient, abundant riffles and some large, deep pools (&gt;2 m at baseflow), substrate rock and gravel.</td>
<td>Qual.</td>
<td>n/a</td>
<td>n/a</td>
<td>n/a</td>
</tr>
<tr>
<td>MAL (Sg. Malua)</td>
<td>5°05'40&quot;N 117°37'30&quot;E</td>
<td>Small river, shallow gradient, some riffles, abundant pools, substrate gravel, sand and some mud.</td>
<td>Qual.</td>
<td>n/a</td>
<td>n/a</td>
<td>n/a</td>
</tr>
<tr>
<td>Ott (unnamed stream)</td>
<td>5°03'00&quot;N 117°37'30&quot;E</td>
<td>Moderate size hillstream, steep gradient, abundant riffles and some small pools, substrate rock and gravel.</td>
<td>Qual.</td>
<td>n/a</td>
<td>n/a</td>
<td>n/a</td>
</tr>
<tr>
<td>Sca (unnamed stream)</td>
<td>5°00'20&quot;N 117°30'10&quot;E</td>
<td>Small hillstream, steep gradient, riffles, cascades and small waterfalls, substrate mostly rock.</td>
<td>Quant.</td>
<td>6</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>San (Sg. Sangitan)</td>
<td>4°59'55&quot;N 117°28'20&quot;E</td>
<td>Large hillstream, moderate-steep gradient, abundant riffles and small cascades, substrate mostly rock and gravel with some sand.</td>
<td>Quant.</td>
<td>7</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Tor (unnamed stream)</td>
<td>5°00'40&quot;N 117°31'40&quot;E</td>
<td>Small hillstream, moderate gradient, abundant riffles and some small pools, substrate pebble with some sand.</td>
<td>Quant.</td>
<td>8</td>
<td>5</td>
<td>1</td>
</tr>
</tbody>
</table>
Table 2. Details of sampling locations for fish collection from lower Segama river (12-17 June 1996)

<table>
<thead>
<tr>
<th>Station</th>
<th>Date</th>
<th>Method</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>LS9602</td>
<td>12 Jun 1996</td>
<td>Cast net</td>
<td>Sg. Segama 20 mins. downstream of Kg. Tomanggong by boat. Edge of main river</td>
</tr>
<tr>
<td>LS9603</td>
<td>12 Jun 1996</td>
<td>Gill net</td>
<td>Sg. Segama 35 mins. downstream of Kg. Tomanggong by boat. Confluence of main</td>
</tr>
<tr>
<td>LS9605</td>
<td>13 Jun 1996</td>
<td>Gill net</td>
<td>Sg. Segama 35 mins. downstream of Kg. Tomanggong by boat. Confluence of main</td>
</tr>
<tr>
<td>LS9606</td>
<td>13 Jun 1996</td>
<td>Cast net</td>
<td>Canal between Kg. Tidong &amp; Kg. Dagat. Still water, mud substrate, abundant water</td>
</tr>
<tr>
<td>LS9608</td>
<td>13 Jun 1996</td>
<td>Gill net</td>
<td>Sg. Segama just downstream of Kg. Tomanggong. Edge of main channel, low muddy</td>
</tr>
<tr>
<td>LS9609</td>
<td>14 Jun 1996</td>
<td>Gill net</td>
<td>Sg. Segama at Kg. Tomanggong. Fisherman’s catch from just downstream.</td>
</tr>
<tr>
<td>LS9610</td>
<td>14 Jun 1996</td>
<td>Gill net</td>
<td>Sg. Segama 5 mins. upstream of Kg. Tomanggong by boat. Edge of main channel.</td>
</tr>
<tr>
<td>LS9611</td>
<td>15 Jun 1996</td>
<td>Cast net</td>
<td>Sg. Segama 30 mins. downstream of Kg. Litong by boat. Mud banks, some grassy</td>
</tr>
<tr>
<td>LS9614</td>
<td>15 Jun 1996</td>
<td>Gill net</td>
<td>Sg. Segama 10 mins. downstream of ferry crossing below Kg. Litong by boat. Edge of main channel at confluence with stream exiting oil palm plantation. Mud banks, some woody debris.</td>
</tr>
<tr>
<td>LS9616</td>
<td>15 Jun 1996</td>
<td>Hook-and-line</td>
<td>Sg. Segama 5 mins. downstream of ferry crossing. Middle of main channel.</td>
</tr>
<tr>
<td>LS9617</td>
<td>15 Jun 1996</td>
<td>Gill net</td>
<td>Sg. Segama 20 mins. downstream of Kg. Litong. Edge of main channel with confuence of two small streams exiting forest. Mud banks and abundant debris.</td>
</tr>
<tr>
<td>LS9618</td>
<td>16 Jun 1996</td>
<td>Gill net</td>
<td>Sg. Segama 10 mins. downstream of ferry crossing. Edge of main channel at confluence with stream exiting oil palm plantation. Mud banks, some woody debris.</td>
</tr>
<tr>
<td>LS9621</td>
<td>17 Jun 1996</td>
<td>Cast net</td>
<td>Sg. Segama 1 hr. upstream of Kg. Bukit Belacong. Edge of main channel, backwater pool grading into shallow rocky riffle.</td>
</tr>
</tbody>
</table>
Evenness values ($J'$) were also calculated for each site as follows: $J' = H'/\ln(S)$, where $S$ is the number of species per site. Species richness, $H'$, abundance and biomass were compared across all sites using a two-way analysis of variance (ANOVA) with factors catchment (Segama or Kuamut) and site (river code). The design was necessarily unbalanced due to unequal sampling effort.

To compare communities between the different sampling locations, canonical discriminant analysis (CDA) was used. This is a multivariate technique designed to reduce the number of variables by creating linear combinations of variables using the variance-covariance matrix and is suited for exploring the relationships within multi-species communities (James & McCulloch, 1990). Since the data were not normally distributed and a plot of log(variance) against log(mean) showed a significant positive regression ($R^2 = 0.964$, $F = 877.5$, $p < 0.001$), data were transformed according to the Taylor Power Law to normalise the variance (Taylor et al., 1980). In this procedure the new variable, $Z = X^p$ where $p = 1 - b/2$ and $b$ is the estimate of the slope of the regression of log(variance) on log(mean). For abundance data this relationship was $Z = X^{0.1652}$.

**RESULTS**

**Species list and notes.** A total of 47 species from 12 families have now been recorded from the catchment of the upper Segama at DYFC. A further 13 species from six families were found during the survey of the lower reaches of the Segama River; and another five species and two families from the headwaters of the Kuamut River (making a total of 68 species known from both upper and lower Segama, and Kuamut headwaters). The following list gives species names, authorities, previous records from the study area, locations and brief notes of interest. **D** indicates specimens obtained from Danum Valley, **L** from the lower Segama and **K** from Kuamut headwaters.

**FAMILY ANGUILLIDAE**

*Anguilla malgumora*  *Kaup, 1856*


Localities: **D, L, K**.

TL to 560 mm. This ubiquitous species is found in the DYFC area, occurring in all sampling locations. Specimens are commonly found under rocks in clear fast-flowing streams. No evers have been found in the headwater streams, smallest specimen obtained from the recent collection is 150 mm SL.

**FAMILY ENGRAULIDIDAE**

*Setipinna melanochir*  *(Bleeker, 1849)*


Localities: **L**.

SL to 250 mm. This predatory anchovy was caught by gill net only in the lower reaches of the Segama river.
Barbodes balleroides (Valenciennes, 1842)
Puntius bramoides (part?)- Inger & Chin, 1962: 75, fig. 33.
Localities: D, L, K.
SL to 250 mm. The major distinguishing feature is the depth of the caudal penduncle which is 1.3-1.5 times in head length in B. balleroides and 1.7-2.0 in B. collingwoodii. This species is very abundant in cast net catches in the main channel of Sg. Segama at DVFC attaining large size, but is less widespread and abundant in tributaries.

Crossocheilus cobitis (Bleeker, 1853)
Localities: D, L, K.
SL to 110 mm. Common species in fast-flowing areas of both main Segama river and tributaries. Detritivorous, found sympatrically with Garra borneensis in schools of up to 50 individuals.

Cyclocheilichthys repasson (Bleeker, 1853)
Localities: D, L, K.
SL to 215 mm. Small individuals are widespread in small streams but never abundant; large individuals were confined to the main Segama river.

Cyclocheilichthys cf. repasson
Cyclocheilichthys apogon - Inger & Chin, 1962: 66, fig. 28
Localities: D.
This species is superficially similar to C. repasson but lacks barbels. Since no material has been examined the identity remains uncertain, but it is possible this species is just a morphological variant of C. repasson.

Garra borneensis (Vaillant, 1902)
Localities: D, K.
SL to 115 mm. Ubiquitous and abundant species in fast flowing water. Found sympatrically with Crossocheilus cobitis. Sexual dimorphism is evident in tuberculation patterns of mature fish (large series had been examined over a two year period), with large spiny tuberculation across snout for females, while in males smaller spiny tuberculation is confined to sides of snout (Fig. 2).

Hampala sabana Inger & Chin, 1962
Hampala macrolepidota sabana x bimaculata - Inger & Chin, 1962: 82, fig. 37.
Hampala macrolepidota sabana - Chin, 1990: SC-12, fig. S12.
Localities: D, L, K.
SL to 410 mm. This species is common in slower, deeper areas of streams but never abundant. Larger individuals are actively predatory and have been observed disgorging frogs and small fish when caught.
Fig. 2. Schematic dorsal view of Garra borneensis showing sexual dimorphism in snout tubercle distribution (left - male, 94.0 mm SL, ZRC 40421; right - female, 98.5 mm SL, ZRC 40421).

**Labiobarbus sabanus** (Inger & Chin, 1962)

*Dangila sabaena* - Inger & Chin, 1962: 94, fig. 44.
Localities: D, L.
SL to 220 mm. Specimens have only been found in the main Segama river, never in the tributaries. Very common in lower reaches of Segama but quite rare around DVFC.

**Leptobarbus melanotaenia** Boulenger, 1894

*Leptobarbus melanotaenia* - Inger & Chin, 1962: 64, fig. 27; Chin, 1990: SC-9, fig. S7; Chin & Samat, 1995: 32.
Localities: D.
SL to 170 mm. This species is found in deeper, slower water and is always rare, except for one location where it was found in schools of 20 or more. It is an extremely strong swimmer and good jumper.

**Lobocheilos bo** (Popta, 1904)

*Lobocheilos* sp. - Chin & Samat, 1995: 33
Localities: D, L, K.
SL to 185 mm. This detritivorous species is extremely widespread and abundant in both the main Segama river and its tributaries. Larger individuals (up to 185 mm SL) are found in the main river while large schools of up to 200 juveniles are common in shallow, fast-flowing areas with gravel substrate.

*Lobocheilos* sp. is figured by Chin & Samat (1995), but it is still undetermined whether the unusual morphology of this species with possession of a large, highly tuberculated secondary rostrum represents secondary sexual characteristics of a variant of *L. bo* or a separate species. Secondary rostra are only found on individuals over 75 mm SL and appear to be present on the majority of large fish from certain locations, perhaps suggesting that this species is merely a different morphotype (Fig. 3).

**Luciosoma pellegrini** Popta, 1905

Localities: D, L, K.
SL to 170 mm. This species is fairly common and sometimes locally abundant. It is usually found in deeper, slower water. It is a very active fish, in constant motion at the surface of
the water, feeding on material dropping into streams and has been observed leaping clear of
the water to prey on material dangling above the river.

**Nematabramis borneensis** Inger & Chin, 1962

*Nematabramis aleses borneensis* - Chin, 1990: SC-6, fig. S2
*Nematabramis aleses* - Chin & Samat, 1995: 35.

Localities: D.
SL to 100 mm. Less common than *N. everetti* but still abundant and widespread. Differs
from *N. everetti* in body depth (3.6-4.2 times in SL for *N. borneensis* vs. 2.5-3.5 for *N. everetti*)
and with shorter barbels.

**Nematabramis everetti** Boulenger, 1894

*Nematabramis everetti* - Inger & Chin, 1962: 49, fig. 17; Chin, 1990: SC-7, fig. S3; Chin
& Samat, 1995: 34.

Localities: D, L, K.
SL to 105 mm. Ubiquitous and often very abundant. Adults found mostly in deeper, slower
areas, while sub-adults found in riffles and juveniles in cut-off areas.

**Osteochilus chini** Karnasuta, 1993

*Osteochilus microcephalus* - Inger & Chin, 1962: 91, fig. 43; Chin, 1990: SC-15, fig. S16; Chin
& Samat, 1995: 35.

Localities: D, L, K.
SL to 180 mm. Differs from its congener *O. ingeri* in the number of scale rows above lateral
line (5-5\(\frac{1}{2}\) for *O. chini* vs. 4-4\(\frac{1}{2}\) for *O. ingeri*) (Karnasuta, 1993) and colour of fins – reddish
for *O. chini* vs. yellowish for *O. ingeri*. Ubiquitous in slow water habitats feeding on detritus
and algae and often extremely abundant occurring in schools of up to 200 individuals.

**Osteochilus ingeri** Karnasuta, 1993

*Osteochilus spilurus* - Inger & Chin, 1962: 90, fig. 42; Chin, 1990: SC-15, fig. S15; Chin & Samat,
1995: 36.

Localities: D, L, K.
SL to 110 mm. Less common than *O. chini* but still locally abundant and often sympatric
with *O. chini*. 
**Osteochilus waandersii** (Bleeker, 1852)

Localities: K.
This species has a central black longitudinal stripe that runs from tip of snout and ends at posterior extremity of median caudal fin rays. The basal body colour was yellowish and all fins were slightly yellowish in colour. Many juveniles were caught with black ectoparasites. Juveniles are all found in the overhanging bank vegetation and near the soft substrate banks.

**Paracrossocheilus acerus** Inger & Chin 1962

*Paracrossocheilus acerus* - Inger & Chin 1962: 100, fig. 47.

Localities: K.
SL to 95 mm. This species has only been collected from headwater streams of the Kuamut area. It is found in large schools sympatrically with *Garra borneensis*.

**Puntioplites bulu** (Bleeker, 1851)

*Puntius bulu* - Inger & Chin, 1962: 70, fig. 31; Chin & Samat, 1995: 36.

Localities: D, L.
SL to 270 mm. Specimens of this species have only been obtained from the main Segama river both around DVFC and in the lower reaches. Lim & Wong (1994) commented on the status of this species.

**Puntius sealei** (Herre, 1933)


Localities: D, L, K.
SL to 110 mm. This is the most common cyprinid species around DVFC found in all stream systems where there is some slow-moving water, attaining high abundance in the absence of other species (schools of more than 200 individuals have been observed). The dispersal abilities of this species are very good, populations being established in stagnant roadside pools and above waterfalls, including the substantial series of falls at Maliau Basin Conservation Area (Martin-Smith et al., in press).

**Rasbora argyrotaenia** (Bleeker, 1850)


Localities: L, K.
SL to 80 mm. These specimens possess a black lateral stripe on the body and a whitish caudal with thick black distal border. Specimens referred to this species are found in the Kuamut headwater streams and in the lower Segama.

**Rasbora hubbsi** Brittan, 1954


Localities: D.
SL to 49 mm. This species is common and sometimes abundant, found in fast-flowing areas in or near riffles. A small species which is distinguished from the similar *R. rutteni* by a circumpenduncular scale count of 14 (occasionally 12) and the dorsal-hypural distance falling at or beyond snout (vs. circumpenduncular scale count of 12 and dorsal-hypural distance falling near anterior margin of eye for *R. rutteni*) (Brittan, 1954).
Rasbora sumatrana (Bleeker, 1852)


Localities: D, K.

SL to 105 mm. The status of the species complex of ‘*R. sumatrana*’ is unclear at the moment, further work being required (Kottelat et al., 1993). This species is ubiquitous and usually moderately abundant. Specimens from DVFC have orange dorsal fins, yellow pelvic and anal fins, whitish caudal fins with black extreme tips; a thin black lateral stripe and a black stripe at supraanal.

Rasbora sp.

Localities: D.

Superficially similar to *R. hubbsi*, this species is distinguished in life by bright red fins. Its taxonomic status is unclear. This species is only found in shallow fast-flowing sections of a very few streams.

Schismatorhynchos holorhynchus Siebert & Tjakrawidjaja, 1998


Localities: K.

SL to 140 mm. It is unclear whether this species occurs in the headwater streams around DVFC. It is found in the Kuantu headwater streams and there are some specimens located at DVFC, but without precise location data. No secondary rostrum development was noted in any of the specimens caught, although very hard and sharp tubercles were present on the rostrum and snout. The tubercles differ in having larger six-pointed star-shaped tips than that of *Lobocheilus bo* (Fig. 4). Live specimens possess a violet sheen over the body (Fig. 5). Siebert & Tjakrawidjaja (1998) recently revised *Schismatorhynchos* genus and described two new species from Borneo - *S. endecarhipis* from Kalimantan Barat (Kapuas basin) and Kalimantan Tengah (Barito basin); *S. holorhynchus* from East Sabah (Kinabatangan basin) and central Sarawak (Rejang basin). The type species *S. heterorhynchus* is known only from the drainages in central Sumatra and the Kapuas basin in Kalimantan Barat.

![Fig. 4. Schematic dorsal view of Schismatorhynchos holorhynchus showing snout tubercle distribution (131.5 mm SL, ZRC 40398). Inset of individual tubercle near tip of snout.](image-url)
**Tor tambra** (Valenciennes, in Cuvier & Valenciennes, 1842)


Localities: **D, K**.

SL to 350 mm. The precise identification of this species is still uncertain with more work required in the region to establish affinities of the different species of *Tor* (T. R. Roberts, pers. comm.). Juveniles are common in high velocity areas of small, rocky streams while larger individuals to 350 mm are found in the main channel of the Segama river.

**Tor tambroides** Bleeker, 1854

Localities: **D, K**.

SL to 140 mm. This species has larger lips and mentum than *T. tambra*.

**Cyprinidae undetermined genus and species**

Localities: **L**.

This species looks superficially similar to *Lobocheilos bo*, but differs by having a different lip morphology. This taxon has also been discussed by Lim & Wong (1994).

**FAMILY BALITORIDAE**

*Gastromyzon danumensis* Chin & Inger, 1989


Localities: **D, K**.

SL to 45 mm. This species is fairly ubiquitous and occasionally highly abundant. It is restricted to riffle areas where it feeds by scraping algae from rocks. It is a small species and generally plain grey in life, with a conspicuous secondary rostrum.

*Gastromyzon lepidogaster* Roberts, 1982


Localities: **D, K**.

SL to 100 mm. This is the most common and abundant *Gastromyzon* in the headwater streams of DVFC. It is currently the largest known species in the genus. A specimen of 101.5 mm SL (Fig. 6) was obtained from the Kuamut area and it exceeds the largest known specimen of *G. borneensis*, recorded by Roberts as 89 mm SL (Roberts, 1982: 502). *Gastromyzon lepidogaster* has a very variable colour pattern, in life varying from uniform bright green to black to barred and lined with orange edges on fins. Colour patterns have been observed to change from plain to barred or vice versa in a few minutes when the fish is transferred to a pail or aquarium (pers. obs.). In preserved specimens, a typical body pattern consists of diamond-shaped brown patches on the lateral although larger specimens (above 50 mm SL) tend to be darkly pigmented and the patterns are obscured. Juvenile specimens (ca. 20 mm SL) have a slim body profile and can be misidentified as *Protomyzon whiteheadi* due to their similar body colour pattern.

*Gastromyzon punctulatus* Inger & Chin, 1961


Localities: **D**.

SL to 65 mm. The rarest species of *Gastromyzon* in the DVFC area. Individuals have a very distinct pattern of light spots on a dark background, small on the head and larger on the body (Fig. 7).
Fig. 5. *Schismatörychus holorhynchus*, ca. 130 mm SL, life coloration, Sg. Malua.

Fig. 6. *Gastromyzon lepidogaster*, 101.5 mm SL, ZRC, Kuamut.

Fig. 7. *Gastromyzon punctulatus*, not preserved, Sg. Bilong.

Fig. 8. *Nemacheilus elegantissimus*, not preserved, Danum Valley.
\textit{Gastromyzon parielavis} Tan \& Martin-Smith, 1998

Localities: K.
SL to 60 mm. This species is only found in the Kuamut headstreams and is described in an earlier paper (see Tan \& Martin-Smith, 1998).

\textit{Gastromyzon ornaticauda} Tan \& Martin-Smith, 1998

Localities: K.
SL to 70 mm. This species is also only found in the Kuamut headstreams and is described in an earlier paper (see Tan \& Martin-Smith, 1998).

\textit{Homalooptera stephensoni} Hora 1932

Localities: D, K.
SL to 65 mm. A common and moderately abundant species of balitorid, found both in fast-flowing water on rocks and in slower water on logs or other woody debris. There appears to be some sexual dimorphism in body shape and colour, males with wider and flatter body and yellowish fins while females have narrower and stocky body and reddish fins (pers. obs.).

\textit{Nemacheilus elegantissimus} Chin \& Samat, 1992

Localities: D, K.
SL to 50 mm. A rare species recently described from the DVFC area. It is further distinguished from its more common congener \textit{N. olivaceus} by having iridescent on lateral body pattern, vs. lack of iridescence (Fig. 8).

\textit{Nemacheilus olivaceus} Boulenger, 1894

Localities: D, K.
SL to 60 mm. Ubiquitous species of balitorid found in interstices in gravel or in loosely packed leaves and debris. A juvenile specimen (ca. 16 mm SL) had no vertical bars, but with a faint brownish stripe along lateral of body.

\textit{Neogastromyzon pauciradiatus} (Inger \& Chin, 1962)

Localities: K.
SL to 43 mm. This species represents a new record for Sabah inland fishes. This species can be easily mistaken for \textit{Protomyzon} due to its elongate body and similar colour pattern (Fig. 9). It can be differentiated by the small lateral opercular opening, ventral mouth structure and fused pelvic fins (see Inger \& Chin, 1962). It is only found in Kuamut headwater streams.

\textit{Parhomalooptera microstoma} (Boulenger, 1899)

Localities: D, K.
SL to 66 mm. This species has a patchy distribution. It is abundant in localised areas and lives in the fastest-flowing areas of riffles. Very abundant in Kuamut headwater streams.

\textit{Protomyzon aphelocheilus} Inger \& Chin, 1962

\textit{Protomyzon aphelocheilus} - Inger \& Chin, 1962: 110, fig. 53.
\textit{Protomyzon aphelocheilus} - Chin \& Samat, 1995: 27
Localities: D.
Fig. 9. *Neogastromyzon pauciradiatus*, not preserved, Kuamut.

Fig. 10. *Protomyzon griswoldi*, not preserved, Danum Valley.

**Protomyzon griswoldi** (Hora & Jayaram, 1951)


Localities: D, K.

SL to 55 mm. Distinguished from congeners by colour pattern (6-8 light vertical bars) and by gill opening reaching pectoral base (Chin, 1990) (Fig. 10). Found in fast-flowing areas with pebble or rock substrate. Moderately rare.

**Protomyzon whiteheadi** (Vaillant, 1893)


Localities: D, K.

SL to 50 mm. Distinguished from *P. aphelochilus* by the presence of a papillose posterior lip. Found sympatrically with *P. griswoldi*.

**FAMILY COBITIDAE**

*Acanthopsis octoactinotos* Siebert, 1991

*Acanthopsis choiropolynus* - Inger & Chin 1962: 116, fig. 55.

Localities: D, K.

The single specimen of this species from DVFC was caught with a cast net on a sandy beach. It might be expected that the species is actually quite common but difficult to catch using normal methods since it is found buried deep in sand or leafbanks emerging only to feed (D. Siebert, pers. comm.). Specimens from the Kuamut headwaters were obtained from submerged leaf litter near the river bank, but were all juvenile specimens (30-45 mm SL).
**Pangio mariarum** (Inger & Chin, 1962)

*Acanthaphthalmus mariae* - Inger & Chin 1962: 118, fig. 56.
*Pangio cf. mariae* - Chin & Samat, 1995: 30

Localities: D, K.

SL to 80 mm. This species has only been found in leaf banks at one location around DVFC. This may represent true patchiness of populations of this species.

**FAMILY BAGRIDAEE**

**Hemibagrus aff. baramensis** (Regan, 1906)


Localities: D, L, K.

SL to 180 mm. Ubiquitous species, sometimes moderately abundant. Always found in slower, deeper water, usually in association with log cover or overhanging rocks which provide shelter.

**Hemibagrus aff. nemurus** (Valenciennes, 1839)


Localities: D, K.

SL to 540 mm. Found in similar habitats to *Hemibagrus aff. baramensis*. Distinguished by thin black mid-lateral line and usually absence of filament on upper lobe of caudal fin.

**Hemibagrus sabanus** (Inger & Chin, 1959)


Localities: L.

SL to 200 mm. This species is distinguished by a long adipose fin (34.8 %SL) compared to other species of *Hemibagrus*.

**Leiocassis sp.**

Localities: D.

This is a new record for the inland waters of Sabah and the Segama basin. This species can be differentiated from other species by its long and narrow head (24.9-25.6% SL). In life, this species is cryptically shaded with bands of yellow, alternating with beige or brown areas. (Fig. 11). This is apparently an undescribed species related to the *L. micropogon* complex (K. K. P. Lim, pers. comm.)

![Leiocassis sp.](image)

Fig. 11. *Leiocassis sp. (micropogon complex)*, 187 mm SL, life coloration, Sg. Segama.
Pseudomystus robustus (Inger & Chin, 1959)


Localities: L.

SL to 250 mm. Caught by gill net in lower reaches of Segama. Lim & Wong (1994) provided figures of the juvenile and adult body patterns.

**FAMILY SILURIDAE**

Kryptopterus parvanalis Inger & Chin, 1959


*Kryptopterus* sp. - Chin & Samat, 1995: 42.

Localities: D, L.

SL to 350 mm. This species is rare at DVFC, 5 specimens have been caught in total during 18 months of fishing, but highly abundant in lower reaches of the Segama river. Specimens obtained invariably had damaged caudal fin.

Ompok sabanus Inger & Chin, 1959


Localities: D, L.

SL to 150 mm. This species is recorded by Chin & Samat (1995) based on a single specimen. It appears that the species is rare in the Segama river at DVFC, but it is abundant in the lower Segama from Kg. Bukit Belacong and downstream.

Wallago maculatus Inger & Chin, 1959


Localities: D, L.

SL to 750 mm. It appears that although silurids may ascend the Segama river from time to time (possibly annual migrations?) they are either present in low numbers or not caught by methods used at DVFC.

**FAMILY PANGASIIDAE**

Pangasius tubbi Inger & Chin, 1959

*Pangasius tubbi* - Chin, 1990: SC-37, fig. S37.

*Pangasius tubii* - Chin & Samat, 1995: 40.

Localities: D, L.

SL to 400 mm. This species is captured infrequently from the main Segama river at DVFC. It may be migratory as local people report it to be caught at particular times of year.

Pangasius micronemus Bleeker 1847.

Localities: L.

SL to 700 mm. This species was sighted in a fisherman’s catch from the lower Segama.
FAMILY SISORIDAE

**Glyptothorax cf. major** (Boulenger, 1894)


Localities: D, K.

SL to 105 mm. This torrent catfish has a fairly wide distribution but is always obtained in low abundance. It is usually found in gravel or sandy runs with fairly fast-flowing water.

**FAMILY AKYSIDAE**

**Acrochordonichthys obscurus** Popta, 1904


Localities: D.

This species exhibits variable body colour, either dark (black or dark brown) or light (yellowish) phase. The colour pattern of the fins of the fresh specimen in dark phase (Fig. 12) corresponds to that of type material (RMNH 7556, 106.7 mm SL). The species status of *A. obscurus* is tentatively viewed as valid (H. H. Ng, pers.comm.), although it had been synonymised under *A. melanogaster* by Weber & de Beaufort (1913: 369).

![Fig. 12. Acrochordonichthys obscurus, 77.4 mm SL, Sg. Segama.](image)

*Acrochordonichthys obscurus* is a new record for the Segama basin. Only seven specimens have been obtained in 18 months of fishing either due to rarity or difficulty in catching because of their benthic habit and preference for deep fast-flowing water habitats. All specimens were caught by cast netting within a few weeks of each other following heavy rains.

**FAMILY CLARIIDAE**

**Clarias teijsmanni** Bleeker, 1857

*Clarias teijsmanni* - Inger & Chin, 1962: 131, fig. 65.

Localities: D.

SL to 200 mm. This species represents a new record for the Segama basin. All individuals were captured in small forest streams in the primary forest in slow-moving or still water and were extremely cryptic. Possibly more widespread in distribution but overlooked due to improper catching techniques.
**FAMILY ARIIDAE**

*Arius truncatus* Cuvier & Valenciennes, 1840

*Arius microcephalus*? - Inger & Chin, 1962: 151, fig. 79.

Localities: L.  
SL to 350 mm. This species is easily identified by its bright yellow colour in life and its elongate body. It was common in gill net catches from the lower reaches of the Segama river.

*Batrachocephalus mino* (Hamilton-Buchanan, 1822)

*Batracocephalus mino* - Inger & Chin, 1962: 149, fig. 76.

Localities: L.  
SL to 150 mm. Two specimens of this species were caught in gill net catches.

*Hemipimelodus borneensis* (Bleeker, 1851)

Localities: L.  
SL to 300 mm. This species is very common in gill net catches from the lower reaches of the Segama river.

**FAMILY HEMIRAMPHIDAE**

*Dermogenys* sp.

Localities: K.  
Lim & Wong (1994) commented upon the presence of a dark brown patch near the pelvic fins, this is also evident in the present series. This is most probably an undescribed species (K. K. P. Lim and B. Collette, pers. comm.).

**FAMILY TOXOTIDAE**

*Toxotes chatareus* (Hamilton, 1822)


Localities: L.  
SL to 170 mm. Specimens were caught by gill nets at the mouths of small tributaries leading into the main channel of the lower Segama river, where the current was moderate.

**FAMILY CICHLIDAE**

*Oreochromis mossambicus*

Localities: L.  
Introduced species for aquaculture purposes which apparently can survive without reaching excessive numbers as has been reported elsewhere. This species has been introduced widely as a cheap source of fish protein.
FAMILY GOBIIDAE

Gobiid sp.
Localities: L.
Unidentified gobiid species caught by cast net in the lower reaches of the Segama river.

FAMILY OSPHRONEMIDAE

Osphronemus laticlavius Roberts, 1992
Localities: D.
Few specimens of this fish have been caught in the Segama river at DVFC over 8 years or so and no specimens had been retained. A drawing made from photographs of an individual caught in 1990s shows it to be O. laticlavius (Campbell, 1994: 55).

Betta ocellata de Beaufort, 1933
Localities: D.
Betta ocellata inhabits the more slow flowing areas of the headwater habitats. It differs from B unimaculata by having more anal fin rays (total 30-31, mode 30, vs. total 27-30, mode 28/29), sharper lateral head profile and more cone-like dorsal head profile (Tan & Ng, in press).

Trichogaster trichopterus (Pallas, 1770).
Trichogaster trichopterus - Inger & Chin, 1962: 162, fig. 84.
Localities: L.
An individual was caught by cast net in a small pond in Kg. Litong.

FAMILY CHANNIDAE

Channa baramensis (Bleeker, 1851)
Localities: L.
One individual of this species was seen in a fisherman’s catch and another was caught by cast net in a small pond in Kg. Litong.

FAMILY MASTACEMBELIDAE

Macrognathus keithi Herre, 1940
Localities: D, K.
SL to 220 mm. This spiny eel is fairly common but never abundant, single or few individuals being found in leaf banks or under log debris or rocks. Juveniles have a much more distinct barred pattern than adults (Fig. 13). Specimens have been collected from small tributaries but also from the main Segama river at DVFC.
FAMILY TETRAODONTIDAE

*Chonerhinos remotus* Roberts, 1982

*Chonerhinos modestus* - Inger & Chin, 1962: 190, fig. 101.
*Chonerhinos remotus* - Chin, 1990: SC41.

Localities: K.

The presence of this species represents a range extension. In life, it had a greenish-gold body colour with a paler underbelly (Fig. 14). This specimen was caught by cast-netting near a fallen log.

*Fish communities.* - Forty-seven species from 12 families were found in the upper Segama streams, 36 species in nine families in the Kuamut streams (Table 3). Significantly more species were caught per location in Segama streams (*t*-test, *t*=3.73, df=9, *p*=0.005). However, there was no overall difference in species richness (*c²*=0.014, df=1, *p*=0.904) indicating more complementary distributions in the Kuamut streams. Although there was similarity in overall species richness there were differences in faunal composition between the two areas. In the Cyprinidae, *Cyclocheilichthys repasson*, *Leptobarbus melanotaenia*, *Nematabramis borneensis*, *Rasbora* sp. and *R. hubbsi* were only found in Segama streams whereas *Osteochilus waandersii*, *Paracrossocheilus acerus* and *Schismatorhynchos holorhynchus* were only found in Kuamut streams (although the last has been reported from the DVFC area). Large differences in faunal composition were also found in the hillstream loaches (Balitoridae); *Gastromyzon punctulatus* was only found in Segama streams whereas *Gastromyzon pariclavus*, *G. ornaticauda* and *Neogastromyzon pauciradiata* were only found
in Kuamut streams. The latter species is a new record for Sabah. The fighting fish family (Osphronemidae), represented by *Betta ocellata*, was found in Segama streams but not in Kuamut streams; this is probably due to insufficient sampling or lack of suitable habitat in the areas sampled. The reverse situation was found for fish from two other families, the half beak *Dermogenys* sp. (Hemiramphidae) and the pufferfish *Chonerhinos remotus* (Tetraodontidae). Both of these species were found in Sg. Malua and represent a range extension for these species in Sabah (see Lim & Wong, 1994).

Univariate measures of community composition were similar between the two catchments. Species diversity ($H'$) was not significantly different between any of the locations sampled (catchment $F=0.10$, df=1, $p=0.891$; site $F=0.95$, df=7, $p=0.624$) and there were also no significant differences in evenness (catchment $F=0.43$, df=1, $p=0.514$; site $F=1.44$, df=7, $p=0.225$) (Fig. 15).

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**Fig. 15.** Mean values of diversity ($H'$) and evenness ($j'$) for fish communities from Kuamut and Segama headwaters.
Canonical discriminant analysis showed that, despite the similarities in species richness, diversity and evenness, there were significant differences between the fish communities (Fig. 3). The first seven axes of the CDA were significant, but only the results from the first two canonical variables are presented. Canonical variable one explained 36.9% and canonical variable two 22.3% of total variance. Distinct clusters were found when the group centroids for the different sites were plotted on these two axes (Fig. 16). The fast water sites (riffles and runs) from the two catchments separated strongly on axis 2, with abundance of *Gastromyzon lepidogaster*, *G. pariclavis* and *G. ornaticauda* contributing significantly to the separation. Both sets of fast water sites separated from slow water sites (pools) on axis 1 with abundance of *N. ematabramis everetti*, *Osteochilus chini* and *Rasbora sumatrana* are significant to the separation. The centroid for the single stream in the Kuamut catchment (TOR) that had slow water sites was intermediate between Kuamut fast water sites and Danum slow water sites.

Fig. 16. Plot of centroids for fish communities from Kuamut and Segama headwaters on two main axes of canonical discriminant analysis. Bi-plot shows fish species contributing substantially to separation between sites.

Qualitative changes in community structure moving longitudinally down the Segama are illustrated by the change in taxonomic composition (Fig. 17). This figure shows composition by order for all species collected at each location during June 1996. Cypriniformes (cyprinids and balitorids) dominate the species composition in the higher reaches of the river and in the headwater streams, whereas Siluriformes and Perciformes are more abundant in the middle and lower reaches.

**Distribution.** - Data for capture locations of all the species above have been used to categorise each species as being found only in hillstreams, only in the main Segama river or in both (Table 4). It is recognised that these classifications are somewhat arbitrary since fish may move into tributaries from the main river to escape flooding or are washed out from tributaries during floods. Twenty-one species have only been captured in hillstreams, 16 in the Segama river and 22 have been caught in both. The affinities of the remaining eight species are uncertain due to complicated taxonomic status (*Rasbora cf. argyrotaenia*), small sample size or difficulty in capture.
Fig. 17. Diversity by taxonomic order of fishes caught at different locations along the Segama River.

DISCUSSION

General. - The total number of fish species collected from the upper Segama and Kuamut catchments around DVFC now stands at 52. This is an increase of 12 species or 30% over the latest checklist of fishes from the area (Chin & Samat, 1995). The freshwater systems around DVFC are some of the most-studied aquatic systems in Sabah and, indeed, Borneo, (Chin 1990; Samat, 1993; Chin & Samat 1995). Chin (1990) lists the number of freshwater fish species from Sabah as 155, including 12 exotics. Thus, the fish fauna of the Segama catchment at DVFC represents over a third of the fish fauna from Sabah. However, this report contains samples of two new species and one new record from Sabah, so it might be estimated that the true number of freshwater fishes in Sabah is higher. In regional terms, the Segama River might be considered to have a moderately rich fish fauna for its size. Twenty-eight species were recorded from the small Gombak river in Peninsular Malaysia (Bishop, 1973), the larger Baram River in Sarawak with at least 57 species (Watson & Balon, 1984, which is a gross underestimation), while the major rivers in Kalimantan - Kapuas (320 species), Barito (over 200 species) and Mahakam (174 species) - are substantially richer (Kottelat & Whitten, 1996a).

Horizontal distribution. - Data given here show that the headwater streams of the Segama and the Kuamut areas appeared to be equally rich in terms of number of species of fish. However, greater sampling effort was expended in the Segama streams around DVFC than the Kuamut streams, due to the distance from DVFC. Thus, although it might be expected that additional species will be found in both areas, it is likely that the true faunal richness of the Kuamut area is higher than that of the Segama area. The area of the Kuamut catchment that was sampled contained substantially less habitat heterogeneity at the scale of 10s of metres than the Segama streams (unpublished data). At the quantitative sampling locations SAN, SCA and TOR there were few areas with slow, deep water which might be expected
to harbour species such as *Leptobarbus melanotaenia* or *Clarias teijsmanni*. The other cyprinid species *Cyprichromis repasson*, *Nematabramis borneensis*, *Rasbora cf. argyrotaenia* and *R. hubbsi* might confidently be expected to be found in the Malua River, given its geomorphological similarity to streams such as Palum Tambun or Sapat Bebandir near DVFC. The Malua river has not yet been sampled using electrofishing which would be expected to yield a higher number of species than would be recorded from cast-netting and kick-netting, the two methods used.

The one family that was represented in Segama collections but not Kuamut collections was the Osphronemidae, specifically *Betta ocellata*. However, *Betta* new species (*B. unimaculata* group) has been collected from the Maliau Basin area (Tan & Ng, in press), and the Maliau River itself is a tributary of the Kuamut. Thus, given appropriate habitat conditions, *Betta* species should be found in other tributaries of the Kuamut. However, in extensive collections using a number of methods in the Segama catchment neither *Dermogenys* sp. nor *Chonerhinos remotus* have been caught and it would appear that these are truly absent from the Segama catchment. This finding is intriguing given that Inger & Chin (1962) caught *Dermogenys pusillus* in the Kinabatangan, Sandakan and Tawau districts but not in Lahad Datu district. Why this species should have such a disjunct distribution is not clear.

*Chonerhinos remotus* was recorded from the larger tributaries of the Kinabatangan by Inger & Chin (1962) as *C. modestus*, and recorded by Lim & Wong (1994) from the main confluence of the Kinabatangan River. *Chonerhinos remotus* either ascends further upriver than other species of freshwater pufferfish in Borneo (except *Carinotetraodon salivator* from the Rajang river in Sarawak; see Lim & Kottelat, 1995) or it is a stray individual.

The catchment of the Kinabatangan river is much larger than that of the Segama, extending to the eastern slopes of the Crocker Range and may well be expected to harbour further species. Detailed qualitative and quantitative collection in locations west of Kuamut is required if the freshwater fish biodiversity of Sabah is to be properly documented. The distinct differences that were found between Kuamut and Segama headwater streams (Table 3) shows the importance of the horizontal species replacements to total regional biodiversity.

There are a suite of species (an ‘assemblage’) which are restricted to small tributaries with fast-flowing waters, including all of the balitorids. It is possible that some of these species such as *Nemacheilus olivaceus*, which inhabit leaf or gravel beds, are found in the Segama river but that it is not possible to catch them with standard methods such as cast nets or hook-and-line. In addition, as the main channel of the Segama becomes rockier and more hillstream-like towards its source it is probable that gastromyzontids would be found in riffle sections. A number of cyprinids have not been captured in the Segama but this may be artifactual owing to capture difficulties because of small size (e.g. *Rasbora hubbsi*) or rarity (e.g. *Schismatorhynchos holorhynchus*). A further two species, *Betta ocellata* and *Clarias teijsmanni* have only been caught in small, slow-flowing forest streams. The former is probably restricted to this habitat but the latter is probably found in the Segama but is difficult to capture.

Conversely, other species of fish appear to be restricted to the main channel of the Segama river at DVFC. *Labiobarbus sabanus*, *Puntioplites bulu*, all species of *Siluridae*, *Pangasius tubbi* and *Acrochordonichthys obscurus* have only been captured in the main river. All of these species, except *Acrochordonichthys obscurus* grow to a large size and are also recorded from the lower Segama. Capture efficiency in smaller tributaries of the Segama around DVFC is high, especially using electrofishing, so it is suggested that these species
Table 3. Distribution of fish species by sampling location.

<table>
<thead>
<tr>
<th>Species</th>
<th>Kuamut headwaters</th>
<th>Segama headwaters</th>
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<tbody>
<tr>
<td></td>
<td>LOB</td>
<td>MAL</td>
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<td><strong>Family Anguillidae</strong></td>
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<td>Crossocheilus cobitis</td>
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<td>Cyclocheilichthys repasson</td>
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<td>Garra borneensis</td>
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<td>Hampala sabana</td>
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<tr>
<td>Paracrossocheilus acerus</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Puntius sealei</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Rasbora cf. argyrotaenia</td>
<td></td>
<td></td>
</tr>
<tr>
<td>R. hubbsi</td>
<td></td>
<td></td>
</tr>
<tr>
<td>R. sumatrana</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>Schismatohynchos holohynchos</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>Tor tambra</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>Tor tambroides</td>
<td></td>
<td>+</td>
</tr>
<tr>
<td><strong>Family Cobitidae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acantopsis octoactinotos</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>Pangio mariarum</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td><strong>Family Balitoridae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gastrostomus danumensis</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>G. lepidogaster</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>G. punctulatus</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>G. parviclavis</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>G. ornaticauda</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>Homaloptera stephensoni</td>
<td></td>
<td>+</td>
</tr>
<tr>
<td>Nemacheilus elegantissimus</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>N. olivaceus</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Neogastrostomus pauciradiatus</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>Parhomaloptera microstoma</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>Protomyzon griswoldi</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>P. whiteheadi</td>
<td>+</td>
<td></td>
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</tbody>
</table>

599
Table 3. (cont.)

<table>
<thead>
<tr>
<th>Species</th>
<th>Kuamut headwaters</th>
<th>Segama headwaters</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>LOB</td>
<td>MAL</td>
</tr>
<tr>
<td><strong>Family Bagridae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hemibagrus aff. baramensis</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Hemibagrus aff. nemurus</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Leiocassis sp.</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Family Sisoridae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gephyrocharax cf. major</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Family Hemiramphididae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dermogenys sp.</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Family Mastacembelidae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Macrognathus keithi</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><strong>Family Osphronemidae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Betta ocellata</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><strong>Family Tetraodontidae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chonerhinus remotus</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total No. Species</td>
<td>13</td>
<td>22</td>
</tr>
</tbody>
</table>

**Longitudinal distribution.** - Despite differences in sampling technique and efficiency there is clear longitudinal change in fish assemblages moving from DVFC down the Segama river (Table 4). Some species are much more abundant (all Siluriformes) whereas families and species were added (e.g. *Toxotes chatareus*) and others disappeared (e.g. many cyprinids). More species were captured at DVFC and in headwater streams around, reflecting higher sampling effort and inability to catch small fish downstream. However, there was a marked decrease in species richness of cyprinids with little or no change in the number of siluroids (although there were species replacements), all of which contributed to much greater dominance by siluroids in lower areas of the Segama river (by species number). It is more difficult to compare abundance between the areas since different capture methods were used, but most of siluroid species that were rare at DVFC (*Kryptopterus parvanalis*, *Ompok sabaus*, *Pangasius* spp. and *Wallago maculatus*) were commonly caught around Kg. Litong and Kg. Tomanggong in the lower Segama.

These changes can be explained by differences in the physicochemical environment moving downstream. Around DVFC the river has numerous rapids, generally rocky substrate with few areas of depositional substrate, high water velocity and rapid changes in water level, while in the lower course of the river the substrate is almost entirely depositional in nature, deep and slow-moving in places of partially or totally isolated ox-bow lakes. The water has some tidal influence (in terms of water level and salinity) from Kg. Tomanggong downstream. These conditions are more favourable for siluroid fishes than for cyprinids.

**Ecology.** - Inger & Chin (1962) gave an important account of the ecology of the fishes that they collected during their expeditions in 1950 and 1956. Much of their information, such
### Table 4. Distribution of fish species by location. Species marked with ‡ were only found during survey of lower Segama river.

<table>
<thead>
<tr>
<th>Species only found in headwater streams</th>
<th>Species only found in main Segama river</th>
<th>‘Ubiquitous’ species found in both</th>
<th>Uncertain affinity</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Betta ocellata</em></td>
<td><em>Acrochordonichthys obscurus</em></td>
<td><em>Anguilla malgumora</em></td>
<td><em>Acantopsis octoactinotos</em></td>
</tr>
<tr>
<td><em>Clarias teijsmanni</em></td>
<td><em>Arius truncatus</em></td>
<td><em>Barbodes balleroides</em></td>
<td><em>Channa baramensis</em></td>
</tr>
<tr>
<td><em>Gastromyzon danumensis</em></td>
<td><em>Hemipimelodus borneensis</em></td>
<td><em>Crossocheilus cobitis</em></td>
<td><em>Osphronemus laticlavus</em></td>
</tr>
<tr>
<td><em>G. lepidogaster</em></td>
<td><em>Batracoccephalus minos</em></td>
<td><em>Cyclocheilichthys repasson</em></td>
<td><em>Pangio mariarum</em></td>
</tr>
<tr>
<td><em>G. punctulatus</em></td>
<td><em>Hemibagrus sabanus</em></td>
<td><em>C. cf. repasson</em></td>
<td><em>Rasbora cf. argyrotaenia</em></td>
</tr>
<tr>
<td><em>G. pariclavis</em></td>
<td><em>Kryptopterus parvanalis</em></td>
<td><em>Garra borneensis</em></td>
<td><em>Trichogaster trichopterus</em></td>
</tr>
<tr>
<td><em>G. ornaticauda</em></td>
<td><em>Labiobarbus sabanus</em></td>
<td><em>Hampala sabana</em></td>
<td></td>
</tr>
<tr>
<td><em>Glyptothorax cf. major</em></td>
<td><em>Ompok sabanus</em></td>
<td><em>Hemibagrus aff. baramensis</em></td>
<td></td>
</tr>
<tr>
<td><em>Homalooptera stephsoni</em></td>
<td><em>Oreochromis mossambicus</em></td>
<td><em>H. aff. nemurus</em></td>
<td></td>
</tr>
<tr>
<td><em>Neogastromyzon pauceiradiata</em></td>
<td><em>Pangasius sp.</em></td>
<td><em>Leiocassis sp.</em></td>
<td></td>
</tr>
<tr>
<td><em>Nemacheilus elegantiissimus</em></td>
<td><em>P. tubbi</em></td>
<td><em>Leptobarbus melanotaenia</em></td>
<td></td>
</tr>
<tr>
<td><em>N. olivaceus</em></td>
<td><em>Pseudomystus robustus</em></td>
<td><em>Lobocheilos bo</em></td>
<td></td>
</tr>
<tr>
<td><em>Osteochilus ingeri</em></td>
<td><em>Puntioplites bulu</em></td>
<td><em>Lobocheilos sp.</em></td>
<td></td>
</tr>
<tr>
<td><em>Paracrossocheilus acerus</em></td>
<td><em>Setipinna melanochir</em></td>
<td><em>Luciosoma pellegrini</em></td>
<td></td>
</tr>
<tr>
<td><em>Parhomalooptera microstoma</em></td>
<td><em>Toxotes chatareus</em></td>
<td><em>Macragnostus keithi</em></td>
<td></td>
</tr>
<tr>
<td><em>Protomyzon aphelochelus</em></td>
<td><em>Wallago maculatus</em></td>
<td><em>Nematabramis borneensis</em></td>
<td></td>
</tr>
<tr>
<td><em>P. griswoldi</em></td>
<td><em>N. everetti</em></td>
<td><em>Osteochilus chini</em></td>
<td></td>
</tr>
<tr>
<td><em>P. whiteheadi</em></td>
<td><em>Puntius sealei</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Schismatotorhynchus holorhynchus</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Rasbora hubbsi</em></td>
<td></td>
<td><em>Tor tambra</em></td>
<td></td>
</tr>
<tr>
<td><em>Rasbora sp.</em></td>
<td></td>
<td><em>T. tambroides</em></td>
<td></td>
</tr>
<tr>
<td><em>R. sumatrana</em></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

No. Species: 22   16   21   8
as their dietary analyses, remain the most comprehensive work that has been done on fishes in the region. Obviously, some of their inferences have had to be modified in the light of further distribution data i.e. their assertion that Osteochilus spilurus (= O. ingeri) replaces O. microcephalus (= O. chini) in interior waters, whereas around DVFC the two species are found sympatrically in most locations. However, much of their information remains valid.

Chin & Samat (1995) emphasize water quality as a key factor in determining species distributions. While not denying the acute effects of water quality on survival outwith physiological tolerances of fishes, there is abundant evidence that water quality fluctuates highly between and within locations around DVFC (Douglas et al., 1992; Samat, 1993). Turbidity, suspended and dissolved solids can fluctuate by two orders of magnitude between sites (Greer et al., 1995), yet similar fish assemblages can be found. Hill-streams which may run clear for much of the time are consistently turbid during protracted rains, yet there appear to be no predictable effects on the fish fauna (unpublished data). Large changes in hydrological regime, including water quality parameters, are the norm for streams and rivers in Borneo (Bruijnzeel, 1990); thus it may be assumed that the fish fauna has evolved to cope with highly fluctuating physico-chemical conditions.

Habitat, microhabitat and food resources have all been shown to be important in determining species diversity, richness and abundance in temperate areas (e.g. Grossman & Freeman, 1987) and it is proposed that similar considerations apply in tropical regions. Many of the fish species found around DVFC show distinct habitat preferences (Martin-Smith, in prep.) and their distribution in streams probably reflects that availability of their preferred microhabitat. It is interesting that Inger & Chin (1962) consider two ‘recurrent groups’, the first consisting of Anguilla malgumora, Clarias teijsmanni, Hampala sabana, Nematabramis everetti, Puntius sealei and Rasbora sumatrana and the second of Cyclocheilichthys repasson, Lobocheilos bo, Hemibagrus aff. nemurus, Nemacheilus olivaceus and Osteochilus chini. Both of these assemblages, with some additional species, have been found around DVFC (except for the presence of C. teijsmanni in the former), but only if streams or large areas within them are considered as the fundamental sampling unit. On a scale of tens of metres or less, reasonably homogeneous habitats tend to have one or more species missing or in very low abundance. This may represent purely stochastic sampling processes, competition at this scale or selection for microhabitats. Such processes warrant further investigation and are the subject of on-going research.

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LITERATURE CITED


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