

## Diversity and spatial distribution of freshwater fish in Great Lake and Tonle Sap river (Cambodia, Southeast Asia)

Puy Lim <sup>(a\*)</sup>, Sovan Lek <sup>(b)</sup>, Seang Tana Touch <sup>(c)</sup>, Sam-Onn Mao <sup>(d)</sup>, Borin Chhouk <sup>(d)</sup>

<sup>(a)</sup> *École nationale supérieure agronomique de Toulouse, avenue de l'Agrobiopole, BP 107, Auzeville Tolosane, 31326 Castanet-Tolosan cedex, France*

<sup>(b)</sup> *Cesac, UMR 5576, CNRS-université Paul-Sabatier, 118, route de Narbonne, 31062 Toulouse cedex, France*

<sup>(c)</sup> *Department of Fisheries, 186 Norodom St., P.O. Box 582, Phnom Penh, Cambodia*

<sup>(d)</sup> *Royal University of Agriculture, Faculty of Fisheries, P.O. Box 2291, Phnom Penh, Cambodia*

Received August 16, 1999; accepted November 25, 1999

---

**Abstract** — Fish catches around the Great Lake, Tonle Sap river and the transitional zone between the lake and the river were studied by professional 'fishing lot' (i.e. fishing zone) from 1995 to 1997. One hundred and twenty species of fish, belonging to 26 families and nine different orders were recorded. Compared to previous studies (1936–1976), only 53 % of families, 32 % of genera and 54 % of species were collected by professional fishing lot. This important loss in biodiversity could have several causes: bias of sampling procedures between professional fishing and research sampling, overfishing, modification of the floodplain by deforestation, etc. The professional fishing data showed that Cypriniformes accounted for 41.6 % of the total number of individuals caught, the Cyprinidae family alone represented 40 species. Siluriformes made up 21.6 %, Perciformes 13.3 %, with six other orders represented by smaller numbers. Eighty-seven percent of the recorded species occur in both habitats depending on the season. Migration takes place from the Mekong river to the Great Lake through the Tonle Sap river at the beginning of the rainy season (May–October), and in the reverse direction at the start of the dry season (November–February). The majority of the species reproduce at the start of the rainy season (May–June) in the flooded plain and the forest floodplain of the Great Lake; the period, the place and the means of reproduction have not been closely studied, particularly for the Belontiiformes, Clupeiformes, Synbranchiiformes, Pleuronectiiformes and Tetraodontiiformes. Multivariate analysis of fishing data (November–February) shows three distinct communities: that of the lake (Perciformes and Siluriformes), of the river (Pleuronectiiformes, Cypriniformes, Clupeiformes and Siluriformes), and of the transitional zone formed from the principal channel, the old river channel and the oxbow lakes (Cypriniformes, Siluriformes and Osteoglossiiformes). © 1999 Ifremer/Cnrs/Inra/Ird/Cemagref/Éditions scientifiques et médicales Elsevier SAS

**Biodiversity / fish fauna / flood plain / Mekong / Cambodia / Southeast Asia**

**Résumé** — **Diversité et distribution spatiale des poissons du Grand Lac et du fleuve Tonlé Sap (Cambodge, Asie du Sud-Est).** Les captures de poissons dans la région du Grand Lac, le fleuve Tonlé Sap et la zone de transition entre le lac et le fleuve ont été étudiées par secteur de pêche professionnelle. Ainsi, 120 espèces de poissons ont été recensées, entre 1995 et 1997, réparties en 26 familles et neuf ordres différents. Par rapport aux données connues entre 1936 et 1976, seulement 53 % de familles, 32 % de genres et 54 % d'espèces sont présentes dans les captures. Cette importante et inquiétante diminution de la diversité pourrait avoir des causes diverses : le biais d'échantillonnage entre les pêches professionnelles et des recensements scientifiques, la surexploitation, la régression de la forêt inondée qui sert de lieu de reproduction et nourricerie, etc. Les données des pêches professionnelles ont permis de constater que les Cypriniformes représentaient 41,6 % des individus capturés avec 40 espèces de la famille des Cyprinidés. Les Siluriformes et les Perciformes sont représentés respectivement par 21,6 et 13,3 %. Enfin, les six autres ordres ne sont représentés qu'en faible quantité. Il y a 87 % des espèces capturées qui sont présents dans les deux habitats (lac et fleuve). Cependant, des variations en fonction de la saison sont observées. La migration se fait du Mékong au Grand Lac via le fleuve Tonlé Sap en début de saison des pluies (mai à octobre), et en sens inverse en début de saison sèche (novembre à février). La majorité des espèces se reproduisent dès le début de la saison des pluies (mai–juin) dans la plaine et la forêt inondées du Grand Lac. Les analyses multivariées des données de pêche (novembre à février) montrent trois communautés distinctes : celle du lac (avec Perciformes et Siluriformes dominants), celle du fleuve (Pleuronectiiformes, Cypriniformes, Clupéiformes, Siluriformes), et celle de la zone de transition formée par des chenaux, des anciens lits ou des bras morts (Cypriniformes, Siluriformes, Ostéoglossiiformes). © 1999 Ifremer/Cnrs/Inra/Ird/Cemagref/Éditions scientifiques et médicales Elsevier SAS

**Biodiversité / peuplement piscicole / plaine inondée / Mékong / Cambodge / Asie du Sud-Est**

## 1. INTRODUCTION

The Mekong river is ranked as the 14th largest river in the world. It has a discharge of  $350 \times 10^9$  cubic meters per year and is ranked 16th in terms of length [19]. The main source of freshwater in Cambodia has a characteristic hydrological system dominated by the Mekong river and its tributaries (62 %) and the Great Lake watershed system (38 %). In south central Cambodia, the Mekong joins the Tonle Sap river. The Tonle Sap river is the outlet of the Great Lake, which is situated at the upper end of the huge floodplain (70 000 km<sup>2</sup>). During the rainy season (May–October), the Mekong (with a mean annual discharge of  $45\,000 \text{ m}^3 \cdot \text{s}^{-1}$  at Phnom Penh) joins the Great Lake via the Tonle Sap river. The depth increases by more than 10 m and the Great Lake increases the water surface area from 2 520 to 15 780 km<sup>2</sup>, a natural reservoir storing 70 billion m<sup>3</sup> ( $\approx 70 \times 10^9 \text{ m}^3$ ) [3].

The floodplain and forest are submerged in one of the most productive seasonal aquatic habitats. Fish migrating upstream invade these inundated areas to feed and reproduce. During the dry season (November–April) and especially from December to February as the Mekong water level recedes, the flow reverses direction and the Great Lake flows out to the Mekong via the Tonle Sap river. Fish migrate from the lake and the floodplain to the Tonle Sap river and the Mekong. During this period all the fishing gear (bagnet or dai fishery, fences seining, etc.) are located around the Great Lake (number of professional fishing lots = 32) and along the Tonle Sap river (number of professional fishing lots = 93) [18]. The peak of fishing is in December and January. A large scale fishery has in recent years (1995–1997) contributed 15–25 % to the total inland fish catch of Cambodia which is estimated at 65 000–75 000 tonnes per year (official fisheries statistics, Department of Fisheries). Nine orders, 27 families, 63 genera and 120 species were recorded in the statistics. Cypriniformes account for 33 % of abundance and 96 % by weight of the fish caught [10]. This study investigates the difference in fish assemblages and analyses statistically the data in order to understand the importance of the various types of habitat for the different families of fish in the large-scale temporal and spatial changes in fish from the lake, the river and the transitional zone. The biodiversity of species, the dietary spectrum, and the period and site of spawning are also analysed.

## 2. MATERIALS AND METHODS

The data for 1995–1997 were provided by the Department of Fisheries. These data include catches from six provinces (*figure 1*). Four of them situated around the Great Lake (sites B, S, P and T) with 32 professional fishing lots using fence (trap fishing, used in combination with weirs extending over several kilometres), capture/killing rooms (weir fishing, lumbers are arranged to partition a section of the river to

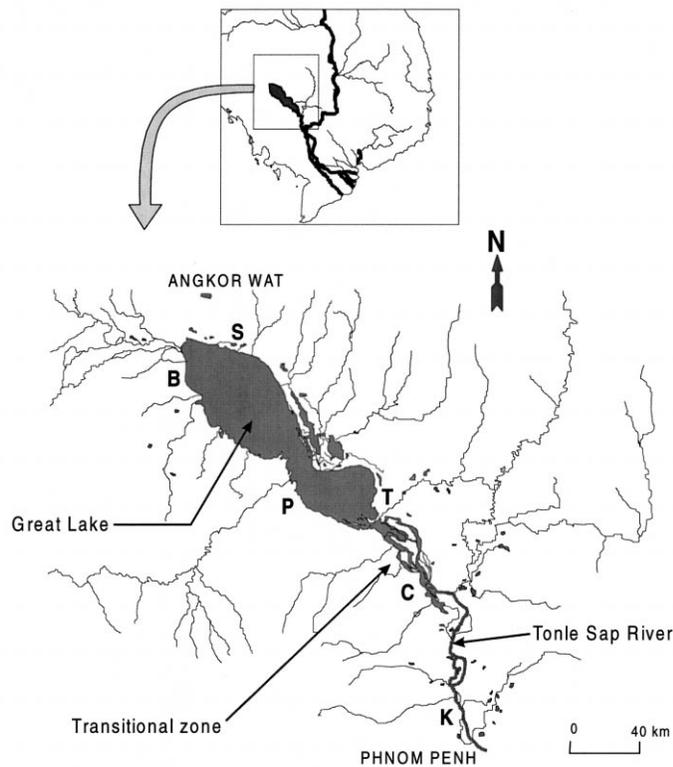
catch all fish that migrate down the stream) and seining methods. One of the two remaining provinces is situated at the outlet of the Great Lake, the transitional zone (site C) with 20 fishing lots operating barricades with yawls (small boat with scoop net), fences and seining. The last province is along the Tonle Sap river (site K) up to the confluence with the Mekong, with 73 fishing lots operating with a fixed bagnet used in combination with a row suspended in the current [10, 18]. These fishing lots are managed by the Fisheries Department (Agricultural Ministry). The data from each province comprised the local and scientific names of the fish, the catch in tonnes and the value in millions of riels (2 500 riels = 1 \$US). For most of the fish (16 %), only the genus and the local name were given, i.e. without the species name. Using the works of Chevey [4], Chevey and Le Poulain [5], Bardach [2], Fily and d'Auberton [6], Banarescu [1], Lagler [9], Touch [16], Penh [13] and Rainboth [14] on the Cambodian Mekong and the Great Lake, each genus and the local name were identified up to the species level. The classifications and scientific names of the fishes are those used by Rainboth [14]. Based on these previous works (1936–1976) cited above, the diversity, the most common size, the place of capture, the feeding habits and the spawning period and site of each species were noted.

Statistical analysis of the data was carried out using version 6.01 of SPSS [11] to consider the spatial and temporal component of fishes caught, with different samples pooled by site for a spatial study and by year for a temporal study. Principal component analyses of the fish caught at different sites and over 3 years (1995–1997) and correspondence analysis of the total pooled by family and sampling site were carried out using StatLab software (OPTIMA-Deltasoftware [12]) to identify the best simultaneous representation (in one or several graphs) of two sets consisting of lines (samples, i.e. statistical individuals) and columns (statistical variables) of the data matrix.

## 3. RESULTS

### 3.1. Population composition

The composition of the fish fauna (orders, families, genera and species) caught by the fishery lots at the Cambodia Mekong and Great Lake, and described previously, is shown in *table I*. One hundred and twenty species were collected belonging to 63 genera, 27 families and nine orders. Compared with species lists for the area, reported in *table II*, 53 % of families, 32 % of genera and 54 % of species were recorded. The composition of the fauna was predominantly Cypriniformes: 41.6 % of the total, with Cyprinidae alone accounting for over 40 %. The Siluriformes represent 21.6 % of the total catch with Bagridae (genus *Mystus*) being dominant. The Perciformes represented 13.3 % of the total. The six other orders each represented only 1.6–7.5 % of the total. Eleven



**Figure 1.** Location of the studied sites (B: Battambang, S: Siem Reap, P: Pursat, T: Kompong Thom, C: Kompong Chhnang, K: Kandal).

percent of the species are below 10 cm in standard length (nine species of Cyprinidae, three Clupeidae and one Chanidae), 64 % between 10 and 30 cm (28 species of Cypriniformes, 13 Perciformes, eight Siluriformes, two to five species for each of the remaining orders), 8 % are between 30 and 50 cm (in particular, Cypriniformes and Siluriformes), and 16 % are from 50 to 150 cm (including *Catlocarpio siamensis*, an endangered species).

Thirty-four percent of the species were piscivorous, in particular the Notopteridae, Engraulidae, Siluridae, Clariidae, Belonidae and Channidae. Twenty-two percent were insectivorous, including some Cyprinidae,

Bagridae, Mastacembelidae, Chadidae, Polynemidae, Soleidae, Cynoglossidae and Tetraodontidae. Forty-four percent of the species were planktivorous and omnivorous including most of the Cyprinidae and Clupeidae.

Most of the species that live in rivers and in the Great Lake spawn in the rainy season. Those living in floodplains or riparian forest spawn between May and August, except the Clupeidae, some species of Cyprinidae, Pleuronectiformes and Tetraodontiformes orders. For some families, such as Engraulidae, Belonidae, Mastacembelidae, Soleidae and Cynoglossidae, the site and period of spawning are unknown.

**Table I.** Fish fauna composition (orders, families, genus and species) caught by all the fishery lots at the Cambodia lower Mekong and Great Lake and described in Cambodia Mekong and Great Lake by Rainboth [14], Bardach [2], Fily and d'Auberton [6] and Chevey [4].

| Order             | Family |           | Genera |           | Species |           |
|-------------------|--------|-----------|--------|-----------|---------|-----------|
|                   | Caught | Described | Caught | Described | Caught  | Described |
| Osteoglossiformes | 1      | 2         | 2      | 2         | 3       | 4         |
| Clupeiformes      | 2      | 3         | 6      | 11        | 9       | 9         |
| Cypriniformes     | 3      | 3         | 28     | 68        | 50      | 103       |
| Siluriformes      | 5      | 11        | 10     | 31        | 26      | 56        |
| Belontiformes     | 2      | 4         | 2      | 6         | 3       | 3         |
| Synbranchiformes  | 1      | 3         | 2      | 5         | 6       | 8         |
| Perciformes       | 10     | 22        | 10     | 69        | 16      | 25        |
| Pleuronectiformes | 2      | 2         | 2      | 4         | 5       | 10        |
| Tetraodontiformes | 1      | 1         | 1      | 4         | 2       | 3         |
| Total             | 27     | 51        | 63     | 200       | 120     | 221       |

Table II. Fish fauna caught by fishery lots in the Tonle Sap River and Great Lake.

| Order                                  | Family                          | Scientific name                       | Nsp/total | Size (cm) | River/Transit.zone       | Lake               | Food                        | Spawning period   | Spawning site       |
|--|---------------------------------|---------------------------------------|-----------|-----------|--------------------------|--------------------|-----------------------------|-------------------|---------------------|
| Osteoglossiformes                      | Notopteridae                    | <i>Chilata blanci</i> A               | 1/3       | 90        | Y                        | Y                  | fish                        | June–July         | inundated forest    |
|  |                                 | <i>Chilata ornata</i> G               | 2/3       | 100       | Y                        | Y                  | fish                        | June–Jul          | inundated forest    |
|  |                                 | <i>Notopterus notopterus</i> P        | 1/1       | 40        | Y                        | Y                  | fish–insects                | June–July         | inundated forest    |
| Clupeiformes                           | Clupeidae                       | <i>Clupeichthys aesarnensis</i> W     | 1/2       | 8         | Y                        |                    | zoopk.                      | June?             | Tonle Sap river     |
|  |                                 | <i>Clupeichthys goniognathus</i> B    | 2/2       | 9         | Y                        |                    | zoopk.                      | June?             | Tonle Sap river     |
|  |                                 | <i>Clupeoides borneensis</i> B        | 1/1       | 8         | Y                        |                    | zoopk.                      | June?             | Tonle Sap river     |
|  |                                 | <i>Tenualosa thibaudeaui</i> D        | 1/2       | 30        | Y                        |                    | phytopk.                    | April             | Tonle Sap river     |
|  |                                 | <i>Tenualosa toli</i> V               | 2/2       | 60        | Y                        | Y                  | phytopk.                    | May–June?         | Tonle Sap river     |
|  | Engraulidae                     | <i>Colia lindmani</i> B               | 1/2       | 20        | Y                        | Y                  | fish–insects–crust.         | u                 | u                   |
|  |                                 | <i>Colia macrogathos</i> B            | 2/2       | 25        | Y                        | Y                  | fish–insects–crust.         | u                 | u                   |
|  |                                 | <i>Lycotrisa crocodilus</i> B         | 1/1       | 30        | Y                        | Y                  | fish–insects–crust.         | u                 | u                   |
|  |                                 | <i>Setipinna melanochir</i> B         | 1/1       | 30        | Y                        |                    | fish–insects                | u                 | u                   |
|  |                                 | <i>Paralauca typus</i> B              | 1/4       | 18        | Y                        | Y                  | zoopk.                      | July              | floodplain          |
| Cypriniformes                          | Cyprinidae                      | <i>Macrochirichthys macrochirus</i> V | 1/1       | 70        | Y                        | Y                  | insects–fish                | May–June          | floodplain          |
|  |                                 | <i>Parachela maculicauda</i> S        | 1/4       | 5         | Y                        | Y                  | insects–zoopk.              | May–June          | floodplain          |
|  |                                 | <i>Opsarus koratensis</i> S           | 1/2       | 10        | Y                        |                    | insects                     | u                 | river ?             |
|  |                                 | <i>Opsarus pulchellus</i> S           | 2/2       | 10        | Y                        |                    | insects–crust.              | u                 | river?              |
|  |                                 | <i>Leptobarbus hoeveni</i> B          | 1/1       | 50        | Y                        | Y                  | insects–zoopk.–plants       | June              | floodplain          |
|  |                                 | <i>Luciosoma setigerum</i> V          | 1/2       | 25        | Y                        | Y                  | fish                        | June              | floodplain          |
|  |                                 | <i>Rasbora daniconius</i> H           | 1/16      | 6         | Y                        |                    | crust.–insects              | May–June?         | river and pond      |
|  |                                 | <i>Rasbora aurotaenia</i> T           | 2/16      | 15        | Y                        |                    | insects–algae               | May–June?         | river and pond      |
|  |                                 | <i>Rasbora hobelmani</i> K            | 3/16      | 6         | Y                        |                    | insects                     | May–June?         | river and pond      |
|  |                                 | <i>Rasbora paviei</i> T               | 4/16      | 10        | Y                        |                    | insects                     | May–June?         | river and pond      |
|  |                                 | <i>Rasbora tornieri</i> A             | 5/16      | 17        | Y                        |                    | insects                     | May–June?         | river and pond      |
|  |                                 | <i>Rasbora pausisquamis</i> A         | 6/16      | 4         | Y                        |                    | insects                     | May–June?         | river and pond      |
|  |                                 | <i>Cyprinus carpio</i> L              | 1/1       | 80        | Y                        |                    | omnivorous                  | July              | river & floodplain  |
|  |                                 | <i>Probarbus jullieni</i> S           | 1/3       | 100       | Y                        | Y                  | u                           | u                 | u                   |
|  |                                 | <i>Albulichthys albuloides</i> B      | 1/1       | 25        | Y                        | Y                  | omnivorous                  | May–June          | inundated land      |
|  |                                 | <i>Amblyrhynchichthys truncatus</i> B | 1/1       | 30        | y                        | Y                  | periphyton                  | May–June          | inundated land      |
|  |                                 | <i>Cosmochilus harmandi</i> S         | 1/1       | 30        | Y                        | Y                  | periphyton                  | May–June          | inundated land      |
|  |                                 | <i>Cyclocheilichthys armatus</i> V    | 1/8       | 15        | y                        | Y                  | zoopk.–crust.–insects       | September         | inundated land      |
|  |                                 | <i>Cyclocheilichthys enoplos</i> B    | 2/8       | 45        | y                        | Y                  | zoopk.–insects–fish         | June              | inundated land      |
|  |                                 | <i>Cyclocheilichthys lagleri</i> S    | 3/8       | 15        | y                        | Y                  | zoopk.–insect–crust.        | September         | inundated land      |
|  |                                 | <i>Puntioptiles bulu</i> B            | 1/5       | 30        | Y                        | Y                  | algae–insects–plants        | June–July         | inundated land      |
|  |                                 | <i>Puntioptiles proctozysion</i> B    | 2/5       | 25        | Y                        | Y                  | algae–insects–plants        | June–July         | inundated land      |
|  |                                 | <i>Barbodes altus</i> G               | 1/3       | 15        | Y                        | Y                  | omnivorous                  | June              | river & floodplain  |
|  |                                 | <i>Barbodes goniotonus</i> B          | 2/3       | 30        | Y                        | Y                  | omnivorous                  | June              | river & floodplain  |
|  |                                 | <i>Hampala dispar</i> S               | 1/2       | 35        | Y                        | Y                  | prawns–crabs–shrimps–fish   | May               | inundated land      |
|  |                                 | <i>Hampala macrolepidota</i> V        | 2/2       | 35        | Y                        | Y                  | fish                        | May               | inundated land      |
|  |                                 | <i>Puntius brevis</i> B               | 1/2       | 10        | Y                        | Y                  | zoopk.–crust.               | May–June          | inundated land      |
|  |                                 | <i>Puntius masyai</i> S               | 2/2       | 3         | Y                        | Y                  | zoopk.–crust.               | May–June          | inundated land      |
|  |                                 | <i>Systemus orphoides</i> V           | 1/6       | 25        | Y                        | Y                  | zoopk.–insects–plants       | April–May         | rivers & floodplain |
|  |                                 | <i>Catlocarpio siamensis</i> B        | 1/1       | 150       | Y                        | Y                  | omnivorous                  | u                 | floodplain?         |
|  |                                 | <i>Thynnichthys thynnoides</i> B      | 1/1       | 12        | Y                        | Y                  | periphy.–phyto–zoopk.       | May–June          | floodplain          |
|  |                                 | <i>Cirrhinus microlepis</i> S         | 1/6       | 60        | Y                        | Y                  | omnivorous                  | May–June          | floodplain          |
|  |                                 | <i>Cirrhinus molitorella</i> V        | 2/6       | 45        | Y                        | Y                  | omnivorous                  | May–June          | floodplain          |
|  |                                 | <i>Dangila cf cuvieri</i> V           | 1/4       | 12        | Y                        | Y                  | phytopk.–zoopk.             | May–June          | floodplain          |
|  |                                 | <i>Dangila kuhli</i> V                | 2/4       | 20        | Y                        | Y                  | phytopk.–zoopk.             | May–June          | floodplain          |
|  |                                 | <i>Dangila lineata</i> S              | 3/4       | 18        | Y                        | Y                  | phytopk.–zoopk.             | May–June          | floodplain          |
|  |                                 | <i>Dangila spilopleura</i> S          | 4/4       | 20        | Y                        | Y                  | phytopk.–zoopk.             | May–June          | floodplain          |
| <i>Henicorhynchus caudimaculatus</i> F | 1/3                             | 13                                    | Y         | Y         | herbivorous              | May–June           | river–floodplain            |                   |                     |
| <i>Henicorhynchus cryptopogon</i> F    | 2/3                             | 15                                    | Y         | Y         | herbivorous              | May–June           | river–floodplain            |                   |                     |
| <i>Henicorhynchus siamensis</i> B      | 3/3                             | 20                                    | Y         | Y         | herbivorous              | May–June           | river–floodplain            |                   |                     |
| <i>Lobocheilus melanotaenia</i> F      | 1/6                             | 15                                    | Y         | Y         | plankton–plants detritus | May                | floodplain                  |                   |                     |
| <i>Morulus chrysophekadion</i> B       | 1/1                             | 60                                    | Y         | Y         | plankton–detritus        | May                | river                       |                   |                     |
| <i>Osteochilus hasselti</i> V          | 1/8                             | 30                                    | Y         | Y         | plankton–detritus        | May–June           | floodplain                  |                   |                     |
| <i>Osteochilus melanopleurus</i> B     | 2/8                             | 40                                    | Y         | Y         | plankton–plants          | May–June           | floodplain                  |                   |                     |
| <i>Osteochilus schlegeli</i> B         | 3/8                             | 40                                    | Y         | Y         | plankton–plants          | May–June           | floodplain                  |                   |                     |
| Cobotiidae                             | <i>Botia helodes</i> S          | 1/8                                   | 25        | Y         | Y                        | molluscs–insects   | June–July                   | floodplain        |                     |
|  | <i>Botia lecontei</i> F         | 2/8                                   | 15        | Y         | Y                        | molluscs–insects   | June–July                   | floodplain        |                     |
|  | <i>Botia modesta</i> B          | 3/8                                   | 25        | Y         | Y                        | molluscs–crust.    | June–July                   | floodplain        |                     |
| Gyrinocheilidae                        | <i>Gyrinocheilus ayonieri</i> T | 1/2                                   | 20        | Y         |                          | periphyton–insects | u                           | probably in river |                     |
|  | <i>Mystus filamentus</i> F & C  | 1/13                                  | 50        | Y         | Y                        | crust.–fish        | May–June                    | floodplain        |                     |
| Siluriformes                           | Bagridae                        | <i>Mystus nemurus</i> V               | 2/13      | 60        |                          | Y                  | insects–shrimps–crust.–fish | May–June          | floodplain          |
|  |                                 | <i>Mystus atrifasciatus</i> F         | 3/13      | 15        | Y                        | Y                  | crust.–zoopk.               | May–June          | floodplain          |
|  |                                 | <i>Mystus albolineatus</i> R          | 4/13      | 35        | Y                        |                    | insects–zoopk.–fish         | May–June          | floodplain          |
|  |                                 | <i>Mystus singaringan</i> B           | 5/13      | 20        | Y                        | Y                  | insects–zoopk.–fish         | May–June          | floodplain          |
|  |                                 | <i>Mystus multiradiatus</i> R         | 6/13      | 15        | Y                        | Y                  | zoopk.–crust.–insects       | May–June          | floodplain          |
|  |                                 | <i>Mystus mysticetus</i> R            | 7/13      | 12        | Y                        | Y                  | zoopk.–crust.–insects       | May–June          | floodplain          |
|  |                                 | <i>Mystus wolffi</i> B                | 8/13      | 20        | Y                        | Y                  | insects–crust.              | May–June          | floodplain          |
|  |                                 | <i>Mystus wicki</i> B                 | 9/13      | 40        | Y                        | Y                  | insects–prawns–fish         | May–June          | floodplain          |
|  |                                 | <i>Mystus wickioides</i> C & F        | 10/13     | 50        | Y                        | Y                  | insects–prawns–fish         | May–June          | floodplain          |

Table II. Continued.

| Order                                | Family                      | Scientific name                        | Nsp/total                       | Size (cm) | River/<br>Transit.zone | Lake          | Food                     | Spawning period       | Spawning site |            |
|--------------------------------------|-----------------------------|--|---------------------------------|-----------|------------------------|---------------|--------------------------|-----------------------|---------------|------------|
|                                      | Siluridae                   | <i>Belodontichthys dinema</i> B        | 1/1                             | 70        | Y                      | y             | fish                     | May–June              | floodplain    |            |
|                                      |                             | <i>Kryptopterus kryptopterus</i> B     | 1/7                             | 35        | Y                      | Y             | fish–prawns–insects      | May–June              | river         |            |
|                                      |                             | <i>Micronema apogon</i> B              | 1/3                             | 77        | Y                      | Y             | fish                     | May–June              | floodplain    |            |
|                                      |                             | <i>Micronema bleekeri</i> G            | 2/3                             | 60        | Y                      | Y             | fish                     | May–June              | floodplain    |            |
|                                      |                             | <i>Micronema micronema</i> B           | 3/3                             | 35        | Y                      | Y             | fish                     | May–June              | floodplain    |            |
|                                      |                             | <i>Ompok bimaculatus</i> B             | 1/3                             | 45        | Y                      | Y             | fish–crust.              | u                     | floodplain?   |            |
|                                      |                             | <i>Ompok hypophthalmus</i> B           | 2/3                             | 30        | Y                      | Y             | fish–crust.              | u                     | floodplain?   |            |
|                                      |                             | <i>Ompok sp cf engeneiatus</i>         | 3/3                             | 20        | Y                      | Y             | fish–crust.              | u                     | floodplain?   |            |
|                                      |                             | <i>Wallago attu</i> S                  | 1/2                             | 80        | Y                      | Y             | fish                     | u                     | floodplain?   |            |
|                                      |                             | <i>Wallago leeri</i> B                 | 2/2                             | 110       | Y                      | Y             | fish                     | u                     | floodplain?   |            |
|                                      |                             | <i>Pangasianodon hypophthalmus</i> S   | 1/2                             | 100       | Y                      | Y             | periphyton–insects       | u                     | Mekong?       |            |
|                                      |                             | <i>Pangasius larnaudieri</i> B         | 1/12                            | 110       | Y                      | Y             | fish–crust.–plant matter | May–June              | floodplain    |            |
|                                      |                             | Pangasiidae                            | <i>Pangasius siamensis</i> S    | 2/12      | 25                     | Y             | Y                        | insects               | May–June      | floodplain |
|                                      |                             |  | <i>Clarias batrachus</i> L      | 1/5       | 40                     | Y             | Y                        | fish–molluscs         | June–July     | floodplain |
|                                      |                             | Clariidae                              | <i>Clarias macrocephalus</i> G  | 2/5       | 35                     | Y             | Y                        | fish–molluscs         | June–July     | floodplain |
| Ariidae                              | <i>Arius stormi</i> B       |  | 1/8                             | 45        | Y                      |               | invertebrates–fish       | May?                  | Mekong        |            |
|                                      | Beloniformes                | Belonidae                              | <i>Xenentodon cancila</i> H     | 1/2       | 35                     | Y             | Y                        | fish–insects          | u             | u          |
| <i>Xenentodon canciloïdes</i> B      |                             |  | 2/2                             | 30        | Y                      | Y             | fish–insects             | u                     | u             |            |
| Hemiramphidae                        |                             |  | <i>Hyporhamphus limbatus</i> V  | 1/1       | 25                     | Y             | Y                        | insects               | u             | u          |
|                                      | Synbranchi-<br>formes       | Mastacembelidae                        | <i>Macrognathus maculatus</i> C | 1/4       | 25                     | Y             |                          | insects–worms–crust.  | u             | u          |
| <i>Macrognathus taeniagaster</i> F   |                             |  | 2/4                             | 15        | Y                      |               | insects–worms–crust.     | u                     | u             |            |
| <i>Macrognathus siamensis</i> G      |                             |  | 3/4                             | 30        | Y                      |               | insects–worms–crust.     | u                     | u             |            |
| <i>Mastacembelus armatus</i> L       |                             |  | 1/4                             | 60        | Y                      | Y             | insects–worms–plants     | u                     | u             |            |
| <i>Mastacembelus erythrotaenia</i> B |                             |  | 2/4                             | 30        | Y                      | Y             | insects–worms–plants     | u                     | u             |            |
| <i>Mastacembelus javus</i> H         |                             |  | 3/4                             | 70        | Y                      | Y             | insects–worms–plants     | u                     | u             |            |
| Perciformes                          | Chandidae                   | <i>Parambassis apogonoides</i> B       | 1/2                             | 10        | Y                      | Y             | invertebrates            | July                  | floodplain    |            |
|                                      |                             | <i>Parambassis wolffi</i> B            | 2/2                             | 15        | Y                      | Y             | insects–crust.–fish      | July                  | floodplain    |            |
|                                      | Polynemidae                 | <i>Polynemus borneensis</i> B          | 1/4                             | 25        | Y                      |               | crust.                   | u                     | u             |            |
|                                      |                             | <i>Polynemus longipectoralis</i> W & B | 2/4                             | 20        | Y                      |               | shrimps–prawns           | u                     | u             |            |
|                                      | Sciaenidae                  | <i>Boesemania microlepis</i> B         | 1/1                             | 30        | Y                      |               | crust.–fish              | u                     | u             |            |
|                                      |                             | Toxotidae                              | <i>Toxotes chatareus</i> H      | 1/2       | 20                     | Y             |                          | insects–zoopk.–crust. | July–August   | floodplain |
|                                      | <i>Toxotes microlepis</i> G |  | 2/2                             | 15        | Y                      |               | insects–zoopk.–crust.    | July–August           | floodplain    |            |
|                                      | Nandidae                    | <i>Pristolepis fasciata</i> B          | 1/1                             | 20        | Y                      | Y             | omnivorous               | x times?              | floodplain    |            |
|                                      | Eleotridae                  | <i>Oxyeleotris marmorata</i> B         | 1/1                             | 30        | Y                      | Y             | fish                     | July–August           | floodplain    |            |
|                                      | Gobiidae                    | <i>Glossogobius aureus</i> A & M       | 1/4                             | 25        | Y                      | Y             | fish–crust.              | u                     | floodplain    |            |
|                                      | Anabantidae                 | <i>Anabas testudineus</i> B            | 1/1                             | 15        | Y                      | Y             | fish                     | x times?              | floodplain    |            |
|                                      | Belontiidae                 | <i>Trichogaster microlepis</i> G       | 1/3                             | 15        | Y                      | Y             | zoopk.–insects           | u                     | floodplain    |            |
|                                      |                             | <i>Trichogaster pectoralis</i> R       | 2/3                             | 15        | Y                      | Y             | zoopk.–insects           | u                     | floodplain    |            |
|                                      | Channidae                   | <i>Channa lucius</i> C                 | 1/6                             | 30        | Y                      | Y             | fish–prawns–crabs        | June–July             | floodplain    |            |
|                                      |                             | <i>Channa micropeltes</i> C            | 2/6                             | 80        | Y                      | Y             | fish–crust.              | June–July             | floodplain    |            |
| <i>Channa striata</i> B              |                             | 3/6                                    | 70                              | Y         | Y                      | fish          | June–July                | floodplain            |               |            |
| Pleuronectiformes                    | Soleidae                    | <i>Euryglossa harmandi</i> S           | 1/3                             | 10        | Y                      |               | invertebrates            | u                     | large river?  |            |
|                                      |                             | <i>Euryglossa orientalis</i> S         | 2/3                             | 15        | Y                      |               | invertebrates            | u                     | estuaries?    |            |
|                                      |                             | <i>Euryglossa panoides</i> B           | 3/3                             | 15        | Y                      |               | invertebrates            | u                     | estuaries?    |            |
|                                      | Cynoglossidae               | <i>Cynoglossus cynoglossus</i> H       | 1/7                             | 15        | Y                      |               | invertebrates            | u                     | estuaries?    |            |
| <i>Cynoglossus jeldmanni</i> B       |                             | 2/7                                    | 25                              | Y         |                        | invertebrates | u                        | estuaries?            |               |            |
| Tetraodontiformes                    | Tetraodontidae              | <i>Chelonodon nigroviridis</i> P       | 1/3                             | 17        | Y                      | Y             | molluscs–crust.inverteb. | u                     | estuaries?    |            |
|                                      |                             | <i>Chelonodon fluviatilis</i> H        | 2/3                             | 17        | Y                      |               | molluscs–crust.inverteb. | u                     | estuaries?    |            |
| Total order: 9                       | Total family: 27            | Total species: 120                     | 20/221                          |           |                        |               |                          |                       |               |            |

Nsp/total: total number of species caught/total number of species described. Size is the mean size (cm); Y indicates presence of species in lake, river and transitional zone; u: unknown.

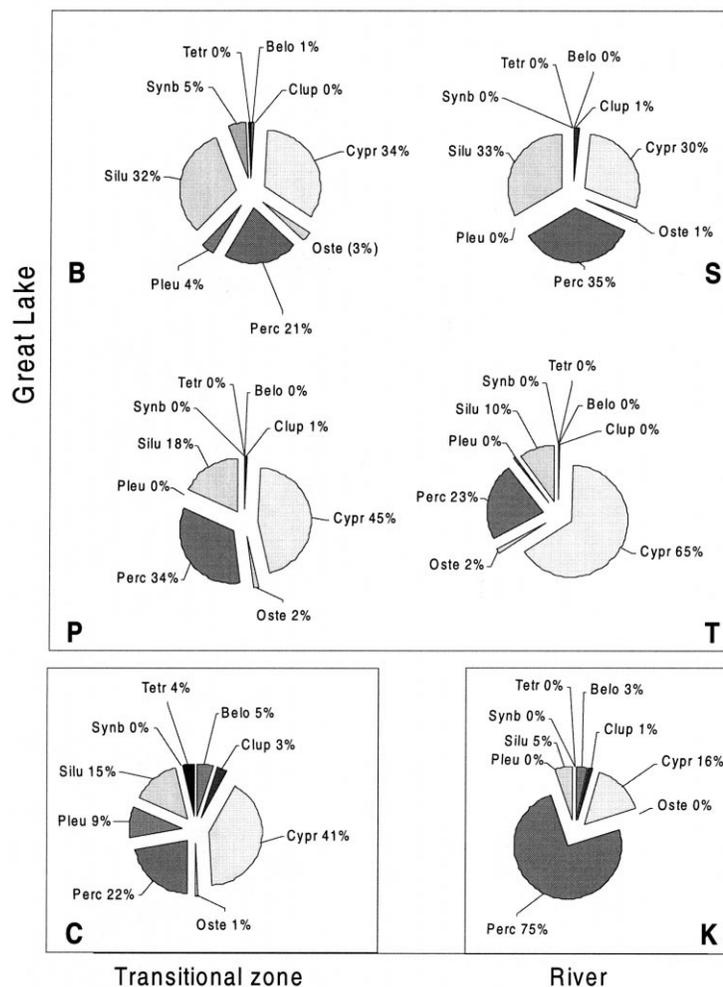
### 3.2. Spatial distribution

Capture data were analysed by species percentage frequency in the two habitats, the river and the Great Lake; 68 % occurred in the river and the lake, 25 % were found only in the river and for 7 % the preferred habitat was the lake. The latter are known as 'black fish' and are of the genera *Channa*, *Trichogaster*, *Anabas*, *Oxyeleotris* and *Mystus*.

Figure 2 shows the relative importance of the different orders in the six fishing sites studied. Three orders were predominant: Perciformes, Cypriniformes and Siluriformes. Perciformes were abundantly

present in the Tonle Sap river, where they represent 75 % of the fish captured at station K. Cypriniformes were most abundant in the transitional zone between the Great Lake and the Tonle Sap river. Siluriformes favoured the lake environment, especially at stations B and S. They were poorly represented at station K where they composed only 5 % of the population.

Performing principal component analysis (figure 3) on the capture data at the six sites for the 3 years (i.e. 18 lines × 75 columns), reveals that the majority of the variables are well correlated (values close to 1 for the first or second component, translated by points situated close to the correlation circle). There was a definite

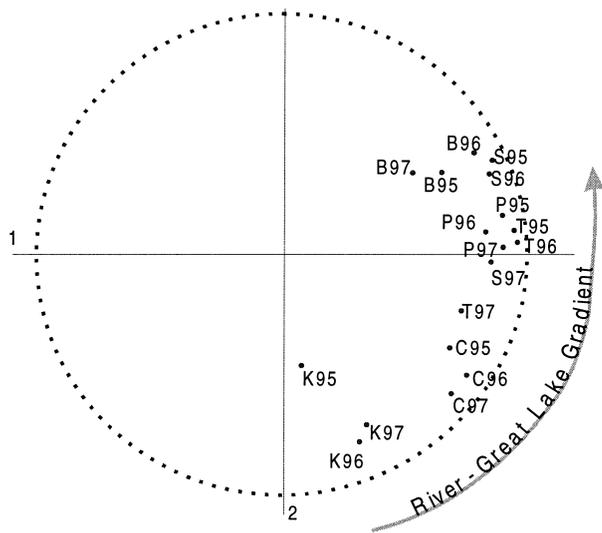


**Figure 2.** Composition of different orders of fishes (% of total catch) at the six studied sites lettered as in figure 1. Cypr: Cypriniformes, Oste: Osteoglossiformes, Perc: Perciformes, Pleu: Pleuronectiformes, Silu: Siluriformes, Synb: Synbranchiformes, Tetr: Tetraodontiformes, Belo: Belontiformes, Clup: Clupeiformes.

consistency in the captures from one year to the next. The site situated in the Tonle Sap river (site K) was independent (perpendicular position) of the sites located in the Great Lake (sites B, S, P, T). Site C, located between the two sites (transitional zone), occupies an intermediate position. Examination of the results shows that the Tonle Sap river fish fauna was dominated by the genera *Thynnichthys*, *Puntioplites*, *Dangila* (Cyprinidae) and *Pristolepis* (Nandidae); the Great Lake was populated by the genera *Barbodes*, *Hampala* (Cyprinidae), *Micronema* (Siluridae), *Pangasius* (Pangasiidae), *Trichogaster* (Belontiidae) and *Channa* (Channidae) and finally the transitional zone was populated by the genera *Cyclocheilichthys*, *Cirrhinus*, *Leptobarbus*, *Osteocheilus* and *Morulus* (Cyprinidae).

Correspondence analysis of catches for 26 fish families (figure 4) gives first and second axes which account for 86.6 % of the total variation. The variables

well represented on the factorial plane, i.e. having high correlation coefficients for one of the two factorial axes, were: B (0.953, 0.041), C (0.774, 0.087) and P (0.005, 0.824). Three other variables were represented with moderate correlation coefficients: K (0.261, 0.443), T (0.023, 0.498) and S (0.199, 0.309). The cluster hierarchical analysis of the factorial coordinates of the first two axes revealed that three groups could be identified: group 1, site B at the far end of the Great Lake characterized by the families Anabantidae and Belontiidae; group 2, sites K and C, the river system characterized by the Cyprinidae and some families of Perciformes; group 3, sites T, P and S corresponding to the middle of the Great Lake, characterized by six orders, accounted for 64.2 % of the variation, representing a spatial gradient of river and lake succession. The second axis of the correspondence analysis accounted for only 22.6 % of variation.

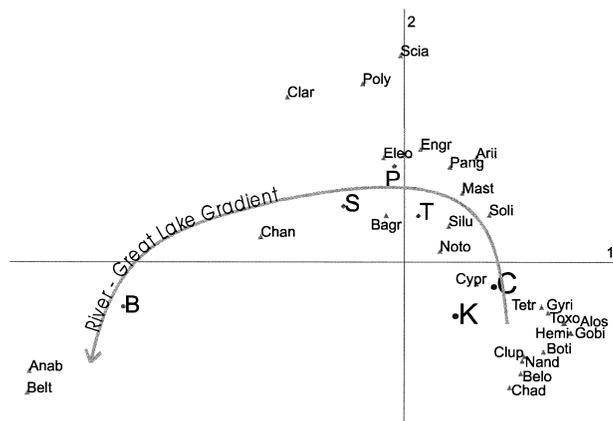


**Figure 3.** Result of standardized principal component analysis of 74 species caught at six sites over 3 years (1995, 1996, 1997). Axes 1 and 2 account for 71.3 % of total variation. Sites are lettered as in figure 1.

**4. DISCUSSION**

Species diversity is generally higher in transitional zones (Shannon index more than 4.2), particularly during a migration period, and higher in floodplains or inundated forest than in an adjacent system [19]. This is because the ecotone not only provides food and cover for a variety of fauna, but is often the only habitat for many rare or endemic species which are adapted to the periodic water-level change [8].

One hundred and twenty species were recorded from the fishing lots out of the 221 listed for the area by Chevey [4], Chevey and Le Poulain [5], Bar-



**Figure 4.** Correspondence analysis of the 26 families of fishes caught at six studied sites lettered as in figure 1. Axes 1 and 2 account for 86.6 % of total variation, i.e. 64 % for axis 1 and 23 % for axis 2. Family names were abbreviated by the first four letters of the full name, except for Belontiidae = Belt and Chandidae = Chad.

dach [2], Fily and d’Auberton [6] and Lagler [9]; 68 % of the species listed frequent the transitional zones, which explains the presence of a large number of waterfowl species which depend on floodplains for food. These transitional zones formed from the principal channel, the old river channel and the oxbow lakes, are also the site of spawning and the nursery habitat for larvae and juvenile stages. Thus, transitional zones and floodplains have a significance for the conservation of biodiversity in general, and endangered and rare species in particular [7]. The standing crop of the Great Lake has been estimated at 10 tonnes per km<sup>2</sup> at high water level and 30 tonnes per km<sup>2</sup> in times of low water by Chevey [4], which proves the high productivity of this type of area.

Although the overall biodiversity has decreased over the last 40 years for the sites studied, between about two-thirds and half of the previously known fishes have disappeared. Certain species were in clear regression owing to human activities (overfishing during the spawning migration and the migration that occurs with the receding water level, the modification of the floodplain by deforestation for rice cultivation, etc.). For example, *Catlocapio siamensis* was abundant in 1962–1963 when catches represented 0.70 % of the total tonnage [6]. This species was very rare in 1994–1997, and only a few individuals were caught. It is the same case with two other species, *Balantiocheilos melanopterus*, Cyprinidae, mentioned by Rainboth [14] and the potamodromous Mekong giant catfish *Pangasianodon gigas* (though this fish has not been listed in the present study areas). The loss of the biodiversity could also be explained by the quality of the data set: on the one hand, catch data do not consider the small and the non-commercial species whilst, on the other hand, all the species described by the authors [1, 2, 4–6, 9, 13, 14] were considered as part of the research investigation. Nevertheless, the transitional zone (site C) should be a protected natural zone where all fishing should be prohibited or at the very least regulated.

The growth studies carried out previously [4] on some Cyprinidae (*Cyclocheilichthys*, *Leptobarbus*, *Hampala* and *Labeo*) in the Great Lake and the Tonle Sap river showed a clear difference between the two areas, i.e. the genus *Labeo* reached 32 cm within 2 years in the lake compared to 17 cm in the Tonle Sap river, the genus *Leptobarbus* reached 29.5 cm in the lake and only 23 cm in the river within 2 years. The higher rate of growth in the lake suggests a greater abundance of food in the flood plain of the Great Lake than in the river. Winemiller and Kelso-Winemiller [20] studying the dietary habits of catfish (Siluriformes) of the Zambezi river (Zambia) showed four size/trophic guilds: large carnivores, medium-sized carnivores, medium-sized omnivores and small omnivores. The Siluriformes in this study showed similar dietary habits: 50 % were medium-sized carnivores, 23 % were large carnivores and 27 % were omnivores.

The result of the data analysis in the Tonle Sap river and the Great Lake showed three habitat types, two with large stocks of fish with some differences in the composition of the fish assemblages among habitats. It is important to note that the grassy floodplains of the Great Lake and the transitional zone located at the outlet of the lake were well utilised by most communities of fish for feeding, spawning, nursery and growth. The Tonle Sap river constitutes the path of migration of fish between the Great Lake and the Mekong river, with the movement of flow dependent on the season [17]. Although significant inter-habitat differences were found between the fish assemblages, most species occurred in more than one habitat type.

Smith and Bokowa [15], in the Fly river (Papua New Guinea), observed four main habitat types within these floodplains. Three out of four studied habitats supported large populations of fish, which is typical for grassed floodplains where few native fishes live. However, a significantly greater mean number of species was found in the blocked-valley lake. Conversely, the present study shows that the transitional zone between the Great Lake and the Tonle Sap river constitutes a remarkable area for the conservation of the biodiversity of fish and other wildlife communities, and the damaging effects of increasing human activity in these areas should be taken as an alarm signal, to ensure the preservation of this rich ecosystem.

### Acknowledgements

We thank the two anonymous reviewers for constructive comments on an earlier version of this paper. We are grateful to the Cambodian Department of Fisheries who provided the fish data set.

### REFERENCES

- [1] Banarescu P., Zoogeography of Fresh Waters, Vol. 2 Distribution and Dispersal of Freshwater Animals in North America and Eurasia, Aula-Verlag, Wiesbaden, 1992, pp. 888–1087.
- [2] Bardach J.E., Étude sur la pêche au Cambodge, USOM/Cambodge, 1959, 89 p.
- [3] Carbonnel J.P., Guiscafré J., Grand Lac du Cambodge. Sédimentologie et Hydrologie 1962–1963, Muséum national d'histoire naturelle, Paris, 1965, 400 p.
- [4] Chevey P., Le Grand Lac du Cambodge, les causes profondes de sa richesse ichthyologique, Notes Inst. Océanogr. Indochine 29 (1936) 39–49.
- [5] Chevey P., Le Poulain F., La pêche dans les eaux douces du Cambodge, Trav. Inst. Océanogr. Indochine 33 (1940) 1–183.
- [6] Fily M., d'Auberton F., Cambodge, Grand Lac-Tonlé Sap, Technologie des pêches 1962–1963, Muséum national histoire naturelle, Paris, 1966, pp. 349–373.
- [7] Gopal B., The role of ecotones (transitional zones) in the conservation and management of tropical inland waters, Mitt. Internat. Verein. Limnol. 24 (1994) 17–25.
- [8] Kushlan J.A., Avian use of fluctuating wetland, in: Sharitz R.R., Gibbons E.W. (Eds.), Freshwater Wetlands and Wildlife, 1990, pp. 593–604.
- [9] Lagler K.F., Fisheries and intergated Mekong river basin development, terminal report of the Mekong basin wide fishery studies, Univ. Michigan, School of Natural Resources, 1976, 407 p.
- [10] Lieng S., Yim C., van Zalinge N.P., Freshwater fisheries of Cambodia, I- The Bagnet (Dai) fishery in Tonle Sap river, Asian Fish. Sci. 8 (1995) 255–262.
- [11] Norusis M.J., SPSS for Windows, Base system User's guide, release 6. 1, SPSS Inc., 1993, 941 p.
- [12] OPTIMA-Deltasoftware, Statlab by SLP, Le logiciel d'exploitation de données, 1995, 530 p.
- [13] Penh K., The freshwater fishes of Cambodia, thesis, Phnom Penh, Cambodia, 1996, 182 p.
- [14] Rainboth W.J., Fishes of the Cambodian Mekong, FAO Rome, 1996, 265 p.
- [15] Smith R.E.W., Bakowa K.A., Utilization of floodplain water bodies by the fishes of the Fly River, Papua New Guinea, Mitt. Int. Verein. Limnol. 24 (1994) 187–196.
- [16] Touch S.T., Status of biodiversity of the Great Lake (Boeung Tonle Sap) an approach for better conservation and future sustainable development, Workshop of the Technical Coordination Unit for the Safeguard and Management of Tonle Sap, Phnom Penh, 1995, 11 p.
- [17] Touch S.T., Status of fisheries resources management in Cambodia. Biodiversity in Asia, Challenge and opportunities for the Scientifics Community, Workshop Unesco Phnom-Penh, 1995, pp. 28–33.
- [18] vanZalinge N.P., Touch S.T., Catch assessment and fisheries management in the Tonle Sap great lake and river, Workshop on Fisheries Statistics, Phnom Penh, 1996, 9 p.
- [19] Welcomme R.L., Fishery Ecology of Floodplain River, Longman, London, 1979, 317 p.
- [20] Winemiller K.O., Kelso-Winemiller L.C., Comparative ecology of catfish of the upper Zambezi river floodplain, J. Fish Biol. 49 (1996) 1043–106.