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Aquatic Sciences

Overview Article

Species diversity and ecology of Tonle Sap Great Lake, Cambodia

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Abstract. Tonle Sap Great Lake in Cambodia, the largest natural freshwater lake in southeast Asia, is situated within the floodplain of the Mekong River. Water levels in the lake vary by about 8 m between the dry season minimum and the wet season maximum when waters from the Mekong River back up the Tonle Sap River. The lake is highly productive – the annual fish catch from the Lake is estimated at between about 180,00–250,000 tonnes while the dai fishery on Tonle Sap River annually harvests about 12,000 tonnes of fish migrating from the lake to the Mekong River early in the dry season. At least 149 species of fish are recorded from the lake and it provides habitat for 11 globally threatened and 6 near-threatened species of vertebrates including globally important populations of Spot-billed Pelican, Greater Adjutant, Bengal Florican, Darter, Grey-headed Fish Eagle and Manchurian Reed Warbler. It also supports significant reptile populations including formerly Siamese Crocodiles, now hunted close to extinction, and probably the world's largest harvest of freshwater snakes. The inundation area around the permanent lake is highly modified, with areas having been cleared for farming and settlements, and many semi-natural areas altered by burning, firewood and timber harvesting. Nevertheless some 200 species of higher plants have already been recorded. Threats to the lake include pressure through growth of the local population dependant on the lake for subsistence and livelihoods, overharvesting of fish and other aquatic species and potential changes in the hydrology of the River due to the construction and operation of dams which could reduce the amplitude of the lake flood cycle. However concerns that the lake is rapidly filling with sediment are unfounded.

Key words. Biodiversity; Tonle Sap; lake; wetland; ecology.

Introduction

Tonle Sap Great Lake, in central Cambodia (Fig. 1), is the largest natural lake in southeast Asia. However its importance arises not just from its size. The lake has played a central role in the history and culture of the Khmer people. It continues to play an important role as a source of livelihoods for modern Cambodia. The lake is also a site of great ecological and conservation significance. It supports a number of unusual ecosystems, and a part of the lake has been zoned as an international biosphere reserve through UNESCO (MRC/UNDP, 1998).

The great temple complex at Angkor Wat is the most prominent cultural feature associated with Tonle Sap Great Lake. The oldest major structures of the complex

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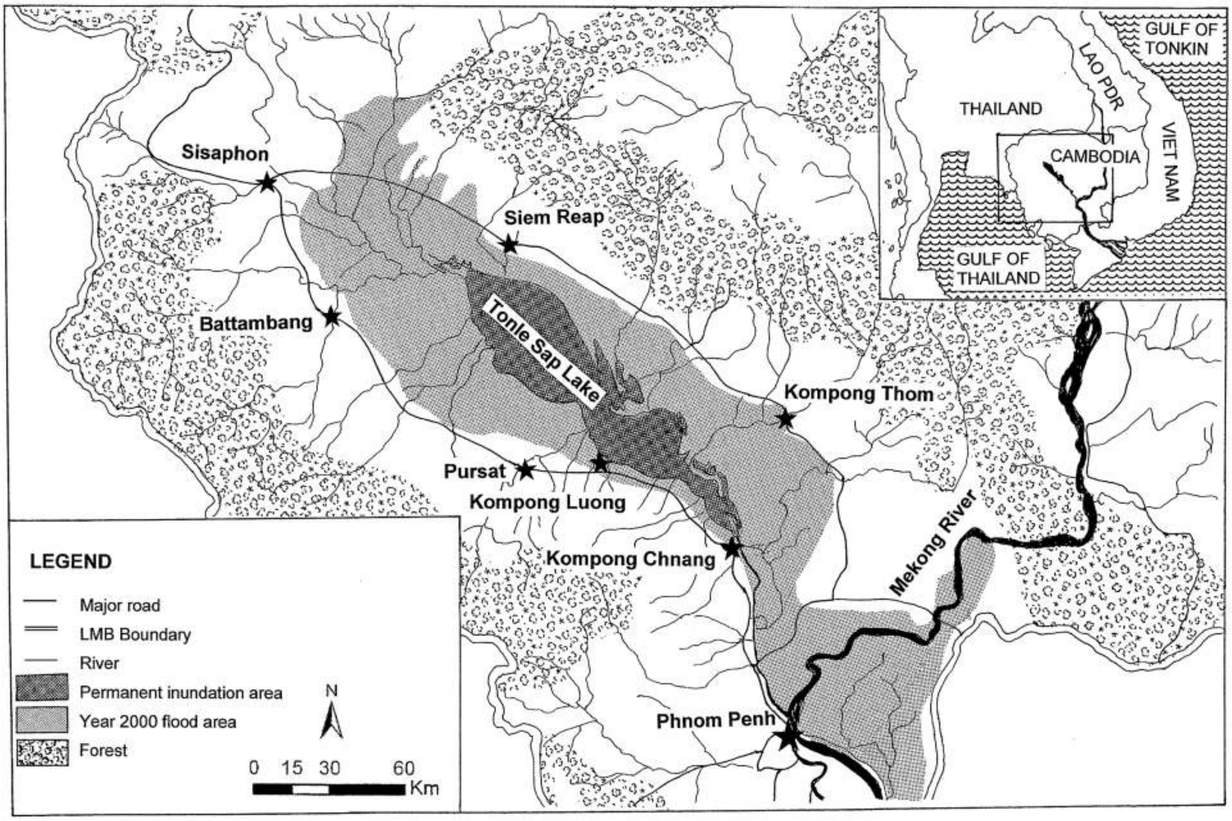


Figure 1. Location map for Tonle Sap Lake, indicating the extent of permanent inundation and the seasonal inundation area.

date from around 800 AD, and although there are differences of opinion about the precise role of the lake in the Khmer civilization (e. g. see Higham, 2001) there is general agreement that the lake was central to the construction of Angkor. At the very least the high productivity of the lake and its floodplain provided sufficient surplus food to support the substantial population needed to build Angkor. Whether, and to what extent, the Angkorian peoples also manipulated the flood by building a flood based irrigation system is still a matter of debate (e. g. see Higham, 2001; Coe, 2003), but clearly the fish from the lake together with the recession rice on the flood plain formed the basis of the economy of Angkor as is evident from the carved galleries at the Angkorian temples.

Ecological characterization of Tonle Sap

Geological history of the lake

The Tonle Sap Great Lake is a shallow lake formed on the recent sediments of the Cambodian plains. The geological history of the Indo-Chinese peninsula is complex (Workman, 1977; Hutchinson, 1989; Rainboth, 1996). Carbonel (1963) considered that the present Great Lake was formed by a subsistence of the Cambodian platform about 5,700 years ago. This is consistent with the data of Tsukawaki (1997) who analysed two cores from the northern basin of the lake and concluded that there was a change in depositional environments about 5,000–6,000 years ago. Okawara and Tsukawaki (2002) suggest that the change found by Tsukawaki (1997) coincided with the lake first becoming linked to the Mekong River at this time, since the upper sediments contain illite and chlorite which are present in clay minerals suspended in the river but not in the soil horizons elsewhere in the basin of the lake. Tuskawaki et al. (undated) indicated that prior to its connection to the Mekong River a palaeo Tonle Sap Lake not connected with the Mekong River and smaller than the present lake existed in the same location between about 7.5 and 5.5 thousand years ago.

Tsukawaki et al. (1994) believed that the presence of two marine diatom species, together with sponge spicules and the presence of balloon fishes and rays living in the lake demonstrated that the lake must have been in recent connection with the sea, however a number of studies of biological remains in sediment cores including pollen (Mildenhall, 2002) diatoms (Akiba, 2002) and foraminiferans (Kato and Oda, 2002) have failed to find any evidence of such a connection. Sponges, though not diverse in freshwaters are often abundant (Smith, 2001a), especially in tropical freshwaters and are common in the Mekong River and its tributaries. Fish species can easily migrate in to the lake and rays and other chondrichthyes are known to have species adapted to freshwaters in many large river systems (Compagno and Cook, 1995).

It seems likely that, prior to its connection with the Mekong River, the Tonle Sap Great Lake was connected to the sea via the Tonle Sap and Bassac Rivers. The Bassac and the Mekong River would, at that time, have had separate entrances to the South China Sea (Rainboth, 1996).

Present geomorphology of the lake

The present Tonle Sap Great Lake varies in area between the wet and the dry season. The dry season area of permanent lake is approximately 2,500 km^2 expanding to as much as 15,000 km^2 in the wet season (MRC, 2003). The lake has a relatively flat bottom, with a maximum dry season depth of 3.3 m (Fig. 2) and is situated within a relatively flat lake basin bordered in the north by the Dongrak Range and in the southwest by the Cardamom and Elephant ranges. A low (<300 m) range of hills separates the lake basin from the Mekong River to the east. The southeastern end of the basin is constricted by an extension of the Cardamom range stretching eastwards towards Kompong Chnang on the southwestern side of the river and some low hills and rocky outcrops on the northeastern side of the river.

Geologically the basin consists of recent sediments overlaying older bedrock which, in a few locations, projects above the plains. The margins of the dry season lake are bordered by a low natural levee caused by sediment deposition as the waters rise during the wet season. Sediment deposition from water flowing up from the Mekong River has also formed an elaborate delta which is evident at the southern end of the lake during the dry season.

Hydrological characterization of the lake

The Tonle Sap Lake basin is located in the wet-dry tropics. Mean daily temperatures at Siem Reap vary between about 20 °C and 36 °C with lowest temperatures in January and highest in April. Average annual rainfall is 1342 mm at Battambang, 1492 mm at Siem Reap and 1561 mm at Kompong Chnang. The rainfall is seasonal, mainly occurring between April and November, with a peak in September (Fig. 3).

The scale of the annual hydrological change in Tonle Sap unusual. Since 1922 the lake water level has varied by an average of 8.2 m on an annual basis between wet and dry seasons (Fig. 4) leading to the change in flooded area to which we previously referred. As the water level in the Mekong River rises during the wet season it begins to flow up the Tonle Sap River channel eventually contributing about 50 % of the maximum wet season water

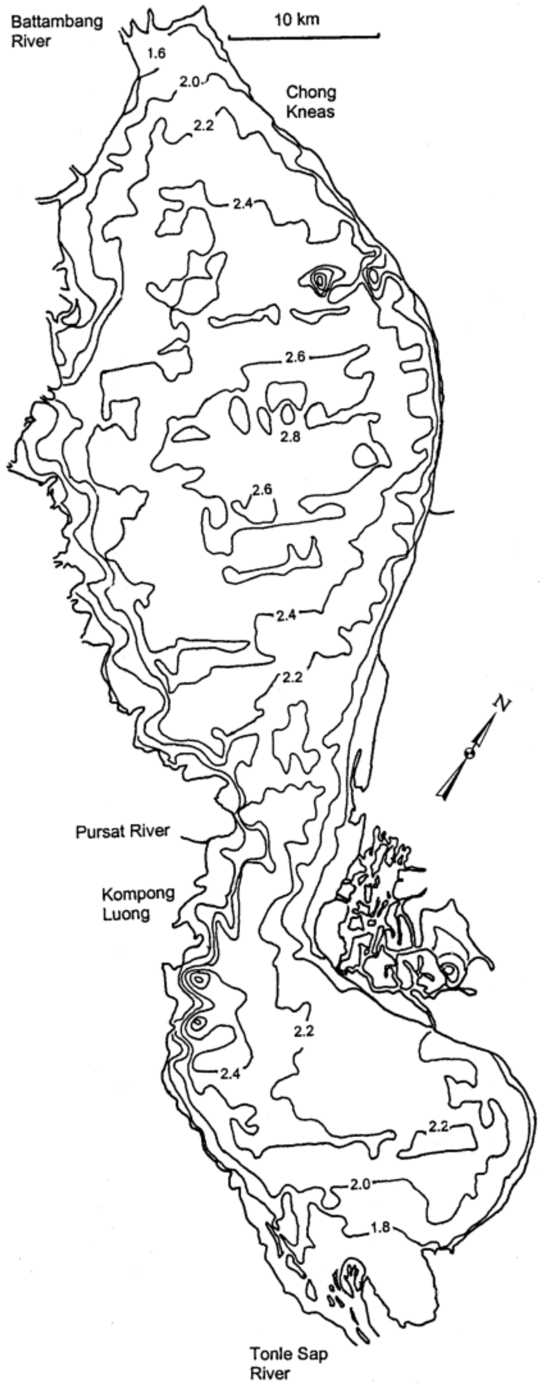


Figure 2. Bathymetric map of Tonle Sap Lake based on the Cambodian Hydrographic Atlas Volume 3 (1999) based on surveys made between 1997 and 1999. Depths shown in metres. Note that in a shallow floodplain lake like Tonle Sap Lake the shape of the inundated area, and the depth of the lake vary substantially through the course of the year depending on the water level.

volume. Once the Mekong River breaks its banks between Kratie and Phnom Penh a further 10 % or so of the final wet season volume flows across the low lying land between the Mekong River and the Lake. DHI (2004)

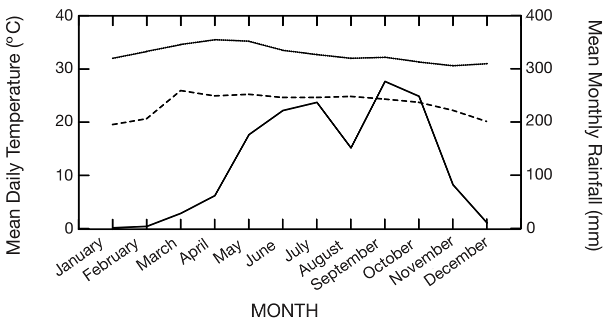


Figure 3. Mean monthly maximum (short dashes) and minimum (long dashes) air temperatures at Siem Reap, and mean monthly rainfall at the same location. Data from World Weather Information Service.

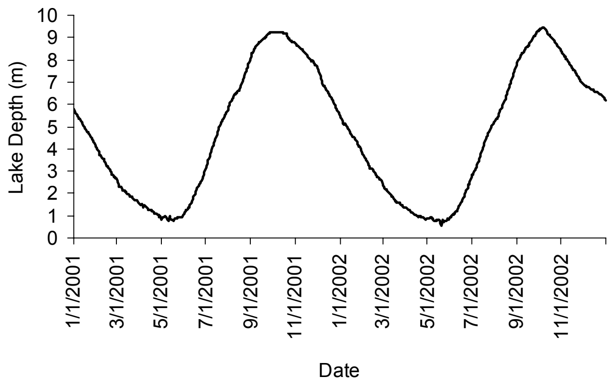


Figure 4. Annual water level cycle Tonle Sap between January 2001 and December 2002.

estimated that about 40 % of the total wet season volume is derived from the immediate catchment of the, but that calculation subtracted the entire Great Basin evaporative losses from the immediate catchment inputs, thus underemphasizing the immediate catchment inflows.

The relative contributions, and importance, of the different water sources vary at different times of the year. Inflows from the Tonle Sap River provide much of the early wet season increase in volume with overland flows increasing in importance in August and September, and runoff from the catchment often greatest in October and November. At the end of the wet season, as the water levels in the Mekong River subside, the water flows out down the Tonle Sap River with October the first month with a net downstream flow in the Tonle Sap River. The stored water from the lake contributes an estimated 16 % of the dry season (December–May) flow in the Mekong River and its distributaries downstream of Phnom Penh (MRC, 2003).

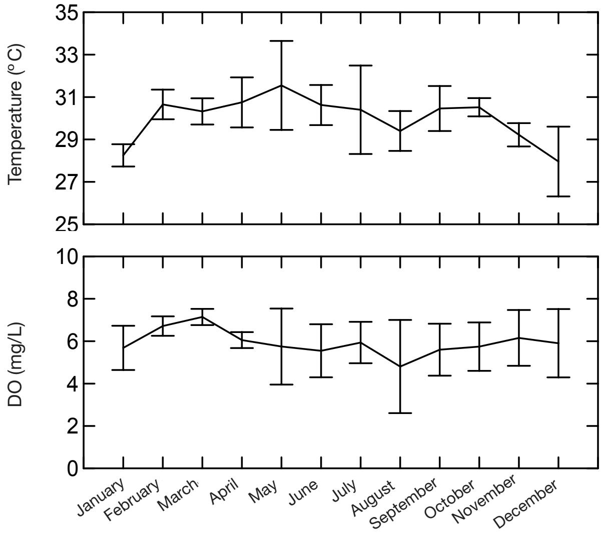
Water levels in the lake were recorded daily at Kompong Luong from 1923 until 1965 and then again from 1999 to the present. There is also a discontinuity in the record from in April 1962 when the level of the gauge was altered by 2 m. The data analysed here have been corrected for that change. Plotting maximum and minimum annual water levels during the period of record it is evident that there have been declines in both the maximum and minimum annual levels of the lake over time and these have been statistically significant ($p = 0.011$ and 4×10^{-4} respectively). Because the most recent data may have had undue leverage on the analysis the analysis was also conducted excluding data since 1965 however the decline was still statistically significant. The decline amounts to a difference of 0.52m between the mean maximum values for the period 1925–35 and 1996–2002. Using the relationship between flooded area and water height developed by the JICA team (WUP-JICA Team, 2004) that would translate into a reduction in flooded area of about 623 km^2.

There are three possible explanations for the decrease in water levels. There may have been an error in the gauge readings, there may have been a change in the hydrological regime resulting from either climate change leading to reduced rainfall in the catchment and reduced flows in the Mekong River, or changes in the catchment either in landuse, storage, or abstraction or some combination of the three.

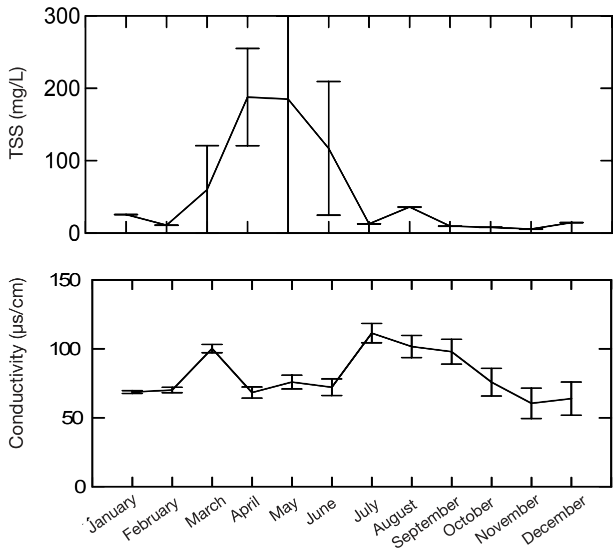
The likelihood of a gauge error causing the result seems remote. It is also difficult to envisage an error becoming progressively greater over time. The gauge was reset in 1962 but the trend continued after that time.

There has been a statistically significant ($p = 0.03$) decrease in maximum annual river heights at Stung Treng over the period 1910–2002. However the difference in mean height between the period 1925–35 and the period 1992–2002 is only 0.17 m compared with the 0.52 m in Tonle Sap Lake, and there was not a statistically significant ($p = 0.07$) decrease in maximum annual river height for the period 1925–2002. At Pakse, where there are discharge records, but no river height records, back to 1925, there has not been a significant decrease on annual discharge over the period of record ($p = 0.051$). In view of this it is not possible that the decrease in water levels in the lake have been caused by dams built within the Mekong Basin as claimed by Bonheur and Lane (2002).

Obstruction of flow in to the lake does not seem to be a likely contributing factor. Suspended sediment levels in the river water in Tonle Sap River are high, although not unusually so for a tropical lowland river. Models of sediment movement in the lake indicate that the main areas of sediment deposition are likely to be the "delta" where the river enters the lake and the region immediately behind the natural levee (Sarkkula and Koponen, 2003), as would be expected. No data are available to determine the extent to which the delta may have accumulated over recent times, but in the absence of dredging it is possible that the inflow to the lake is becoming increasingly obstructed. However if the obstruction were sufficient to



Figures 5 (top) and 6 (bottom). Annual temperature and dissolved oxygen cycles for Tonle Sap Lake showing means and standard errors of monthly measurements at Kompong Luong from 1995–2000.



Figures 7 (top) and 8 (bottom). Annual cycle of suspended solids and conductivity in Tonle Sap Lake showing are the mean and standard errors of monthly measurements at Kompong Luong during the period 1995–2000.

cause appreciable interference to water flow in to the lake it would be expected that minimum annual levels would be remaining stable or even increasing as the "sill" at the lake entrance grew higher. However, as previously noted, minimum depths have also been decreasing.

The most likely explanation for the change is a change in rainfall in the Tonle Sap Lake catchment possibly compounded by small decreases in Tonle Sap River flows. There are no adequate rainfall records from the Lake catchment so it is not possible to directly test this hypothesis, but by a process of elimination it remains the most likely.

Limnology of the lake

Tonle Sap Great Lake is tropical (latitude 12°30´ to 13°30´) and the water temperatures reflect this reaching lows of about 28 °C in December and January – the cold season in the region, and highs of 31.6 °C towards the end of the dry season in May (Fig. 5). With increasing cloud cover and the beginning of the influx in wet season flows in June temperatures then begin to decline.

Based on monthly samples collected at Kompong Luong since 1995, the waters of the lake generally reflect the sources of the water. The geological nature of the lake basin means that runoff is generally dilute while the Mekong River water is relatively high in dissolved ions, notably calcium, magnesium, sulphate and silicate which reflect the Mekong River's passage through karst areas in central Lao PDR. The chemical composition of the Lake is intermediate between these sources with considerably lower ionic strength than the Mekong River (Table 1). The size of the differences in chemical composition between the lake and the Mekong River would also seem to indicate that the DHI figure for the proportion of water derived from the catchment of the lake is an underestimate.

The annual patterns of water chemistry within the lake reflect the seasonal patterns of water inflows and evaporation. Dissolved oxygen at the surface (Fig. 6) shows maximal values in the early dry season when transparency is highest, and a slight drop in August when overland and Mekong River inflows are at their peak, presumably bringing with them high organic loads. At that time water is also rapidly inundating the floodplain so the impact of decomposition of terrestrial vegetation would also be greatest. Eloheimo et al. (2002) found oxygen saturation at depth of 3.5 m dropping to 0 % on a

Table 1. Mean composition of river waters of the world, the Mekong River at Kratie in Cambodia and the Tonle Sap Great Lake at Kompong Luong. (All values in mg/L). Data for world average from Wetzel (1983) other data from MRC water quality database.

	Ca^{2+}	Mg^{2+}	Na^{+}	K^{+}	Fe^{3+}	SO_4^{2-}	Cl^{-}	SiO_2	NO_3^{-}
World Average	15	4.1	6.3	2.3	0.67	11.2	7.8	13.1	1
Mekong – Kratie	15.5	4.1	6.9	1.4	1.21	9.3	5.0	11.4	0.1
Tonle Sap Lake	7.3	2.3	5.1	1.6	0.55	4.0	3.0	4.0	0.1

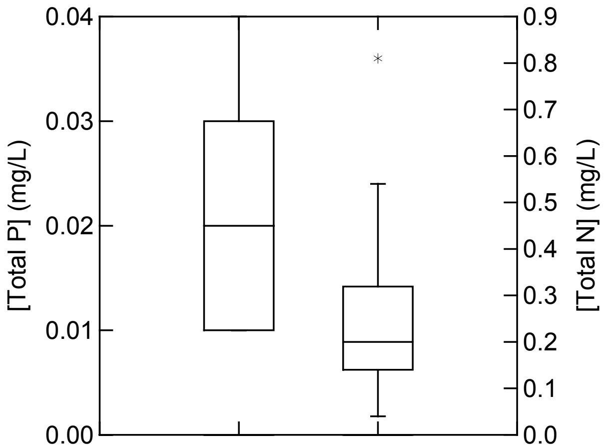


Figure 9. Median, 75th percentile and range of concentrations of total Nitrogen and total Phosphorus in Tonle Sap for the period 1995–2000. Data from MRCS water quality database.

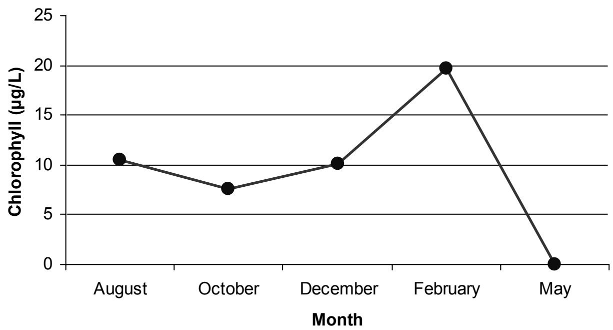


Figure 10. Total Chlorophyll concentrations measured at Kompong Luong in Tonle Sap Lake between August 2003 and May 2004.

number of occasions at sites in flooded forest inundated by the lake in October and November 2001, and found profiles at several sites over flooded fields showing rapid declines in oxygen saturation with depth. Lamberts (2002) also found some evidence of oxygen stratification at times in swamp forest sites.

pH of the lake also reflects the water sources. In general pH is relatively stable with a mean of 7.0 and a standard deviation of 0.34. On average the pH is lowest in April, at 6.6, the season of low water level and presumed highest algal productivity, and highest in September at 7.2, when the inflow from the relatively high pH Mekong River is greatest.

Concentrations of suspended solids in the lake water peak in April–June, at the end of the dry season (Fig. 7). This is the period when the lake water levels are lowest (c.f. Fig. 4), less that 0.5 m over most of the lake, and the high suspended solids concentrations reflect the resuspension of bottom sediment due to wind action at this period. Conductivity, on the other hand, peaks in July to September (Fig. 8) with the influx of Mekong River water. There is another minor peak in March which may reflect evaporative concentration.

The concentrations of total phosphorus and nitrogen are both consistent with the concentrations that would be expected in a shallow lake (Fig. 9). The P/N ratio is approximately 10 indicating, contrary to the comments of Sarkkula and Koponen (2003), that the lake productivity tends towards nitrogen limitation although there is no experimental confirmation of this, and during much of the late dry season light limitation is most likely.

There is limited data on chlorophyll in the lake. Insitu fluorimeter measures taken every two months from August 2003 to May 2004 indicate that, over that period, the phytoplankton was dominated by green algae (61 %) and cyanobacteria (35 %) with a few diatoms (4 %) also present. Chlorophyll levels peaked in February at about 20 µ/L (Fig. 10) during the period when turbidity is relatively low (c.f. Fig. 6). As turbidity increases chlorophyll concentrations are reduced presumably due to light limitation. The zero chlorophyll value recorded in May is probably an erroneous reading due to turbidity interfering with the fluorimeter operation, light transmission was only 0.03 %. Nevertheless the chlorophyll levels in the water column were undoubtedly low at that time. Sarkkula and Koponen (2003) comment that *Aulacoseira* diatoms dominated the phytoplankton during their field studies presumably conducted in 2002. The wet season in late 2003 was unusual and the lake levels were unusually low during the fluorimetric survey which may have influenced the composition of the phytoplankton, especially diatoms which are characteristic of riverine plankton.

Species diversity of plant and animal groups

Algae

There is little data on the phytoplankton of Tonle Sap Great Lake. Blache (1951) provided some information on the phytoplankton of Prek Andor, a tributary river to the, and five months of data for a site in the Lake inundation area. During the period of these surveys (September to January) highest plankton densities were recorded in September. Bacillarieae were dominant from September to December with Myxophyceae abundant in December and dominant in January. *Melosira granulata* was the predominant species in September, with a species of *Microcystis* replacing it in January. A survey conducted by Tran Truong Luu and Bun Ny between 1986–1988 (Department of Fisheries, 1993 Vol. 3) identified a total of 123 species present in the Lake. This included 37 species of Bacillariophyta (diatoms), 34 species of Chlorophyta (green algae), 34 species of Cyanobacteria (blue green algae), 15 species of Euglenophyta and smaller numbers of several other groups.

Higher plants

Pattern of vegetation types. The vegetation of the Tonle Sap floodplain has undergone a long history of alteration, mainly due to human disturbances, and is now largely secondary in nature. In its most pristine form, it consists of an almost closed canopy of small to medium-sized trees, while at the other end of the spectrum it consists of herbaceous, seasonally inundated or floating vegetation. Most of floodplain habitat, however, consists of something intermediate: usually scrubland with shrubs and stunted trees, and an occasional scattered taller tree, interspersed with swards of herbaceous vegetation dominated by grasses. Submerged aquatic macrophytes are generally lacking, due to a combination of turbidity and large seasonal fluctuations in water levels. Seasonally, large parts of the floodplain are utilised by local communities, and higher-lying zones exhibit a dense web of ox-cart trails as areas are cyclically opened for establishing vegetable plots, fuel wood cutting, grazing, and cultivation of recession rice as floodwaters recede. Fires – either intentional (for clearing or hunting) or accidental – play an important role in modifying the habitat, and during the dry months plumes of smoke are a common sight throughout the floodplain.

The end result is a mosaic of swamp scrubland in various stages of regeneration, herbaceous swamps and seasonal farmland, along with swamp forest occurring in more deeply flooded areas nearest to the dry season edge of the lake and along perennial streams. Some authors (McDonald et al., 1997; Smith, 2001b) attribute this vegetation distribution at least partly to edaphic factors, hypothesizing that a lack of water leads to stunting of vegetation further from the lake edge. However, this seems unlikely, as similar vegetation patterns in seasonal swamps elsewhere in the region have well documented histories, all based on human interference (e.g. van Steenis, 1957; Paaijmans, 1976; Giesen, 2000). Also, village elders in Tonle Sap lake-edge communities confirm that most of the swamp scrubland was swamp forest in the not-too-distant past.

A confused terminology hinders attempts to reconstruct the history of the vegetation of the Tonle Sap. Older – mainly French – literature refers to all seasonally inundated vegetation dominated by woody species as forêt inondee (e.g. Rollet, 1972; Légris and Blasco, 1972), and based on this classification it can be concluded that the area of forêt inondee has declined from more than one million hectares during the 1930s, to 614,000 ha in the late 1960s and 360,000 ha in the 1990s (Woodsworth, 1995). However, it should be noted that most of this 'forêt' is flooded scrubland, often very patchy in distribution. At the same time, the area of herbaceous seasonal swamp and farmland has increased.

A total of about 200 higher plant species have been recorded in the Tonle Sap area (CNMC et al., 1998; Triet, 2002), but this figure is far from exhaustive, as years of instability in Cambodia and a subsequent lack of capacity has not been conducive to in-depth studies. Nevertheless, some clear patterns emerge. The vegetation of the Tonle Sap floodplain has a relatively simple floristic composition. About 35 % of the flora consists of trees and shrubs, 8 % consists of climbers, and most of the rest of herbaceous terrestrial species. Vines are a common component of floodplain vegetation, occurring as herbaceous twiners (e.g. *Ipomoea chryseides, Merremia hederacea*) in floating vegetation, or as slender perennial vines (e.g *Cissus hexangularis, Derris laotica, Stenocaulon kleinii*) and stout woody liana's (e.g. *Acacia thailandica, Breynia rhamnoides, Combretum trifoliatum, Tetracera sarmentosa, Uncaria* sp.) in the swamp forests and scrublands (McDonald et al., 1997; Smith, 2001b). According to Rollet (1972) and McDonald et al. (1997), other peculiarities of these flooded forests are the absence of pneumatophores and a lack of epiphytes. The latter can be explained by the high degree of human disturbance, which has lead to a lack of older trees available as stable substrates. Palms are generally uncommon, although rattans (climbing palms) – notably *Calamus salicifolius* and *Calamus palustris* – are a feature of both swamp forest and scrublands.

Most trees and shrubs of the flooded forests of Tonle Sap are deciduous, and leaves are shed underwater during the monsoonal flooding period. When waters recede, new leaves rapidly grow and flowering follows several months later – usually occurring profusely in July–August. When flooding occurs again, the trees and shrubs generally bear fruit and seeds, which are subsequently dispersed by floodwaters and herbivorous fish. Certain species, such as the small tree *Barringtonia acutangula* (Lecythidaceae) and the climber *Combretum trifoliatum* (Combretaceeae) do not follow this pattern, however, and keep their (actively photosynthesising) leaves even when submerged for several months.

Swamp forests. Swamp forests commonly line the shores of the lakes and rivers of the region, and extend over less than 10 % of the Tonle Sap floodplain. These forests are flooded by a maximum of 4–6 m of water up to 8 months per year, and trees are usually 7–15(–20) m tall. A similar community once occurred as a gallery forest in the floodplains of many major rivers in southern Cambodia, following channels or other waterways and occasionally occurring in isolated depressions which hold surface water through the dry season. Rather than forming a continuous forest, this community is broken into a mosaic of stands of large trees and open areas with floating aquatic herbs typical of the lake itself (see below). In most of the country this habitat has now disappeared, and the stands at Tonle Sap represent some of the last examples.

The two main tree species are *Barringtonia acutan-*

gula and *Diospyros cambodiana* (Ebenaceae), often accompanied by the woody climbers *Acacia thailandica* (Mimosoidae), *Breynia rhamnoides* (Euphorbiaceae), *Combretum trifoliatum* (Combretaceae), *Connarus semidecandrus* (Connaraceae), *Tetracera sarmentosa* (Dilleniaceae) and *Uncaria* sp. (Rubiaceae). Other common tree species include *Coccoceras anisopodum* (Euphorbiaceae), *Crataeva nurvala* (Capparaceae), *C. roxburghii, Crudia crysantha* (Caesalpinoidae), *Elaeocarpus griffithii* (Elaeocarpaceae), *Garcinia loureiri* (Guttiferae), *Homalium brevidens* (Flacourtiaceae), *Lophopetalum fimbricatum* (Celastraceae), *Terminalia cambodiana* (Combretaceae) and *Xanthophyllum glaucum* (Xanthophyllaceae). Common shrub species include *Brownlowia paludosa* (Tiliaceae), *Cudrania cambodiana* (Moraceae), *Dalbergia entadoides* (Papillionoidae), *Ficus heterophylla* (Moraceae), *Gmelina asiatica* (Verbenaceae), *Hymenocardia wallichii* (Euphorbiaceae), *Salacia verrucosa* (Celastraceae) and *Vitex holoadenon* (Verbenaceae). Well represented families of predominantly woody species are the Annonaceae (3 spp.), Caesalpinioidae (6 spp.), Capparaceae (4 spp.), Combretaceae (6 spp.), Ebenaceae (3 spp.), Elaeocarpaceae (3 spp.), Eupborbiaceae (13 spp.), Flacourtiaceae (4 spp.), Guttiferae (3 spp.), Mimosoidae (6 spp.), Moraceae (4 spp.), Papilionoidae (7 spp.), Rubiaceae (6 spp.) and Verbenaceae (3 spp.).

Swamp scrublands. Swamp scrublands form the dominant vegetation cover over approximately 80 % of the Tonle Sap floodplain, often in various stages of regeneration in a mosaic with farmland clearings. Woody species dominate – mostly no taller than 2–4 m – but many of the species with a shrubby growth form in this community are capable of reaching tree size if left undisturbed. The flora of these short tree-scrublands is dominated by species of Euphorbiaceae, Fabaceae and Combretaceae (McDonald et al., 1997). Several species (e. g. *Combretum trifoliatum*) that form woody lianas under more favourable conditions, maintain a shrubby growth form in this habitat. Common (stunted) tree and shrub species are *Barringtonia acutangula, Bridelia cambodiana* (Euphorbiaceae), *Brownlowia paludosa* (Tiliaceae), *Capparis micrantha* (Capparaceae), *Crataeva nurvala, C. roxburghii*, *Coccoceras anispodum*, *Croton mekongensis* (Euphorbiaceae), *Cudrania cambodiana*, *Dalbergia entadoides*, *Dalbergia pinnata* (Papilionoidae), *Ficus heterophylla*, *Gardenia cambodiana* (Rubiaceae), *Gmelina asiatica*, *Hymenocardia wallichii*, *Phyllanthus taxodiifolia* (Euphorbiaceae), *Powpowia diospyrifolia* (Annonaceae), *Terminalia cambodiana* (Combretaceae) and *Vitex holoadenon*.

Aquatic macrophytes and herbaceous vegetation. Submerged aquatic vegetation is virtually absent, and rooted-submerged species that are common elsewhere in Southeast Asia – mainly members of the Hydrocharitaceae, Najadaceae, Nymphaeaceae and Potamogetonaceae – are not found at Lake Tonle Sap. The reason for this absence is the combination of a significant annual fluctuation in lake water levels (6–8 m) and high turbidity (TSS of up to 450 mg/l; CNMC et al., 1998). Water lilies *Nymphaea nouchali* (Nymphaeaceae), *Nymphoides indica* (Menyanthaceae), and lotus *Nelumbo nucifera* (Nelumbonaceae) are present but uncommon, found only in occasional pools and ponds around the periphery of the lake. Submerged-suspended (i. e. non-rooting) species such as *Utricularia aurea* (Bladderwort) and *Chara* (Stonewort) are also encountered in these pools, but they also occur in sheltered waters in swamp forests during the flooded season.

The shallow shoreline of Tonle Sap supports dense mats of 1–3 m-tall herbaceous vegetation that may be emergent from shallow water, but typically becomes dislodged and forms floating mats (McDonald et al., 1997). Large mats of these species float freely over the lake, colonising large openings and gaps within the swamp forest. These mats are dominated by a wide variety of grasses (*Brachiaria mutica, Echinochloa stagnina, Leersia hexandra, Leptochloa chinensis, Oryza rufipogon, Paspalum scrobicularum, Sacciolepis interrupta, Vossia cuspidata*) and sedges (*Cyperus halpan, Rhynchospora corymbosa, Scirpus grossus*), along with *Colocasia esculenta* (Araceae), *Commelina salicifolia* (Commelinaceae), *Ipomoea aquatica* (Convolvulaceae), *Ipomoea chyseoides, Ludwigia adscendens* (Onagraceae), *Merremia hederacea* (Convolvulaceae) and *Polygonum barbatum* (Polygonaceae). Conspicuous in these floating mats are two woody legume species that may reach 1.5–2 m above the lake surface, namely *Sesbania javanica* and *Aeschynomene indica.* Other floating herbs include water-hyacinth *Eichhornia crassipes* (Pontederiaceae), *Lemna minor* (Lemnaceae), *Pistia stratiotes* (Araceae) and *Salvinia cucullata* (Salviniaceae). *Eichornia*, *Pistia* and *Salvinia* are all exotic to the system. Reeds *Phragmites karka* and wild sugarcane *Saccharum spontaneum* form dense stands along perennial streams entering the lake, and at the mouth of the Tonle Sap river (e. g. near Snoc Trou).

Aquatic invertebrates

We have been unable to find any quantitative information on zooplankton or zoobenthos in Tonle Sap Lake. Brehm (1951) recorded two copepods (*Heliodiaptomus elegans* and *Diaptomus javanus*) and one cladoceran (*Diaphanosoma paucispinosum*) from the lake and a further 2 species of copepods, 4 of cladocerans and 2 rotifers in influent streams. Nguyen and Nguyen (1991) reported 46 species of zooplankton, 23 species of rotifers, 16 of cladocerans and 7 copepods from the Tonle Sap River but provide no data on the lake fauna. They note that both the number of species and the abundance of zooplankton in flooded areas was greater than in the rivers, and at Kompong Chnang density was two orders of magnitude higher in the dry season than the wet season. Sarkkula and Koponen (2003) refer to high biomass of copepods in the lake but the species are not identified. O'Connor identified 125 aquatic macroinvertebrate taxa in surveys around Siem Reap and Banteay Meanchey, but the taxa are not specified and it is not clear how many were collected in the lake. MRC/UNDP (1998) included an appendix listing 33 crustacea and mollusc species recorded from the lake.

Balzer et al. (2002) reported six species of *Sommaniathelphusa* crab and the freshwater shrimp *Macrobrachium lanchesteri* from lowland rice fields in Kompong Thom. A new species of ricefield crab *Sommanniathelaphusa lacuvita* was described from the Tonle Sap by Ng (1995).

Fish

Diversity. Although Mekong River fishes have been subject to studies for almost 150 years (Valbo-Jørgensen and Visser, 2003) knowledge about them is still unstable. The long history of studies reflects the overriding importance of the fishery to the economies and livelihoods of people in the Mekong Basin. However, the extraordinary richness of the fish fauna and the lack of consensus among the taxonomists working in the region mean that scientific names and classification are in a state of flux, and it is almost impossible to get a reliable estimate for the total number of species even for the better-studied parts of the basin.

So far 149 fish species from 35 families have been recorded from Tonle Sap Lake (Table 2). The fish diversity reflects connection between the lake and the Mekong River system which has one of the richest fish faunas of any comparable river (MRC, 2003a; Visser et al., 2003) with 923 named species from 91 families recorded (MRC, 2003). This list includes many estuarine species that occur in the lower parts of the Mekong River. Out of 439 species recorded from the Cambodian Mekong about 5 % are brackish water visitors that may penetrate several hundred kilometres upstream. However, visitors are normally restricted to the main river channel and are only rarely seen in the Tonle Sap Lake.

Bonheur and Lane (2002) claimed 500 fish species in Tonle Sap citing as their source the total number of fish species recorded from the Cambodian Mekong by Rainboth (1996). They also claimed that Kottelat "recorded 215 fish species from the Tonle Sap Lake" but this is an erroneous citation from Kottelat and Whitten (1996) who actually give this number as the total number of freshwater fish species from Cambodia. Since the Tonle Sap Lake is connected to the Mekong River it is likely that, in time, most if not all the Mekong species will be recorded in the lake at some time, but we are restricting our total to species already definitely recorded from the lake.

The Mekong River has a high degree of endemism (24 %), however most of the endemic species are restricted to upland areas, and none of the species recorded from the Tonle Sap Lake are endemic to this waterbody. Most occur widely in large rivers of the basin. The ostariophysean species in particular tend to occur also in the Lower Chao Phraya basin in Thailand and the Greater Sunda Islands (Taki, 1975, 1978; Rainboth, 1991).

Table 2. A list of fish families and the number of species from each presently recorded from the Tonle Sap Lake.

Family	Common Name	No. of Species
Carcharhinidae	Requiem sharks	1
Dasyatidae	Stingrays	1
Pristidae	Sawfish	1
Notopteridae	Featherbacks	4
Anguillidae	True eels	1
Clupeidae	Herrings and shads	3
Engraulididae	Anchovies	4
Cyprinidae	Minnows and carps	60
Balitoridae	River loaches	1
Cobitidae	Loaches	4
Bagridae	Bagrid catfishes	12
Siluridae	Sheatfishes	10
Pangasiidae	River catfishes	10
Clariidae	Airbreathing catfishes	4
Ariidae	Sea catfishes	2
Plotosidae	Eel-like catfishes	1
Belonidae	Needlefishes	2
Hemiramphidae	Halfbeaks	1
Syngnathidae	Pipefishes	1
Synbranchidae	Swampeels	2
Mastacembelidae	Spiny eels	1
Chandidae	Asiatic glassfishes	3
Datnioididae	Tigerperches	1
Polynemidae	Threadfins	2
Sciaenidae	Croakers	1
Toxotidae	Archerfishes	1
Nandidae	Leaffishes	1
Eleotridae	Sleepers	1
Gobiidae	Gobies	1
Scombridae	Mackerels and tunas	1
Anabantidae	Climbing perches	1
Osphronemidae	Giant gouramies	3
Channidae	Snakeheads	3
Soleidae	Tonguefishes	1
Tetraodontidae	Puffers	3

Most of the fish species recorded from the lake belong to four families: Cyprinidae (39 %), Bagridae (8 %), Siluridae (7 %) and Pangasiidae (7 %) (Table 2). The river catfishes include the famous Mekong giant catfish (*Pangasianodon gigas*) one of the the largest freshwater fish in the world, which may reach 3 m in length and a weight of 300 kg.

Lim et al. (1999) claim that there has been a substantial drop in fish diversity in the Tonle Sap area, including both the lake and the river, based on a comparison of fish catch data from the period between 1936–76 and the period between 1995–97. There are two obvious weaknesses in their comparison. Firstly they are comparing a 40 year data set with a two year data set. A 40 year catch data set would be expected to contain more species than a two year data set. Secondly the earlier data set was obtained by field based ichthyologists working with local fishers, while the second data set was obtained by reports from government fisheries officers. The second data set would have focused on the size of the catch, rather than its taxonomic composition, and may also have been subject to underreporting. Lim et al. recorded a total of only 89 species occurring in the lake, 40 % fewer than we record here, and we consider their conclusion that "between about two-thirds and half of the previously known fishes have disappeared" between the two time periods they investigated as unsupported.

Lifecycles. Knowledge of the lifecycles of even the most conspicuous Mekong River species is still incomplete. Comparative ecological research in the basin has been limited by taxonomic problems, political instability and lack of resources, so although there is a good general understanding of the factors influencing fish production in the Lower Mekong Basin detailed understanding of the biology of many critical species is still in its infancy. Only recently, a general idea about the distribution, and the migration and spawning habits of some of the most important commercial fish species has started to emerge (Poulsen and Valbo-Jørgensen, 2000).

Hardy black fishes (*sensu* Welcomme, 2001) with anatomical and ethological adaptations to withstand hypoxia and desiccation dominate in many parts of the lake floodplain where oxygen levels can drop to zero shortly after inundation. Species with such adaptations include the labyrinth fishes (Anabantoidei) and snakeheads (Channidae), which possess accessory breathing-organs above the reduced gills allowing them to breath atmospheric air. Parental care is also a common trait in these groups. The male labyrinth fishes construct a froth nest where the eggs are deposited in the more oxygen rich surface water, while male snakeheads defend their nests, built from vegetation, and their larvae and juveniles.

Black fish species such as the walking catfish (*Clarias batrachus*), climbing perch (*Anabas testudineus*) and chevron snakehead (*Channa striata*) are capable of crossing dry land in search of water when their ponds dry up. Some black fishes survive the dry season in small waterbodies on the floodplain, but most of them move to the permanent part of the Great Lake as the water draws down.

The Great Lake is seasonally also a habitat for a number of white fish species although they constitute a less prominent part of the fishery than they do along the Mekong and Tonle Sap Rivers. Many white fish species (including several species of Cyprinidae and probably all species of Pangasiidae) spawn in tributaries and mainstream rapids in the border area between Cambodia and Lao PDR when the rainy season starts. From the spawning grounds, eggs and larvae drift downstream and distribute themselves in the flooded areas. The ichthyoplankton that reaches the junction of the Mekong and Bassac Rivers (Quatre Bras) may continue downstream or be caught by the reverse flow of the Tonle Sap and carried towards the Tonle Sap Lake. So far 88 fish species have been recorded from the drift in the Tonle Sap River (Chea Tharith et al., 2003), however the mechanisms that determine exactly where the individual larvae end up are not well known.

After gorging on food on the floodplains throughout the flood season the white fishes leave the Great Lake destined for the Mekong River. Most fish movement is concentrated in the six days before the full moon (Baird et al., 2003). Many of the white fish species find their dry season shelters in deep pools or canyons that are located in the mainstream between Kompong Cham in Cambodia and Siphandone in southern Lao PDR (Poulsen et al., 2002).

Fisheries. Fish and fishing have been central to Cambodian culture since ancient times, and with an annual consumption of fish and other aquatic animals of at least 720,000 tonnes the inland fisheries of Cambodia are among the most significant in the world (Hortle et al., 2004b). Few countries in the world are so dependant on inland fisheries as is Cambodia where fish provides people with 80 % of their animal protein, and fish also contribute 16 % to the country's GDP (Baird et al., 2003).

The fishery in Tonle Sap Lake, like the Cambodian fishery generally, is very intensive, highly organized and includes both small and large scale operations. The latter focus mainly on black fish moving out of the floodplains (lateral migration). In the Tonle Sap Lake the giant snakehead (*Channa micropeltes*) contributes most to the catch, while catches of in the dai fisheries in the Tonle Sap River are dominated by small migratory cyprinids, mainly *Henicorhynchus* spp. (Van Zalinge et al., 2000). Estimates of the catch have varied widely. CNMC/

Table 3. Turtles recorded occurring from the Tonle Sap Great Lake and their global conservation status. Data from Long (2003) and Stuart and Platt (2004).

Family	Species	Common Name	IUCN status	CITES status
Geoemydidae	*Batagur baska*	Mangrove Terrapin	Cr	I
Geoemydidae	*Cuora amboinensis*	Asian Box Turtle	Vu	II
Geoemydidae	*Hieremys annandalii*	Yellow-headed Temple Turtle	En	II
Geoemydidae	*Malayemys subtrijuga*	Malayan Snail-eating Turtle	Vu	
Trionychidae	*Amyda cartilaginea*	Asiatic Softshell Turtle	Vu	

Nedeco (1998) gave annual estimates of the lake for the years from 1981–1996. These ranged from 30,000 to 41,000 tonnes per year. These estimates are derived from government statistics and are certainly far lower than the true catch for a number of reasons. Lieng and Van Zalinge (2001) cite an annual catch range of 179,500–246,000 tonnes. Lamberts (2001) cites an estimate of the annual catch from Van Zalinge at between 177,000 and 252,000 tonnes. These later figures are based on consumption survey data and may be overestimates (Hortle pers. comm.), but are likely to be closer to the true figure than earlier estimates. In addition there are reasonably good estimates of the dai or bag net catch of fish migrating from the lake down the Tonle Sap river early each dry season and this fluctuates around about 12,000 tonnes (Hortle et al., 2004a).

Amphibians and reptiles

The herpetological fauna is the least studied of the major vertebrate groups in the region and René Bourret's works of the 1930s and 1940s still remain some the major published works on the snakes, amphibians and turtles of Cambodia (Bourret, 1936; 1941 and 1942).

Recent work has focused on turtles (Stuart and Platt, 2004), homalopsine watersnakes (Stuart et al., 2000) and crocodiles (Platt et al., in press). A Cambodian and English language guide to the reptiles of the Tonle Sap has also recently been produced (Long, 2003).

Five species of turtle have been confirmed to occur in and around the Tonle Sap Lake (Long, 2003; Stuart and Platt, 2004) (Table 3). One species, Mangrove Terrapin *Batagur baska* is documented to have gone extinct in the Tonle Sap. The complete shells of two adults were obtained from local fishermen in 1985 and are now in the Siem Reap Department of Fisheries Office. The shells were found buried in the lake mud and are not believed to represent recent occurrences. According to elderly residents, small numbers of Mangrove Terrapin were present in the Tonle Sap during the early 1900's. However, recent surveys have found no evidence for the continued persistence of the species in the Tonle Sap, and the species has almost certainly been locally extirpated (Platt et al., 2003). All turtle species in and around the Tonle Sap are under great threat from trade, primarily to China (Touch et al., 2000; Holloway, 2003).

Table 4. Snake species confirmed from the Tonle Sap. Data from Stuart et al. (2000) and Long (2003).

Family	**Genus and Species**	**Common Name**
Colubridae	*Enhydris enhydris*	Rainbow Watersnake
Colubridae	*Enhydris longicauda*	Tonle Sap Watersnake
Colubridae	*Enhydris bocourti*	Bocourt's Watersnake
Colubridae	*Enhydris jagorii*	Striped Watersnake
Colubridae	*Enhydris plumbea*	Plumbeous Watersnake
Colubridae	*Erpeton tentaculatum*	Tentacled Watersnake
Colubridae	*Homalopsis buccata*	Puff-faced Watersnake
Colubridae	*Xenochrophis piscator*	Checkered Keelback
Cylindrophiidae	*Cylindrophis ruffus*	Red-tailed Pipe Snake
Acrochordidae	*Acrochordus grunulatus*	Granulated File Snake
Elapidae	*Ophiophagus hannah*	King Cobra
Elapidae	*Naja kaouthia*	Monocled Cobra
Pythonidae	*Python reticulatus*	Reticulated Python
Pythonidae	*Python molurus bivittatus*	Burmese Python
Viperidae	*Trimeresurus macrops*	Big-eyed Pit Viper
Xenopeltidae	*Xenopeltis unicolor*	Sun-beam Snake

Stuart et al. (2000) documented seven species of Homalopsine watersnakes occurring in the Tonle Sap based on observations of catches and trade, and these are the first 7 included in Table 4.

Market data gathered at the peak of the wet season during 1999 and 2000 estimated that upwards of 8,500 watersnakes, of the first five species listed above, were harvested and sold per day, primarily for crocodile and human food. It is probable that this represents the greatest exploitation of any single snake assemblage in the world. Little is yet known as to whether this harvest is sustainable and further research is continuing (Stuart et al., 2000).

Other snakes have not been systematically surveyed but nine additional species (Table 4) were incidentally recorded by Stuart et al. (2000) or documented by Long (2003). Other species of reptiles recorded from the Tonle Sap include Tokay Gecko *Gekko gecko* and Water Monitor *Varanus salvator*. There is no systematic published work on the amphibians of the Tonle Sap, but two species

Table 5. Globally threatened breeding birds of the Tonle Sap swamp forest. Data from Goes (2001) and Seng et al. (2002).

		IUCN status	Conservation significance
Masked Finfoot	*Heliopais personata*	Vu	Unknown
Grey-headed Fish Eagle	*Ichthyophaga ichthyaetus*	NT	Largest popn. in mainland SE Asia
Darter	*Anhinga melanogaster*	NT	Largest colony in SE Asia. >30 % of global popn.
Black-headed Ibis	*Threskiornis melanocephalus*	NT	Largest colony in SE Asia. c. 5 % of reg. popn.
Spot-billed Pelican	*Pelecanus philippensis*	Vu	Largest colony in world. c. 25 % of global popn.
Milky Stork	*Mycteria cinerea*	Vu	Only freshwater colony in the world
Painted Stork	*Mycteria leucocephala*	NT	Largest colony in SE Asia. c. 20 % of reg. popn.
Lesser Adjutant	*Leptoptilos javanicus*	Vu	c. 2 % of global popn.
Greater Adjutant	*Leptoptilos dubius*	En	Only colony in SE Asia. c.10 % of global popn.

were reported to be abundant in lowland rice fields in Kompong Thom by Balzer et al. (2002).

Siamese Crocodiles *Crocodylus siamensis* still occur in small numbers in the Tonle Sap Lake, particularly in the Prek Toal Core Area, but are much reduced from earlier numbers. Formally they were reportedly common through the lake system, but have been heavily impacted through capture for farming and trade and must now be close to extirpation in the wild on the Tonle Sap. Siamese Crocodile is recognized by IUCN as being Critically Endangered and is listed on CITES Appendix I. It is now confined to remote wetland areas in Cambodia, with a stronghold in the rivers of the Cardamom Mountains to the south of the Tonle Sap Lake (Platt et al. in press.). Finally in late 2004 a lower jaw of a crocodilian species was discovered in the lake mud near Siem Reap by a local fisherman. It is now in the GECKO Centre in Chong Kneas and is believed on size alone to be from an Estuarine Crocodile *Crocodylus porosus*, the first confirmation of this species from the Tonle Sap. However, the jaw is not believed to be of recent origin and the species has long been extirpated from the lake (Steve Platt pers comm., 2004).

Birds

Birds are the best studied of the terrestrial faunal groups on the Tonle Sap, detailed information beginning with the 4th Franco-British Expedition to Indochina which visited Siem Reap and the Tonle Sap in 1928 (Delacour, 1929) and with further records, particularly from the Siem Reap area, up until the 1960s (Thomas and Poole, 2003). All work then was suspended through the civil war and began again with the first surveys in 1992 and 1993 (Archibald, 1992; Scott, 1992; Carr, 1994). About 220 species are known from the Lake area.

The Tonle Sap Lake is one of the most important areas for bird conservation in the region and has long been understood to be extremely important for gregarious large waterbirds, particularly storks, pelicans, ibises and cormorants. Seventeen Globally Threatened or Near Threatened species are known to occur regularly around the Tonle Sap Lake, and a recent project to identify Important Bird Areas (IBAs), based on the global criteria of BirdLife International, identified ten IBAs within the inundation zone (Seng et al., 2002). These are divided between two key habitat types; swamp forest and inundated grassland, both only seasonally flooded. The swamp forest, particularly of the Prek Toal Core Area is home to large breeding colonies of colonial waterbirds, while the inundated grassland has its own unique suite of threatened breeding birds, and during the early flood season hosts many feeding birds from the swamp forest.

A true understanding of the global importance of the colonial waterbirds of the swamp forest began with work in the Prek Toal Core Area in 1996 and 1997 (Parr et al., 1996; Ear-Dupuy et al., 1998) (Table 5). This work, and that of Goes and Hong (2002), resulted in a long term conservation initiative undertaken by the Government and the Wildlife Conservation Society working with local people to protect the colonies from large-scale egg and chick collection. This has been extremely successful and has resulted in the rebounding of waterbird populations in the area (Goes in prep.).

The Tonle Sap inundated grassland bird communities were unknown until the recent work of the late Sam Veasna (Sam, 1999). They are now known to support a unique community of birds (Table 6), including the world's largest population of the Globally Endangered Bengal Florican *Houbaropsis bengalensis*, and number of small grassland birds including Red Avadavat *Amandava amandava*. They are also significant for post-breeding populations of large waterbirds from the swamp forest and non-breeding *Aquila* eagles from the northern Palearctic (Goes et al., 2001; Seng et al., 2002). Again all these species were formerly widely persecuted, but recent local level conservation interventions are having successful results.

Only one bird species, the Greater Flamingo (*Phoenicopterus ruber*), is known to have gone extinct on the Tonle Sap, having last been recorded in 1935. It is diffi-

Table 6. Globally threatened birds of the Tonle Sap grasslands. Data from Seng et al. (2002).

Genus and Species	Common Name	IUCN status	Local status/origins
Houbaropsis bengalensis	Bengal Florican	En	Breeding
Grus antigone	Sarus Crane	Vu	Non-breeding from northern Cambodia
Aquila clanga	Greater Spotted Eagle	Vu	Non-breeding from Palearctic
Aquila heliaca	Imperial Eagle	Vu	Non-breeding from Palearctic
Threskiornis melanocephalus	Black-headed Ibis	NT	Non-breeding from swamp forest
Pseudibis davisoni	White-shouldered Ibis	Cr	Breeding/non-breeding?
Pelecanus philippensis	Spot-billed Pelican	Vu	Non-breeding from swamp forest
Mycteria cinerea	Milky Stork	Vu	Non-breeding from swamp forest
Mycteria leucocephala	Painted Stork	NT	Non-breeding from swamp forest
Ephippiorhynchus asiaticus	Black-necked Stork	NT	Non-breeding from northern Cambodia
Leptoptilos javanicus	Lesser Adjutant	Vu	Non-breeding from northern Cambodia/ swamp forest?
Leptoptilos dubius	Greater Adjutant	En	Non-breeding from swamp forest
Acrocephalus tangorum	Manchurian Reed Warbler	Vu	Non-breeding from Palearctic
Ploceus hypoxanthus	Asian Golden Weaver	NT	Breeding/non-breeding?

cult to comment on the status of this species and it may only ever have been a vagrant. The mudflats exposed by the receding Tonle Sap from April to June would provide an excellent nesting area for flamingos, so it is possible that they were once part of the lake's breeding avifauna. However, easily accessible nests and large nutritious eggs would have made this species highly vulnerable to exploitation (Thomas and Poole, 2003).

Mammals

Mammal faunal diversity of the Tonle Sap Lake is not particularly high. Three species of primate (O. Primates) occur in the swamp forest; Slow Loris *Nycticebus coucang*, Long-tailed Macaque *Macaca fascicularis* and Silvered Langur *Semnopithicus cristatus*. All have been confirmed from the Prek Toal Core Area. Long-tailed Macaque is widely distributed around the lake and Silvered Langur has also been recorded in the Stung Sen Core Area and in Kompong Thom (Goes and Hong, 2002). Long-tailed Macaques are now being trapped and traded in large numbers all around the lake in response to the recent demand from "monkey farms", in both Cambodia and Vietnam, established to serve the overseas pharmaceutical industry.

Two species of otters (O. Carnivora) have thus far been confirmed from the Tonle Sap Lake: Smooth Otter *Lutra perspicillata* and Hairy-nosed Otter *Lutra sumatrana*. The latter, thus far confirmed by the identification of captive animals from the Prek Toal and Stung Sen Core Areas is especially important as it is globally very little known and the Tonle Sap Lake may represent its major global stronghold (Poole, 2003). All otter species in Cambodia are under great threat from the local demand for skins for traditional medicine.

Colonies or roosts of flying-foxes *Pteropus* sp. (O. Chiroptera) have been recorded throughout the year, although primarily in the wet season, from swamp forest areas in Siem Reap, Pursat and Kompong Thom (Goes and Hong, 2002). From information elsewhere in the country it is likely that two species are involved Large Flying-fox *P. vampyrus* and Lyle's Flying-fox *P. lylei* (J. Walston pers. comm. to C.M. Poole, 2004). All flying-foxes are hunted throughout Cambodia and either eaten or sold for the restaurant trade.

Of the other carnivores, the small Asian Mongoose *Herpestes javanicus* is widespread around the lake. Leopard Cat *Prionailurus bengalensis* has been recorded once with an animal captured from the local area being held at the Phet Sanday Fisheries Office at the mouth of the Stung Sen in December 1998 (Goes and Hong, 2002). Reports of Fishing Cat *Prionailurus viverrinus* from the Tonle Sap Lake area remain unconfirmed. Asiatic Jackal *Canis aureus* was recorded in 2000 and 2001 in small numbers from the grasslands of the inundation zone in Kompong Thom, however they were being actively persecuted for food, particularly in the wet season, and none have been recorded since (Hong Chamnan pers. comm. to C.M. Poole, 2004).

Several larger species of mammal previously understood to have occurred around the Tonle Sap Lake are now locally extinct. Village elders claim within living memory to remember Asian Elephant *Elephas maximus* (O. Proboscidea) making annual seasonal migrations to the lake, but the nearest populations are now small, fragmented and well to the north of the Tonle Sap. Irrawaddy Dolphins *Orcaella brevirostris* (O. Cetacea) certainly used to occur in the Tonle Sap Lake, but were decimated during the Khmer Rouge era when they were harvested to provide fuel oil.

The role of invasive alien species

More than a dozen exotic plant species have become established in the Tonle Sap floodplain (CNMC et al., 1998; Oertzen and Smith, 2001). These include two grass species: *Brachiaria mutica* and *Echinochloa stagnina* that were introduced at some time in the past from Africa as high quality species for grazing, and have become dominant in many parts of the floodplain. Noxious invasive species are water hyacinth and giant mimosa *Mimosa pigra*, both of which are from South America. Water hyacinth occurs along waterways with slow-moving water, and in pools and ditches, and to a certain extent it is regarded as useful by local communities as it may be used as pig fodder and in fish attracting devices (*samras*). However, as water hyacinth forms dense mats it tends to de-oxygenate waters, and subsequently reduces water quality and fish production, especially in smaller bodies of water. Giant mimosa invades fallow fields and cleared and burnt swamp forest and scrubland areas, forming dense, impenetrable thickets that are very difficult to eradicate. It is also of little value to wildlife, although its effects on fisheries have not been well documented. At Tonle Sap it has recently become established along the length of the Tonle Sap River, scattered along the lake shores from Siem Reap to Snoc Trou, and in the Prek Toal Biosphere Reserve Core Area (CNMC et al., 1998).

Several exotic species, including silver carp (*Hypophthalmichthys molitrix*), tilapia (*Oreochromis* spp.), and common carp (*Cyprinus carpio*), are commonly seen in some parts of the Mekong Basin, but until now none of them have established large populations in the Great Lake. This may be due to small releases because the aquaculture sector is relatively small in Cambodia and in particular around the Great Lake where the fish supply from capture fisheries is plentiful. Fish culture is mainly based on the indigenous species giant snakehead (*Channa micropeltes*) and iridescent shark-catfish (*Pangasianodon hypophthalmus*) that are raised from wild seed. It may also be due to competition from the diverse range of native species already present in the lake. With future habitat degradation alien fish species could become a greater problem than at present.

Three non-native reptile species: Chinese Softshell Turtle, *Pelodiscus sinensis*, Estuarine Crocodile, *Crocodylus porosis*, and Cuban Crocodile, *C. rhombifer*, are recorded from farms around Tonle Sap Lake. The Chinese Softshell is present in at least two floating farms at Chong Kneas and has already been recorded from Cambodian markets (Holloway, 2003). On the evidence from other countries escaped animals are likely to establish feral populations (Stuart et al., 2001). Cuban Crocodile and Estuarine Crocodile are both present along with apparent hybrids in the Seam Reap crocodile farm (Platt et al. in press). Hybrid Estuarine x Siamese Crocodiles are also now apparently regularly, although illegally, imported to stock Cambodian crocodile farms around the Tonle Sap Lake. This is a major concern as the crocodile stock of the Cambodian farms was previously believed all to derive from wild caught genetically uncontaminated Siamese Crocodiles.

The South American Golden Apple Snail, *Pomacea* sp, was first recorded from lowland ricefields in Cambodia in 1995 and was subsequently reported as being raised for food in at least nine provinces (Jahn et al., 1996). It is a serious rice pest in other Asian countries and has been demonstrated to have a negative effect on wetland ecosystem function in Thailand through the loss of aquatic plants (Carlsson et al., 2004). In central Thailand it is now believed to be the main prey species of a burgeoning population of Asian Openbills *Anastomus oscitans* (Round, 2002).

Threats and protection

Human population growth in the basin, over harvesting of aquatic resources and the possible impacts of hydrological changes in the Mekong River are the three most pressing threats to the Tonle Sap lake ecosystem. Population growth and over-harvesting are obviously linked, because increases in harvesting pressure have partly arisen, and are likely to continue to rise in the short term, because of the increased numbers of people harvesting, and the increased market for the harvest. In contrast potential hydrological changes are driven by factors outside the basin, and indeed outside Cambodia, through the impacts of dams in China, Lao and Vietnam. Exotic species are present in the basin, as previously noted, but at present seem to pose less of a threat than other factors.

Population growth

The Tonle Sap basin, including the catchment of the lake and the Tonle Sap River, has an estimated population of 4.5 million people (Leang, 2003) giving an average population density of 53 people per km^2. Population growth in the basin is rapid at 4.8 % (Leang, 2003). This results partly from high fecundity due partly to the relatively young age structure. For example all of the seven provinces in the basin have more than 40 % of their population age 14 or less and more than 15 % between 15 and 24 years old (Hook et al., 2003).

There are also high rates of migration into the basin. People are drawn partly by employment prospects particularly in the tourism and construction industries. Tourism accounts for more than 4 % of Cambodia's GDP (Countrywatch.com, 2004) and the major national tourist attraction is Angkor Wat in the Tonle Sap Basin. The number of hotels beds in Siem Reap, the town servicing tourists visiting Angkor, was predicted to increase by 112% between 2003 and 2004 with 25 new hotels under construction of awaiting an operating licence (Yuan, 2004).

Apart from the attraction of potential employment in the tourist industry, the Tonle Sap Basin, and especially the region around the lake, is seen as an area where better subsistence livelihoods are available than in many other areas in Cambodia. There is flat land available for cultivation, a range of forest products including both wood and non-wood products and access to fish. Many families migrate to the area temporarily during the fishing season, while others migrate permanently.

Overharvesting

Evidence is growing that the aquatic resources in the Tonle Sap have suffered, and continue to suffer from overharvesting. For example, as previously noted, the rarity of crocodiles in the lake and the apparent absence of dolphins are both attributed to excessive hunting by humans, and hunting is identified as a major threat to bird and turtle populations. Of greater concern, from a human livelihoods point of view, is a growing concern about overfishing (Hortle et al., 2004a; Hortle et al., 2004b).

Until recently decline in species composition and size of fish caught was the main evidence of pressure on the Tonle Sap fishery. Total fish catch was believed to have increased between 1940 and the mid 1990's although catch per fisher declined (Van Zalinge et al., 2001). However during this period the contribution of large fish species to the catch has decreased and many of the largest are now rare. In addition the average size of the smaller fish in the catch has also decreased (Hortle et al., 2004b), which is often a sign of over fishing.

The past three years have seen a decline in the catch of the Tonle Sap River dai fishery, one of the few for which there is reliable data. The dai fishery uses large fixed nets in the river to catch fish moving from the lake and the floodplain during the dry season migration. Data since 1995 indicated that the extent of the previous wet season flood was a good predictor of the catch in a given year (Hortle et al., 2004a), but from 2002 to 2004 the catch declined rather than track the flood level. This could have been because of other features of the flood, such as timing or length of inundation period, were also having an impact, or because competition from other fishers impacted the dai fishery. In 2005 the dai catch recovered, a recovery which corresponded to a higher flood and to renewed government efforts to reduce illegal fishing. This has been taken to indicate that previous low dai catches were being impacted by overall fishing pressure. It also indicates that governments are beginning to assert necessary control to manage the fishery more effectively.

Hydrological change

Several reservoirs have already been constructed in the Mekong Basin upstream of the junction between the Mekong and the Tonle Sap Rivers, several more are under construction or in the final planning stages and many more have been proposed. Nam Ngum Dam in Lao PDR, Yali Falls Dam in Vietnam and both Manwan dam and Dachaoshan dam in China are already operational (Dore and Yu, 2004). Xiaowan Dam is under construction, due for completion in 2012, and Nam Theun II dam proposed in Lao PDR is undergoing environmental impact evaluation. A number of additional dams are proposed, particularly in the Chinese section of the river (e.g. see Hori, 2000), at least 7 or 8 as part of the "Mekong Cascade".

Virtually all the proposed dams are single purpose hydropower dams. In the headwaters of the Mekong River there is relatively little flat land available so there is little potential for irrigation. The only significant non-hydropower proposals involving Mekong waters are proposals to divert water to the Chao Phraya basin in Thailand through the Kok-Ing-Nan scheme, and proposals to divert water in to north east Thailand for irrigation.

The major impact of large scale hydro development on the River will be an increase in dry season flows and a decrease in wet season flows downstream. Hydro dams retain some of the wet season flows which are excess for generation power needs to augment dry season flows which may be insufficient for power needs. The extent of the change will depend on the stored capacity of the dams and their operational rules.

This change in flow pattern will reduce the area of land subject to seasonal inundation around Tonle Sap Lake. Modelling exercises conducted at MRCS (Halcrow, 2004, Beecham pers. comm.) indicate that development of two large dams in China could result in an increase in dry season minimum water levels in Tonle Sap Lake of about 0.3 m and a decrease in wet season maximum water levels of about 0.4 m. Based on the relationship between lake depth and area developed by JICA (2004) that would result in the seasonally inundated area decreasing from 10,620 km^2 to 9164 km^2, a drop of about 11%.

Changing land subject to annual inundation to permanently flooded or rarely flooded will in turn alter the plant communities and the productivity of the system. Seasonally flooded forest, for example, would not be able to adapt to permanent inundation. If the change resulted in a similar average reduction in the fish harvest it would also have serious consequences for the livelihoods both of those living around the lake and those living downstream who depend on the fish "exported" during the seasonal migration down the Tonle Sap River.

Sedimentation

One concern that has been raised in the grey literature and also occasionally in the popular press is that the lake is rapidly filling with sediment. Bardach (1959) estimated that, "based on recent estimates by local fishermen not supported by measurements" the lake would disappear as a permanent body of water in not more than 50 years. Csavas (1990) commented that "deposition in the bed of the Great Lake is currently occurring at a rate of 4 cm/year and, as the lake has an average depth of 40 cm in the dry season, it could cease to exist as a lake in the dry season in ten years time". Recent work, including several coring studies (Penny, 2002; Tsukawaki, 1997), and hydrodynamic modeling studies (FINWUP) all indicate that this is false. There is no danger of the two lake basins infilling in the short or medium term (Penny, 2002) and recent sedimentation in the lake basin proper appears to be insignificant. Most sedimentation in the lake basin would be expected to occur on or behind the natural levees which form the perimeter of the dry season lake rather than in the lake itself (WUPFIN). Were a problem to arise from sediment deposition it would most likely occur due to sediment deposition or rearrangement where the Tonle Sap river enters the lake, and this area does require monitoring.

Protection

In recognition of the importance of Tonle Sap Lake it was designated by the Cambodian Government as a Multiple Use Area under the 1993 Royal Decree on Protected Areas. In October 1997 UNESCO accepted the nomination of the Tonle Sap as a biosphere Reserve. Three Core Areas: Prek Toal; Boeng Chmar and Stoeng Sen were confirmed in April 2001 by the passage of a specific Royal Decree implementing the Tonle Sap Biosphere Reserve. These three Core Areas total 70,837 ha and are "devoted to the long term protection and conservation of natural resources and the ecosystem" specifically "to preserve flooded forest, fish, wildlife, hydrological systems and natural beauty". These core areas are surrounded by a buffer zone totaling 510,768 ha and a transition area totaling 899,652 ha. The Biosphere Reserve is managed through an inter-ministerial Tonle Sap Biosphere Reserve Secretariat which includes representatives from the Ministry of Environment, Mnistry of Agriculture, Forestry and Fisheries and Ministry of Water Resources and Meteorology.

Many of the temples and ruins at Angkor and surrounds were included in a 400 km^2 World Heritage Area listed in 1992. The area encompasses the Angkor complex the Roulos group of temples and Banteay Srei.

Other Cambodian environmental legislation also impinges on the management of the Tonle Sap Lake. This includes various legislative instruments to manage the fisheries of the Lake and the Mekong system in Cambodia. At present these are managed through a combination of fishing lots and community based fisheries, both of which have social and management shortcomings.

Discussion and conclusion

The Tonle Sap Lake is a fascinating system of great intrinsic value, and of great economic and cultural value to the people of Cambodia. The lake and its inundation zone are already showing the impacts of over-exploitation of resources which is reducing both the biodiversity value and its potential to support livelihoods.

The next decade is likely to be a critical period which will determine the future status of this important wetland. Many of the pressures presently impacting the lake are likely to greatly increase in the short term, including population growth, especially around Siem Reap, fishing pressure and hydrological changes.

Stable and effective governance systems in Cambodia are as yet not well established, and Bonheur and Lane (2002) identified governance deficiencies as a significant threat to the biodiversity of the Tonle Sap Lake. Management of the system requires cooperation from a range of government agencies. In addition the relationships between government officials and civil society, the people in the basin, will be key if the resources are to be well managed. Government legislation is of little value without public support.

It is of serious concern that Tonle Sap may be impacted by developments initiated in countries outside Cambodia. In particular the development of hydropower schemes on the Mekong River in countries upstream of Cambodia present a real and present danger to the ecosystems and fisheries of the Tonle Sap Lake. It is essential that the Cambodian Government use all the influence at its disposal to ensure that environmental impacts in downstream countries are considered in the design, implementation and operation of these projects. Where these projects proceed ameliorative measures, including appropriate operational rules and, where necessary, flow regulation structures should be included.

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References

Akiba, F., 2002. Nonmarine diatom floral changes in the core TS21-2 C-9-4 from the northern part of Lake Tonle Sap, Cambodia. Paper presented to International Symposium on Environmental Changes of the Tonle Sap. 16 October 2002, Ministry of Industry, Mines and Energy, Cambodia.

Archibald, G., 1992. A bird's eye view of Cambodia. The Bugle **18**(2): 1–3.

Baird, I. G., M. S. Flaherty and Bounpheng Phylavanh, 2003. Rhythms of the river: lunar phases and migrations of small carps (Cyprinidae) in the Mekong River. Nat. Hist. Bull. Siam Soc. **51**: 3-36.

Balzer, T., P. Balzer and S. Pon, 2002. Traditional use and availability of aquatic biodiversity in rice-based ecosystems. I. Kampong Thom Province, Kingdom of Cambodia. FAO Inland Water Resources and Aquaculture Service, Rome.

Bardach, J., 1959. Report on Fisheries in Cambodia. USOM, Phnom Penh, 80 pp.

Blache, J., 1951. Apercu sur le Plancton des eaux douces du Cambodge. Cymbium **6**: 62–94.

Bonheur, N. and B. D. Lane, 2002. Natural resources management for human security in Cambodia's Tonle Sap Lake biosphere reserve. Environment Science and Policy **5**: 33–41.

Bourret, R., 1936. Les Serpents de l'Indochine. 2 vols. Henri Basuyau, Toulouse, France, 141 and 505 pp.

Bourret, R., 1941. Les Tortues de l'Indochine. l'Institut Océanographique de l'Indochine. Hanoi, 235 pp.

Bourret, R., 1942. Les Batraciens de l'Indochine. Memoires de l'Institut Océanographique de l'Indochine, Hanoi, 547 pp.

Brehm, V., 1951. Cladocera und Copepoda Calanoida von Cambodja. Cymbium **6**: 95–124.

CNMC, NEDECO and MIDAS Agronomics, 1998. Natural resources-based development strategy for the Tonle Sap area, Cambodia. (CMB/95/003), Final report, volume 2, Sectoral studies, 1. Environment in the Tonle Sap area. Cambodia National Mekong Commission for Mekong River Commission and UNDP, Phnom Penh, 95 pp. + appendices.

CNMC (Cambodia National Mekong Committee)/Nedeco, 1998. Sectoral studies: environment in the Tonle Sap area. Natural resources-based development strategy for the Tonle Sap area, Cambodia. Final Report, Volume 2, Part B. MRC/UNDP Phnom Penh, 269 pp.

Carbonnel, J. P., 1963. Vitesse dáccumulation des sediments récents du Grand Lac du Cambodge d'après le carbonne 14. Corréations stratigraphiques et morphologiques. C. R. Acad. Sci., Fr. **257**: 2514–2516.

Carlsson, N. O. L., C. Brönmark and L. Hansson, 2004. Invading herbivory: the Golden Apple Snail alters ecosystem functioning in Asian wetlands. Ecology **85**: 1575–1580.

Carr, P., 1994. Cambodia, the last refuge for rare and endangered waterfowl in South-East Asia. Sea Swallow **43**: 35–37.

Chea Tharith, Lek Sophat and Thach Phanara, 2003. Fish larvae and juvenile drift at the confluence of four rivers near Phnom Penh: the Mekong upstream and downstream, the Tonle Sap and the Bassac River June–September 2002. MRC Conference Series **4**: 20–27.

Coe, M. D., 2003. Angkor and the Khmer Civilisation. Thames and Hudson, London, 240 pp.

Compagno, L. J. V. and S. F. Cook, 1995. The exploitation and conservation of freshwater elasmobranches: status of taxa and prospects for the future. Journal of Aquariculture and Aquatic Science **7**: 62–90.

Countrywatch.com, 2004. http://biz.yahoo.com/ifc/kh.html. Accessed December 2004.

Csavas, I., 1990. Report of the Mekong Secretariat Mission to Cambodia. Appendix 3d.

Csavas, I., D. J. Doulman, T. O. Petr, J. Prado and L. Debas, 1994. Cambodia – rehabilitation and development needs of the fishery sector. FAO, Rome, 87 pp.

DHI, 2004. Study on Natural Reverse Flow in the Tonle Sap River. DHI – Water and Environment. Consultants Report to Mekong River Commission.

Delacour, J., 1929. On the birds collected during the fourth French expedition to French Indochina. Ibis **12 (5)**: 193–220.

Dore, J. and Yu Xiaogang, 2004. Yunnan Hydropower Expansion: Update on China's energy industry reforms and the Nu, Lancang and Jinsha hydropower dams. Working Paper from Chiang Mai University's Unit for Social and Environmental Research and Green Watershed, 32 pp.

Ear-Dupuy, H., E. Briggs, C. Hong and O. Keo, 1998. Waterbird Conservation in the Prek Toal Area, Battambang Province, Cambodia. Wetlands International, International Crane Foundation and the Wildlife Protection Office, Phnom Penh, 24 pp.

Eloheimo, K., S. Hellsten, T. Jantunen, J. Jozsa, M. Kiirikki, H. Lauri, J. Koponen, J. Sarkkula, O. Varis and M. Virtanen, 2002. Data Report March 2002, revised August 2002. Water Utilization Program – Modelling of the Flow Regime and Water Quality of the Tonle Sap. Consultants Report by the Finnish Environment Institute, 122 pp.

Giesen, W., 2000. Flora and vegetation of Danau Sentarum: Unique lake and swamp forest ecosystem of West Kalimantan. Borneo Research Bulletin **31**: 89–122.

Goes, F., in prep. Three years of waterbird conservation activities in Prek Toal Core Area, Tonle Sap Biosphere Reserve (2001–2004). Wildlife Conservation Society, Cambodian Program, Phnom Penh.

Goes, F. and C. Hong, 2001. The status and conservation of large waterbirds on the Tonle Sap, Cambodia 2000–2001, Wildlife Conservation Society, Phnom Penh, 109 pp.

Goes, F. and C. Hong, 2002. The status and significance of waterbirds of the Tonle Sap. Cambodia Bird News **8**: 3–19.

Goes, F., C. Hong, P. Davidson and C. M. Poole, 2001. Bengal Florican *Houbaropsis bengalensis* conservation in Kampong Thom province, Cambodia. Wildlife Conservation Society, Phnom Penh, 59 pp.

Halcrow, 2004. Mekong River Commission Decision Support Framework. Water Utilization Project Component A: Final Report. Volume No. 1. DSF 100 Main Report. Consultants report to Mekong River Commission Secretariat by Halcrow Group Limited. 40 pp.

Higham, C., 2001. The Civilization of Angkor, Wiedenfeld and Nicolson, London, 192 pp.

Holloway, R. H. P., 2003. Domestic trade of tortoises and freshwater turtles in Cambodia. Chelonian Conservation Biology **4(3)**: 733–734.

Hook, J., S. Novak and R. Johnston, 2003. Social Atlas of the Lower Mekong Basin, Mekong River Commission, Phnom Penh, 154 pp.

Hori, H., 2000. The Mekong, Environment and Development, United Nations University Press, Tokyo, 398 pp.

Hortle, K. G., P. Ngor, R. Hem and S. Lieng, 2004a. Trends in the Cambodian dai fishery: floods and fishing pressure. Catch and Culture **10(1)**: 7–9.

Hortle, K. G., S. Lieng and J. Valbo-Jorgensen, 2004b. Cambodia's Inland Fisheries. Mekong Development Series No. 4. Mekong River Commission and the Inland Fisheries Research and Development Institute, Phnom Penh, 41 pp.

Hutchinson, C. S., 1989. Geological evolution of Southeast Asia. Oxford Monographs on Geology and Geophysics, Clarendon Press, Oxford, 368 pp.

Jahn, G. C., B. Kiev, S. Pheng and C. Pol, 1996. Pest management in rice. In: H. J. Nesbitt, (ed.), Rice Production in Cambodia, University Press, Phnom Penh, pp 134–147.

JICA, 2004. The study on hydro-meteorological monitoring for water quantity rules in Mekong River Basin. Draft Final Report. Volume II Supporting Report (1/2). Paper IV. Development of Hydro-Hydraulic Model for the Cambodian Floodplains, 109 pp.

Kato, M. and M. Oda, 2002. The possibility of the occurrence of modern Foraminifera (Order Sarcodina) from Lake Tonle Sap and the basin of the Mekong River, Cambodia. Paper presented to International Symposium on Environmental Changes of the Tonle Sap. 16 October 2002, Ministry of Industry, Mines and Energy, Cambodia.

Kottelat, M. and T. Whitten, 1996. Freshwater Biodiversity in Asia with special reference to fish. World Bank Technical Paper No. 343. World Bank Washington DC, 59 pp.

Lamberts, D., 2001. Tonle Sap fisheries: a case study on floodplain gillnet fisheries in Siem Reap, Cambodia. FAO Regional Office for Asia and the Pacific, Bangkok, Thailand. RAP Publication 2001/11, 133 pp.

Leang, P., 2003. Sub-Area Analysis, The Tonle Sap Sub-Area. Report for the Basin Development Plan, Mekong River Commission, Phnom Penh, 79 pp.

Légris, P. and F. Blasco, 1972. Notice de la carte de végétation du Cambodge au 1:1,000,000. Travaux de Section Sci. Techn. Inst. Fr., Pondichéry **11**: 1–238.

Lieng, S. and N. Van Zalinge, 2001. Fish yield estimation in the floodplains of the Tonle Sap and River, Cambodia. In IFReDI (ed.) Cambodia Fisheries Technical Paper Series, Vol. III, MRC and Department of Fisheries Phnom Penh, pp. 23–26.

Lim, P., S. Lek, S. T. Touch, S. Mao and B. Chhouk, 1999. Diversity and spatial distribution of freshwater fish in and Tonle Sap river (Cambodia, Southeast Asia). Aquatic Living Resources **12(6)**: 379–386.

Long, K., 2003. Understanding the conservation status of reptiles and small mammals of the Tonle Sap, Tonle Sap Biosphere Reserve Secretariat, Phnom Penh, 24 pp.

MRC, 2003a. State of the Basin Report. 2003. Mekong River Commission, Phnom Penh, 300 pp.

MRC, 2003b. Mekong Fish Database version 2003. CD-ROM, Mekong River Commission, Phnom Penh, Cambodia.

MRC/UNDP, 1998. Natural Resources-Based Development Strategy for the Tonle Sap Area, Cambodia. (CMB/95/003). Final Report. Volume 2, Part B. Sectoral Studies. Environment in the Tonle Sap Area, 122 pp.

McDonald, A., B. Pech, V. Phauk and B. Leeu, 1997. Plant communities of the Tonle Sap Floodplain. Final Report in contribution to the nomination of Tonle Sap as a UNESCO Biosphere Reserve, UNESCO, IUCN, Wetlands International and SPEC (European Commission), Phnom Penh, 30 pp.

Mildenhall, D. C., 2002. Palynology of Holocene and last glaciation samples from Lake Tonle Sap, Cambodia. Paper presented to International Symposium on Environmental Changes of the Tonle Sap. 16 October 2002, Ministry of Industry, Mines and Energy, Cambodia.

Ng, P. K. L.,1995. *Somanniathelhusa lacuvita*, a new ricefield crab from Tonle Sap, Cambodia. Asian Journal of Tropical Biology. **1**: 26–30.

Nguyen, X. T. and V. H. Nguyen, 2001. A summary of the Report on the Freshwater Fisheries Reources Survey in Cambodia (1986–1988), Ministry of Fisheries, Socialist Republic of Vietnam. Hanoi 1991, 12 pp.

O'Connor, R., 2001. Aquatic macroinvertebrates of Cambodia (freshwater). In: J. Smith (compiler and editor). Biodiversity, the life of Cambodia. Cambodia's Biodiversity Status Report – 2001,Cambodia Biodiversity Enabling Activity. Phnom Penh, Cambodia, pp. 81–86.

Oertzen, I. and J. Smith, 2001. Focus on Invasive Alien Species in Cambodia. In: J. Smith, (compiler and editor). Biodiversity, the life of Cambodia. Cambodia's Biodiversity Status Report. 2001, Cambodia Biodiversity Enabling Activity, Phnom Penh, Cambodia, pp. 230–239.

Okawara, M. and S. Tsukawaki, 2002. Composition and provenance of clay minerals in the northern part of Lake Tonle Sap, Cambodia. Journal of Geography **111**: 311–359.

Paaijmans, K., 1976. (ed.). New Guinea Vegetation. ANU Press, Canberra, 213 pp.

Penny, D., 2002. Sedimentation rates in Tonle Sap, Cambodia. Report to the Mekong River Commission, 12 pp.

Parr, J. W. K., J. C. Eames, H. Sun, C. Hong, H. Som, V. L. Pich and K. H. Seng, 1996. Biological and social aspects of waterbird exploitation and natural resource utilization of Prek Toal, Tonle Sap Lake, Cambodia. Cambridge, UK: IUCN/SSC, 57 pp.

Platt, S. G., B. L. Stuart, Heng Sovannara, K. Long, K. Kalyar, and K. Heng, 2003. Rediscovery of the critically endangered river terrapin, *Batagur baska*, in Cambodia, with notes on occurrence, reproduction, and conservation status. Chelonian Conservation and Biology **4(3)**: 691–695.

Platt, S. G., S. Heng, K. Long, J. B. Thorbjarnarson and T. R. Rainwater, in press. Population status and conservation of wild Siamese Crocodiles (Crocodylus siamensis) in the Tonle Sap Biosphere Reserve, Cambodia. Nat. Hist. Bull. Siam Soc.

Poole, C. M., 2003. The first records of Hairy-nosed Otter *Lutra sumatrana* from Cambodia with notes on the national status of three other otter species. Nat. Hist. Bull. Siam Soc. **51(2)**: 273–280.

Poulsen, A. F. and J. Valbo-Jorgensen (eds.), 2000. Fish migrations and spawning habits in the Mekong mainstream – a survey using local knowledge. AMFC Technical Report, Mekong River Commission.

Poulsen, A. F., O. Poeu, S. Viravong, U. Suntornratana and N. T. Tung, 2002. Deep pools as dry season fish habitats in the Mekong river basin. MRC Technical Paper No. 4. Mekong River Commission, Phnom Penh, 22 pp.

Rainboth, W. J., 1991. Cyprinids of South East Asia. In: I. J. Winfield and J. S. Nelson (eds.), Cyprinid fishes: systematics, biology, and exploitation, Chapman and Hall, London. Fish and Fisheries Series 3, pp. 156–210.

Rainboth, W. J., 1996. Fishes of the Cambodian Mekong. FAO, Rome. 265 pp.

Rollet, B., 1972. La végétation du Cambodge. Bois et Forêts de Tropiques **144**: 3–15; 145:24–38; 146: 4–20.

Sam, V., 1999. Survey for Sarus Crane and other endangered bird species in southern Kampong Thom province, Cambodia. Unpublished report to the Oriental Bird Club. Sandy, UK, 22 pp.

Sarkkula J. and J. Koponen, 2003. Modelling Tonle Sap for Environmental Impact Assessment and Management Support. Draft Final Report, Finnish Environment Institute, 109 pp.

Scott, D. A., 1992. Survey of Cambodian wetlands, 26 November to 5 December 1992. Unpubl. manuscript.

Seng, K. H., B. Pech, C. M. Poole, A. W. Tordoff, P. Davidson and E. Delattre, 2002. Directory of Important Bird Areas in Cambodia: key sites for conservation. Phnom Penh: Department of Forestry and Wildlife, Department of Nature Conservation and Protection, BirdLife International in Indochina and the Wildlife Conservation Society Cambodia Program, 116 pp.

Smith, D. G., 2001a. Pennak's Freshwater Invertebrates of the United States. Porifera to Crustacea. 4th Edn, John Wiley and Sons, New York, 638 pp.

Smith, J., 2001b. Biodiversity, the life of Cambodia. Cambodia's Biodiversity Status Report – 2001. Ministry of Environment, UNDP, GEF & FAO, Phnom Penh, 244 pp.

Stuart, B. L. and S. G. Platt, 2004. Recent Records of Turtles and Tortoises from Laos, Cambodia, and Vietnam. Asiatic Herpetological Research **10**: 129–150.

Stuart, B. L., J. Smith, K. Davey, Prom Din and S. G. Platt, 2000. Homalopsine watersnakes: The harvest and trade from Tonle Sap. TRAFFIC Bulletin **18(3)**: 115–124.

Stuart, B. L., P. P. van Dijk and D. B. Hendrie, 2001. Photographic Guide to the Turtles of Thailand, Laos, Vietnam and Cambodia, Wildlife Conservation Society, New York, 84 pp.

Taki, Y., 1975. Geographic distribution of primary freshwater fishes in four principal areas of Southeast Asia. Southeast Asian Studies (Kyoto Univ.) **13 (2)**: 200–214.

Taki, Y., 1978. An analytical study of the fish fauna of the Mekong basin as a biological production system in nature. Res. Inst. Evol. Biol. Tokyo, Spec. Publ. **1**: 1–77.

Thomas, W. W. and C. M. Poole, 2003. An annotated checklist of the birds of Cambodia from 1859–1970. Forktail **19**: 103–127.

Touch, S. T., L. H. Prak, T. Chul, S. Lieng, S. Chun, P. Hout and K. Heng, 2000. Overview of turtle trade in Cambodia. In: P. P.Van Dijk, B. L. Stuart, and A. G. J. Rhodin (eds.). Asian Turtle Trade: Proceedings of a Workshop on Conservation and Trade of Freshwater Turtles and Tortoises in Asia. Chelonian Research Monographs 2. Chelonian Research Foundation, Lunenburg, pp. 55–57.

Triet, T., 2002. Wetland vegetation of Ang Trapaeng Thmaw Nature Reserve, Banteay Meanchey Province, Cambodia. Report for the International Crane Foundation, Baraboo, Wisconsin, USA, 6 pp.

Tsukawaki, S., 1997. Lithological features of cored sediments from the northern part of Lake Tonle Sap, Cambodia. Proceedings of the International Conference on Stratigraphy and Tectonic Evolution of Southeast Asia and the South Pacific. Bangkok, Thailand, 19–24 August 1997.

Tsukawaki, S., M. Okawara, K. Lao and M. Tada, 1994. Preliminary study of sedimentation in Lake Tonle Sap, Cambodia. Journal of Geography **103**: 623–636.

Tsukawaki, S., D. C. Mildenhall, B. Ben, S. Touch and M. Oda, 2002. Lithological features and radiocarbon ages of cored sediments from the northern part of Lake Tonle Sap, Cambodia. Paper presented to International Symposium on Environmental Changes of the Tonle Sap. 16 October 2002, Ministry of Industry, Mines and Energy, Cambodia.

Valbo-Jørgensen, J. and T. Visser, 2003. The MRC Mekong Fish Database: An Information Base on Fish of a Major International River Basin. MRC Conference Series **4**: 55–69.

van Steenis, C. G. G. J., 1957. Outline of vegetation types in Indonesia and some adjacent regions. Eighth Pacific Science Congress, **IV Bot**: 61–97.

Van Zalinge, N. P., T. Nao and N. Sam, 2001. Status of the Cambodian inland capture fisheries sector with special reference to the Tonle Sap. In: N. P. van Zalinge, R. Ounsted and S. Lieng, S. (eds.). Cambodia Fisheries Technical Paper Series 3. Mekong River Commission and Department of Fisheries, Phnom Penh, pp. 10–17.

Van Zalinge, N., Nao Thuok, Touch Seang Tana and Deap Loeung, 2000. Where there is water, there is fish? Cambodian fisheries issues in a Mekong River Basin Perspective. In: M. Ahmed and P. Hirsch, (eds.) Common Property in the Mekong: issues of sustainability and subsistence. ICLARM Studies and Reviews **26**: 37–48.

Visser, T. A. M., J. Valbo-Jørgensen and T. Ratanachookmanee, 2003. MFD 2003, Introduction and data sources. Mekong River Commission, Phnom Penh, Cambodia, 63 pp.

Welcomme, R. L. (compiler), 2001. Inland Fisheries: Ecology and Management. Fishing, News Books, Oxford, UK, 358 pp.

Wetzel, R. G., 1983. Limnology, 2nd Edn, Saunders College Publishing, New York, 767 pp.

Woodsworth, G., 1995. Disappearing Lakes – What is to be Done ? A Case of the Tonle Sap, Cambodia. In: Proceedings of the Regional Dialogue on Biodiversity and Natural Resources Management in Mainland Southeast Asian Economies, Kunming, China, 21–24 February 1995. Natural Resources and Environment Program of the Thailand Development Research Institute, and Kunming Institute of Botany (Chinese Academy of Sciences), pp. 99–109.

Workman, D. R., 1977. The Geology of Laos, Cambodia, South Vietnam and the eastern part of Thailand. Overseas Geology and Mineral Resources. **50**: 1–33.

WUP-JICA Team, 2004. Development of hydro-hydraulic model for the Cambodian Floodplains. Paper IV, Draft Final Report. In: The Study on Hydro-meteorological Monitoring for Water Quantity Rules in Mekong River Basin. Draft Final Report. Volume II. Supporting Report (1/2). CTI Engineering International Co. Ltd and Nippon Koei Co. Ltd. MRC and JICA, Phnom Penh, 109 pp.

Yuan, L. F., 2004. Up, up, up go hotels in Siem Reap. The Searchlight. **1(2)**: 1–2.