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The Holocene history and development of the Tonle Sap, Cambodia

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Abstract

The Tonle Sap, the 'Great Lake' of central Cambodia, is the central component of wetland ecosystems in the lower Mekong River basin, and is of enormous conservation value. The lake's unusual hydraulic relationship with the Mekong River, and its consequent sensitivity to monsoon variability, makes the Tonle Sap sensitive to climate change. Exploring the dynamics and development of this system under different climate regimes of the past offers a perspective on possible future impacts, which is critical for sound management. Biostratigraphic and sedimentological data derived from cores of lake sediment indicate that during the period >7000 to ca. 5500 ^{14}C years Before Present the lake was less variable than present in terms of depth during the annual cycle of flood, and may have been strongly influenced by saline tidal waters associated with higher-than-present seas levels. As regional environments became drier and more seasonal in the late Holocene, more sediment was re-suspended during the increasingly marked dry season lake level minimum, lowering the effective sediment accumulation rate. Contrary to current interpretations of the history of the lake and associated wetland ecosystems, the data presented here imply that regional hydraulic connections between the lake and the Mekong River existed from at least the early Holocene.

1. Introduction

The lower Mekong River basin supports the largest and most significant remnant wetland ecosystems in Southeast Asia (MRCS/WUP-FIN, 2003a; Bonheu and Lane, 2002). The central component of these wetlands is the Tonle Sap, a large fluvial lake in central Cambodia (Fig. 1) which receives flood water from the Mekong River while the southeast monsoon is active. During its flooding phase, the Tonle Sap receives more than 51 000 million m^3 of water from the Mekong River via the Tonle Sap River, and expands more than five-fold to flood the surrounding alluvial plain (MRCS/UNDP, 1998; Puy et al., 1999), covering an area of up to 16 000 km^2 (MRCS/WUP-FIN, 2003a). The lake, then, acts as a natural spillway for the Mekong River and plays a significant role in mitigating flooding in Cambodia and Vietnam. This, in concert with the delayed release of flood water from the lake back into the Mekong River during the dry season, means that the Tonle Sap plays an important role in mitigating extremes of seasonal hydrology associated with the contrasting wet and dry monsoons.

The hydrodynamics of the Tonle Sap are highly dependent upon the magnitude of wet season flows in the Mekong River, which are in turn dependent upon the timing and strength of the southwest monsoon. Consequently, the Tonle Sap and its riparian ecosystems and economies are extremely sensitive to variation in monsoon behaviour. Critically, predicted climatic changes are likely to have significant implications for the Asian monsoon (Anderson et al., 2002; Black, 2002; Gupta et al., 2003) and, consequently, for the wetlands of the lower Mekong River basin, which will represent a significant challenge to management, particularly at the intergovernmental level (Jacobs, 1996). Bhaskaran and Mitchell (1998) predict an increase of 20–25% in peak monsoon rainfall over mainland Southeast Asian under a greenhouse climate scenario, driven by a greater moisture carrying capacity of southwest winds from the Indian Ocean. The result will be a "noticeable increase

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in the frequency of flooding" in mainland Southeast Asia (p. 1460). Nijssen et al. (2001) calculate a more seasonal climate for the Mekong Basin under elevated greenhouse gas climate but, with higher than present rainfall during the early part of the southwest monsoon season, higher rainfall overall. Evapotransporation is predicted to be in phase with increased precipitation in most tropical river basins, but this may mean little if rainfall becomes more markedly seasonal and flooding may occur more rapidly. Higher and more seasonal monsoon rainfall will have enormous implications for the riparian provinces of Cambodia and southern Vietnam. For example, Zeidler (1997) reports that the Vietnamese coastline is inherently susceptible to climate change, particularly flooding as a result of higher-than-present sea levels and stronger early wet season monsoon rainfall. Fourteen million people living in the Mekong Delta of Vietnam will be subject to annual flooding that could be as extensive as 40 000 km^2, with capital value losses of US$17 billion. The impact of higher sea-levels under a predicted greenhouse climate scenario is likely to be larger inland than on the coastal fringe, as 'backflooding' during the wet season becomes more extensive. Under this scenario, flooding in southern Cambodia, and particularly around Phnom Penh, may become extremely problematic.

Understanding the long-term development of wetlands in the lower Mekong River basin is important in understanding how they might respond to predicted climate scenarios. In particular, the response of the system to higher-than-present sea levels (Nguyen et al., 2000; Ta et al., 2001, 2002), and to 'surges' in the strength of the southeast monsoon during the Holocene (Gupta et al., 2003; Maxwell and Liu, 2002) offer an opportunity to forecast the likely impact of greenhouse climates. Lake sediments are valuable archives of environmental information (Last and Smol, 2002a, b; Smol et al., 2002a, b), and offer the opportunity to reconstruct climatic variability and hydrodynamics over long time-scales. This paper presents a record of climatic and hydrologic variability for the past ca. 7000 years based on the analysis of sediment cores from lake Tonle Sap, Cambodia.

2. Materials and methods

The Tonle Sap lake is large, mesotrophic 'fluvial' lake, the hydrodynamics of which are strongly dependent upon the character of the regional climate. The climate is monsoonal and markedly seasonal (Köppen's 'Aw'), characterised by the contrasting influence of surface winds from the Indian Ocean and central east Asia, respectively. Average annual rainfall is between 1300 and 1500 mm, the majority of which falls while the southwest summer monsoon is active (May–October), peaking in September (18% of annual rainfall) (MRCS/WUP-FIN, 2003a, b). The seasonal flood pulse supports a unique freshwater 'flooded forest' plant community which forms a substantial fringe at the dry season lake edge, and is partly or wholly submerged for several months during the peak of the flood (McDonald et al., 1997). This community is dominated by *Barringtonia acutangula* and *Diospyros cambodiana*, with sub-dominant taxa including *Crataeva* spp., *Terminalia cambodiana*, *Coccocera anispodum*, and the "ubiquitous" woody lianes *Combretum trifoliatum*, *Breynia rhamnoides* and *Acacia thailandica* (McDonald et al., 1997, p. 12).

The Tonle Sap lake is essentially two primary lacustrine basins—a large northwest basin and a smaller southeast basin—linked by a relatively narrow strait (Fig. 2). Cores of sediment were collected in November 1999 using a Kullenberg-type corer (Glew et al., 2001) from the smaller southeast basin (Site 2: 12°35′32″N: 104°17′20″E). Water depth at this site was 7.9 m. Upon recovery, cores were cut into 1 m lengths, sealed, packed and freighted to the laboratory.

Whole cores were analysed for variation in volume magnetic susceptibility over depth (Dearing, 1999) and X-rayed with a Scanray-AC120L to reveal stratigraphic features in situ prior to longitudinal sectioning of the core tubes. Samples were taken for mineral particle size analysis at 0.5, 1, and 10 cm intervals, with resolution decreasing as depth increased. Samples were treated with 10% w:w sodium pyrophosphate to disaggregate the sediment, and 30% w:w hydrogen peroxide to remove organic material (Gale and Hoare, 1991). Particle size analyses were conducted on a Coulter LS100 laser diffraction particle size analyser (McManus, 1995).

Samples for AMS-^{14}C dating were taken from five locations in the core. The pollen fraction of the sediment was used for dating, and was isolated following the procedure described by Regnell (1992). The results were calibrated (Bronk Ramsey, 1995, 2001; Stuiver et al., 1998) and are expressed below as both radiocarbon (BP) and calibrated (cal. BP) ages.

Sub-samples for pollen analysis were taken at 10 cm intervals. Pre-treatment followed Berglund and Ralska-Jasiewiczowa (1986), with the inclusion of a heavy-liquid separation stage (sodium polytungstate s.g. = 2.0 g/cm^3). Pollen and spores were identified and counted under 400–1000 times magnification using standard transmitted light microscopy. Pollen and spore taxonomy is based on a pollen reference set of 328 Southeast Asian phanerogams. Nomenclature follows Punt et al. (1994). Pollen data are expressed here as percentages of either a primary pollen sum that includes all woody taxa, or secondary pollen sum which includes herbaceous and aquatic plants, and ferns. Microscopic charcoal particle and total pollen concentrations per unit volume were calculated following Stockmarr (1971). These were found to be covariant ($r^2 = 0.69$), suggesting the primacy

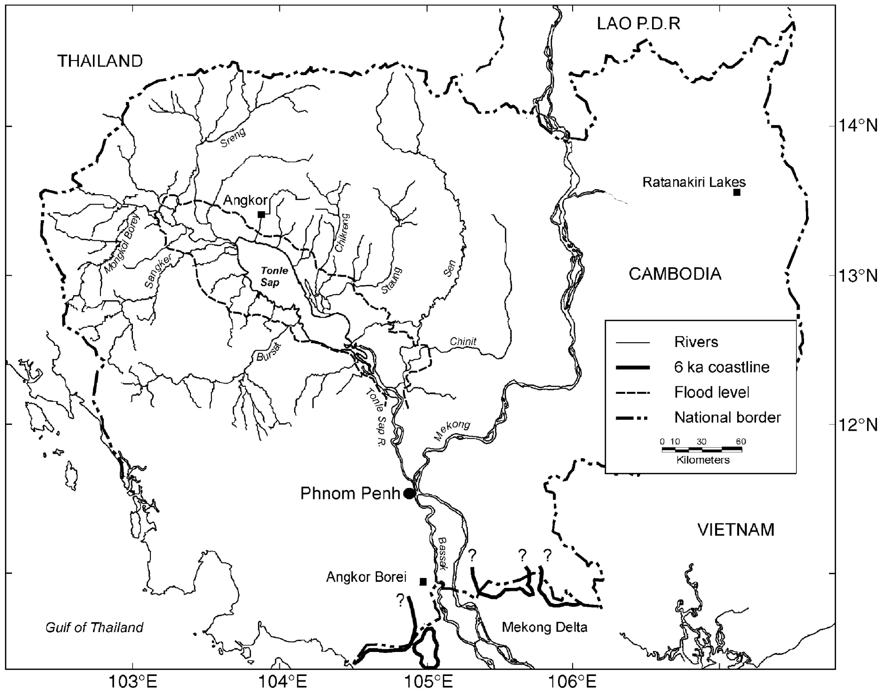

Fig. 1. Map of Cambodia, showing the regional hydrology, approximate dry and wet season lake levels (wet season level based on year 2000 flood, from MRCS/WUP-FIN 2003), and reconstructed coastline at ca. 6000 BP (from Nguyen et al., 2000).

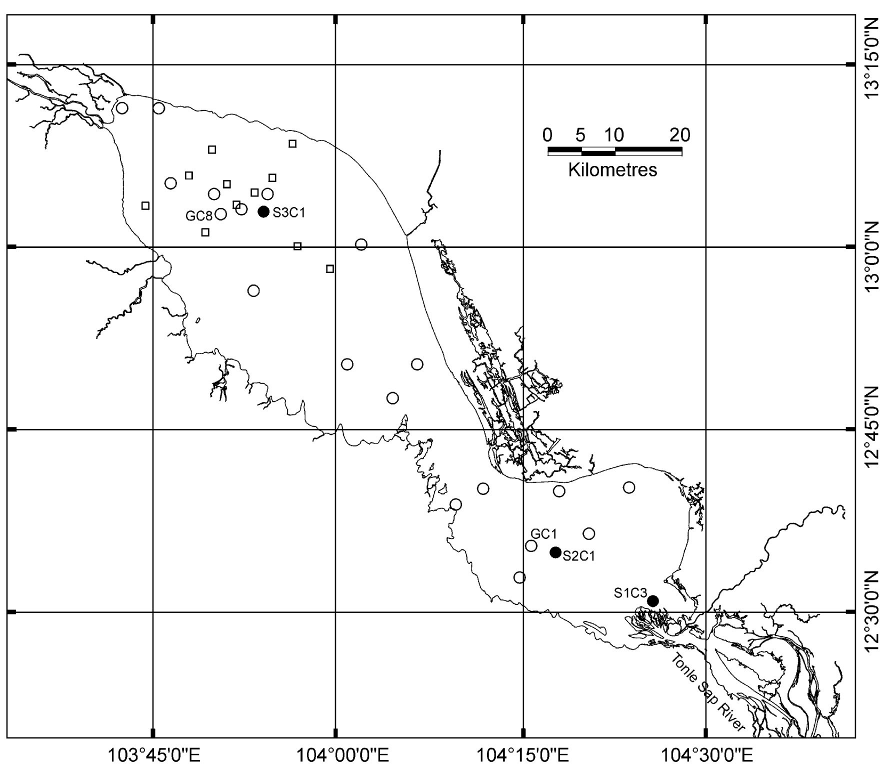

Fig. 2. Map of the Tonle Sap Lake, showing the two primary lacustrine basins, and coring sites relative to the dry season lake level. Core sites are taken from this study (closed circles), Carbonnel and Guiscafré (1965) (open circles), and Tsukawaki (2002) (open squares).

of taphonomy rather than fire regime in controlling concentrations of charcoal in the sediments of the lake. In order to correct this, charcoal is expressed as a ratio of total pollen concentration. Pollen influx from the catchment is independent of the rate of sediment accumulation, and is here assumed to be relatively stable over time. The relative concentration of palynomorphs, then, can be used to indicate the relative rate of sediment accumulation, against which variations in sedimentary charcoal concentrations can be corrected.

Samples for diatom analysis were taken at 10 cm intervals, and pre-treated with 10% w:w hydrochloric acid and 10% w:w hydrogen peroxide (Krammer and Lange-Bertalot, 2000b; Battarbee, 1986). Samples were mounted with Naphrax and counted at 1000 × magnification. Taxonomy and nomenclature follows Krammer and Lange-Bertalot (1991, 1999a, b, 2000a, b), with reference to Round et al. (1990).

3. Results

3.1. Stratigraphy and sedimentology

The longest core recovered from Site 2—S2C1—was 3.74 m in length. X-radiographs indicate a largely homogenous profile, with the exception of shells above 0.15 m depth (Fig. 3; cores S1C3 from Site 1 and S3C1 from Site 3 are also shown in Fig. 3 for the purposes of cross-basin comparison, and to document the occurrence of shells in the lake stratigraphy. See Fig. 1 for site locations). Visual description of core S2C1 following longitudinal sectioning revealed a thick (>3.7–0.46 m depth) horizon of olive grey (5Y 5/2) homogenous mud overlain by a greyish brown (10YR 5/2) mud (0.46–0.00 m depth). Susceptibility (κ) values are stable and relatively low between the base of the core and 0.6 m depth, excepting a discrete increase between ~3.0 and 3.18 m depth. Susceptibility values increase in the upper 0.6 m of the core, with maxima at 0.42, 0.24, 0.14 and 0.04 m depth (Fig. 4). Particle size analysis indicates the profile is dominated by silt, particularly medium to very fine silt, and clay. Mean mineral particle size is relatively low and stable from the base of the core to 0.9 m depth, with the exception of a discrete increase in the coarse-silt to very-fine sand fraction at 3.1 m depth. Mean particle

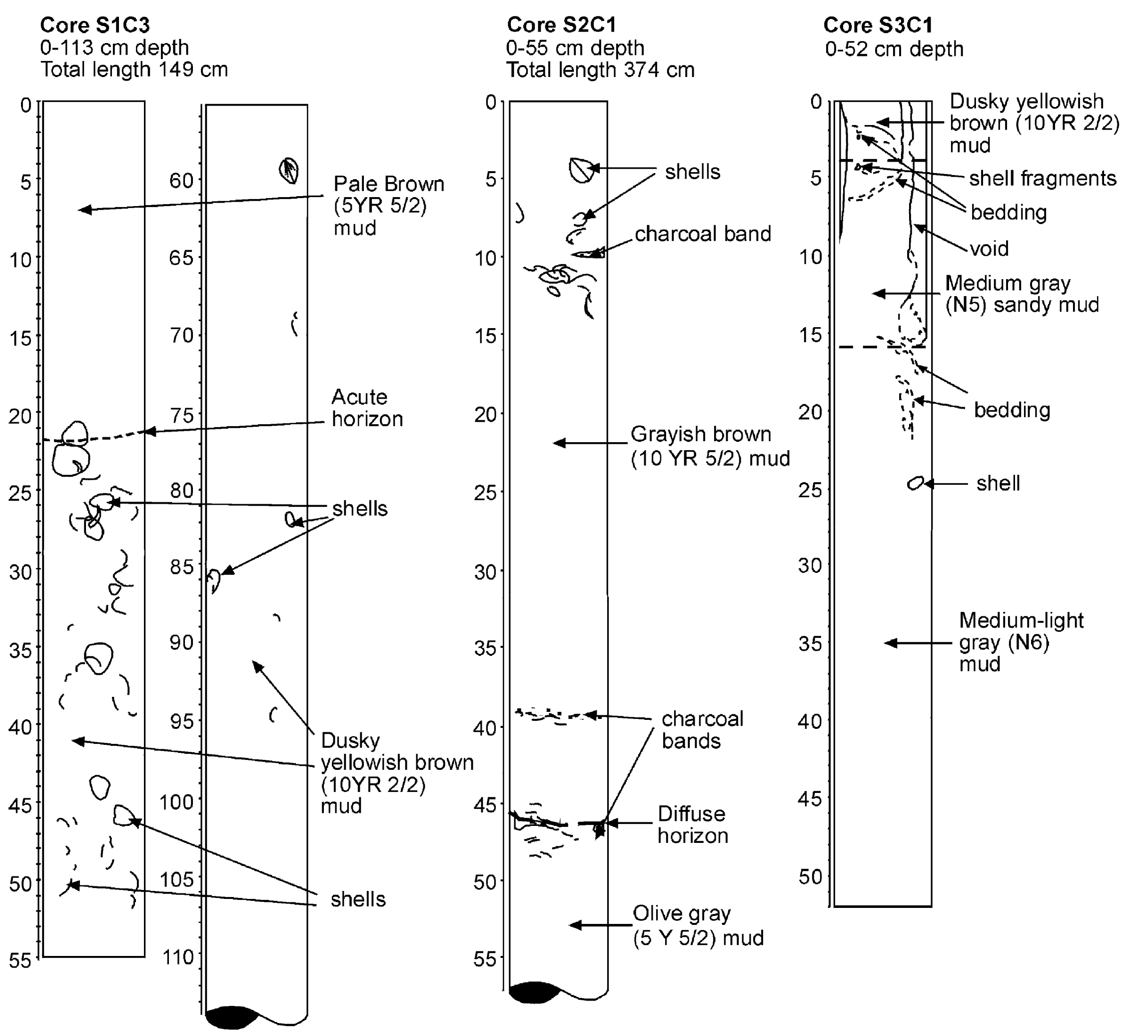

Fig. 3. Line drawings for cores S1C3, S2C1 and S3C, based on X-ray negatives, showing stratigraphic features and the location and abundance of *Corbicula fluminaea* shells. Only the upper sections of cores S1C3 and S2C1 are shown, as the remainder of these cores are highly uniform.

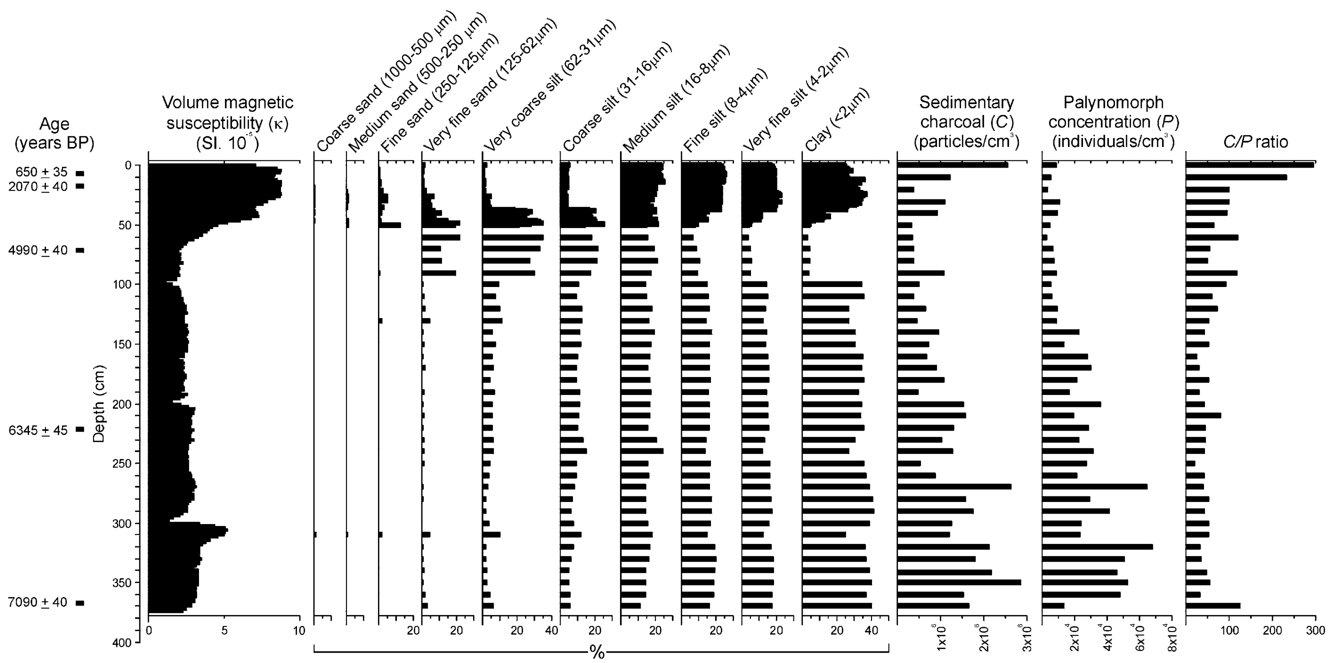

Fig. 4. Sedimentological data, core S2C1. Note that marked decreases in magnetic susceptibility at ca. 1, 2, 3 and 3.7 m depth are due to the MS2C sensor measuring air at the end of each 1 m section of the core.

Table 1
Radiocarbon dating results from core S2C1

Lab. code	Depth (cm)	^{14}C Enrichment (% modern ± 1σ)	δ ^{13}C$_{PDB}$‰ + 0.1	Conventional age (years BP ± 1σ)	Calibrated age (years BP ± 2σ)	Calibrated age (years AD/BC ± 2σ)
AA-39964	6–8	NA	−27	650 ± 35	670–550	AD 1280–1400
CAM-66653	14–18	77.2719 ± 0.30	−25.70	2070 ± 40	2150–1920	BC 200–30
CAM-66654	70–74	53.7075 ± 0.20	−19.40	4990 ± 40	5890–5800 (20.4%) 5770–5610 (75.0%)	BC 3940–3850 (20.4%) BC 3820–3660 (75.0%)
AA-39963	220–222	NA	−24.60	6345 ± 45	7420–7160	BC 5470–5210
CAM-66655	376–370	41.3895 ± 0.20	−25.50	7090 ± 40	7980–7820 (91.2%) 7810–7790 (4.2%)	BC 6030–5870 (91.2%) BC 5860–5840 (4.2%)

size increases markedly above 0.9 m depth to reach a maximum at 0.50 m depth (~61-µm), driven by increases in the proportion of the coarse silt to fine sand fraction.

3.2. Radiocarbon dating

Radiocarbon determinations are presented in Table 1. The chronology thus derived is internally consistent, indicating that the core represents the period 7090 ± 40 BP to the present. The chronology infers a marked and consistent decrease in the rate of sediment accumulation at the core site over time, a pattern that appears consistent across the two lake basins (Penny et al., 2005; Tsukawaki et al., 1997). The relatively slow accumulation rate apparent over the past few millennia makes the impact of well-resolved decadal/centennial scale climate variations (Paulsen et al., 2003; Anderson et al., 2002) on the hydrology of the lake difficult to observe in the sediment record. Equally, information on the interaction between the hydrology of the lake and the dynamics of the great Angkorian civilisation on its northern shore (Harms, 2003) is unlikely to be derived from study of sediment cores from the Tonle Sap. In core S2C1, the entire span of the Classic Angkorian period (AD 802–1431) is recorded in ca. 4.5 cm of sediment accumulation.

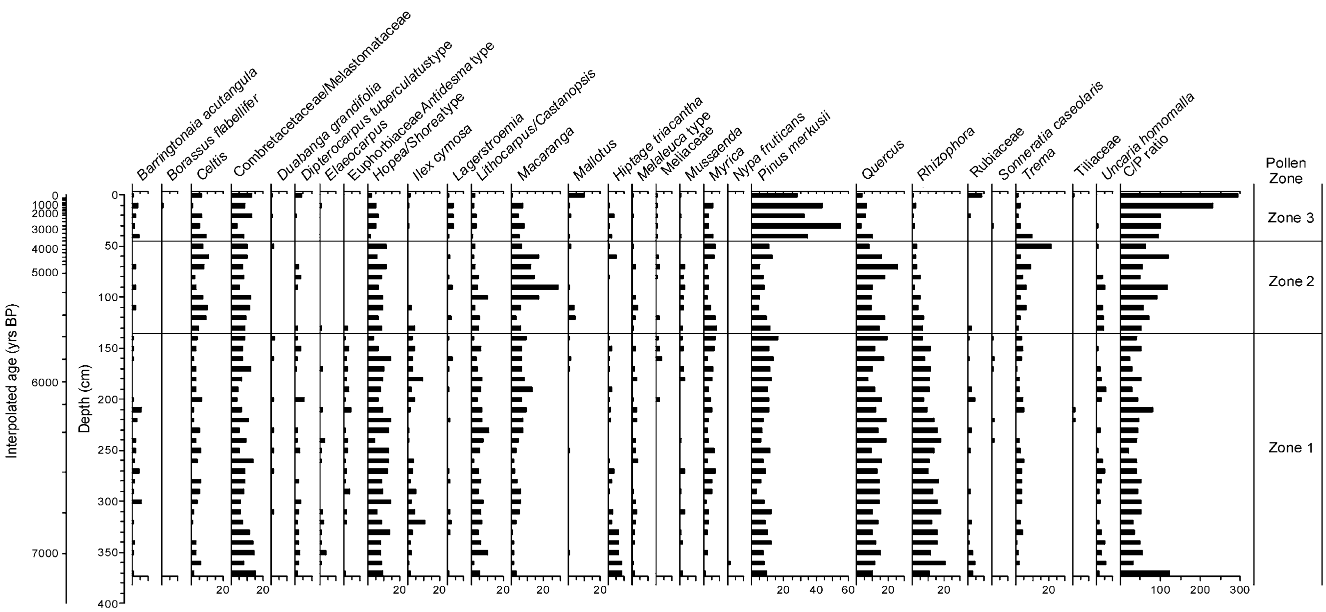

Fig. 5. Selected ($n = 28$) arboreal pollen types and sedimentary charcoal data, core S2C1. Samples groups based on stratigraphically constrained classification of full pollen dataset ($n = 98$).

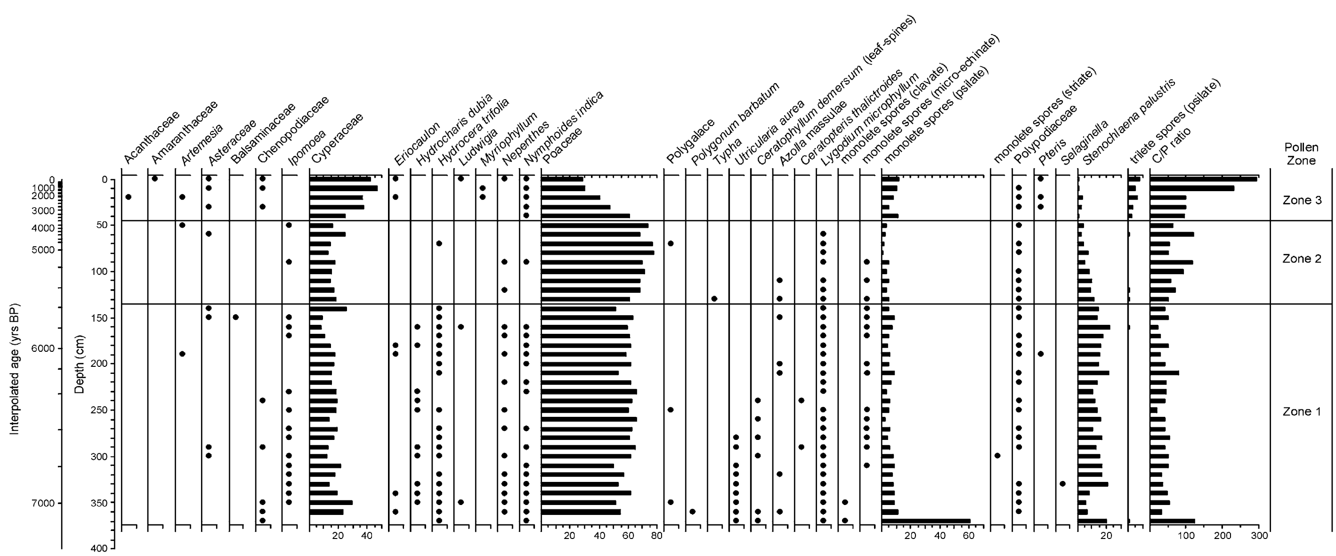

Fig. 6. Non-arboreal pollen types, fern spores and sedimentary charcoal data, core S2C1. Closed circles represent rare taxa that do not exceed 5% of the pollen sum in any sample, and are used here to indicate presence/absence.

3.3. Palynology

Ninty-eight pollen types were recorded in 37 samples, with an average of 513 specimens per sample. Classification of the total pollen data set (Grimm, 1987: Euclidean distance, stratigraphically constrained) indicates three pollen 'zones' (Figs. 5 and 6), which are used here as a basis for description.

3.3.1. Zone 1: 370–140 cm depth

The most common pollen type in this zone is Poaceae, which has an average value of 57% of the secondary pollen sum. Cyperaceae, the epiphytic fern *Stenochlaena palustris* and the monolete (psilate) fern spore group are also common.

The primary pollen sum is dominated by anemophilous pollinators, particularly *Quercus*, *Lithocarpus/Castanopsis* and *Pinus merkusii*, while the common lowland forest elements *Hopea/Shorea* type and Combretaceae/Melastomataceae are also notable. *Rhizophora* (or *Rhizophora*-type *sensu* Muller (1964, pp. 37–38) maintains an average representation of 12.4%, and a maximum value of 20.8% at 360 cm depth, but decreases, with some minor variation, as depth decreases. Sedimentary charcoal concentrations (C/P ratio; Fig. 4) are relatively low and stable, with minor peaks at 370 and 210 cm depth.

3.3.2. Zone 2: 130–50 cm depth

Rhizophora pollen values are lower than the preceding zone (<7%) and demonstrate a declining trend as depth decreases. Similarly, *Stenochlaena palustris* spores decrease in relative abundance by 47% as depth decreases, while taxa such as *Ilex cymosa*, *Antidesma* type (*Antidemsa* sub-type *sensu* Punt, 1961, p. 22) and *Melaleuca* type are absent or sporadic. Both *Macaranga* and *Trema* are more abundant in these samples than at any point in the record, reaching maximum values at 90 and 50 cm depth, respectively. Poaceae pollen is slightly more abundant (an average of 72% of the secondary pollen sum, compared with 57% for zone 1 samples). Charcoal concentrations increase gradually in these samples, with two peaks at 60 and 90 cm depth.

3.3.3. Zone 3: 40–0 cm depth

Poaceae pollen declines dramatically and consistently between 40 and 0 cm depth, from 61% to 29% of the secondary pollen sum, while Cyperaceae and unidentified monolete and trilete fern-spore groups increase. *Pinus merkusii* pollen increases very rapidly at 40 cm depth to become the dominant arboreal pollen type. *Macaranga*, *Trema*, *Hopea* and *Quercus* are all lower than in the previous zone, whereas Combretaceae/Melastomataceae, *Celtis*, *Lithocarpus/Castanopsis* and *Myrica* maintain a comparable representation. *Rhizophora* is very poorly represented (<2% of the primary pollen sum). Charcoal concentrations are relatively high and stable, but increase sharply at 10 cm depth.

3.4. Diatom analysis

Samples prepared for diatom analysis from core S2C1 were in most cases too sparse or poorly preserved to warrant quantitative analysis. This is due presumably to efficient recycling of algal biomass by pelagic zooplankton (MRCS/WUP-FIN, 2003a). However, adequate preservation occurred at 0, 0.05, 2.3, 2.4 and 2.6 m depth, and some qualitative remarks can be made. In all cases, assemblages were overwhelmingly dominated by the euplanktonic colonial genus *Aulacoseira*. Assemblages in the uppermost 5 cm of the core were characterised by *Gyrosigma acuminatum*, *Cyclostephanos tholiformis*, *Surirella elegans*, *Actinocyclus normanii*, and some rare species such as *Fragilaria capucina* and *Nitzschia levidensis*. Samples between 2.3 and 2.6 m depth were less diverse, and characterised by *Thalassiosira bramaputrae* and *Amphora ovalis* var. *lybica*, with rare species including *Staurosira construens* and *Pseudostaurosira brevistriata*.

4. Discussion

4.1. Palaeoclimate and palaeohydrology

Maxwell (2004, 2001), based on pollen cores from Ratanakiri province in northeast Cambodia, concluded that the widely recorded Holocene monsoon maximum (Maxwell and Liu, 2002) became manifest in Cambodia between ca. 8400 and 5300 BP. During this time, water levels in the Ratanakiri lakes increased in response to higher summer monsoon rainfall. Given the regional extent of the monsoon maximum in Asia (Maxwell and Liu, 2002), it is probable that seasonal flow in the Mekong River and its tributaries would also have reached a pre-modern maximum at this point.

In the Tonle Sap pollen record this period of higher and/or less seasonal rainfall is indicated by the presence of a swamp forest community subtly distinct from the modern 'flooded forest' (McDonald et al., 1997). Swamp-forest elements such as *Ilex cymosa*, *Melaleuca* type, and the epiphytic fern *Stenochlaena palustris* imply a different inundation regime in the early Holocene.

The strong presence of pollen from the mangrove *Rhizophora*, in particular, implies a flooding regime quite distinct from the current situation, and may indicate a stronger tidal influence in the lake under higher-than-present sea levels. The coastline during the sea-level maximum penetrated well into southern Cambodia (Nguyen et al., 2000: Fig. 1) and, given the extremely low relief of the lower Mekong River basin, it is quite probable that tidal influence extended inland along the Mekong and Tonle Sap Rivers, and possibly into the Tonle Sap lake itself. Wolanski et al. (1996) claim that tidal influence in the Mekong River during the dry season currently extends some 228 km inland, less than 100 km south of the Tonle Sap River. The extent of tidal influence in central Cambodia is not precisely known as an hourly water-level sampling regime is yet to be fully established. However, recent measurements indicate a daily tidal variation during the dry season of ca. 0.2–0.25 m at Prek Dam on the Tonle Sap River, approximately 60 km upstream of Phnom Penh, and approximately 70 km downstream of the Tonle Sap (Matti Kuumu, MRCS/WUP-FIN Lower Mekong Modeling Project, pers. comm., Feb. 2005). Mangrove communities are known to have maintained a local presence at Angkor Borei in Southern Cambodia during the late Holocene (Bishop et al., 2003), demonstrating the significant influence of saline tidal waters in southern Cambodia even during the regressive sea-level phase when the delta front was ca. 150 km to the south (Nguyen et al., 2000).

Apart from the presence of *Rhizophora*, and other mangal taxa such as *Sonneratia caseolaris* and *Nypa fruticans*, there is no evidence in the palynological data for higher salinities in the early mid Holocene. However, the occurrence of the diatom *Thalassiosira bramaputrae* (syn. *Thalassiosira lacustrus* (Grunow) Hasle, *Coscinodiscus lacustris* Grunow) in samples below 2.3 m depth is unequivocal evidence of brackish water or estuarine conditions (Sato et al., 2001; Ta et al., 2001; Hemphill-Haley and Lewis, 2003), suggesting conditions were indeed suitable for local mangrove growth. The dominance of the modern and fossil phytoplankton by *Aulacoseira* species is, in large part, a result of the huge biomass of algae washed into the lake from the Mekong River during floods, in addition to an autochthonous population. Ta et al. (2001) record its common occurrence in diatom assemblages from the Mekong Delta, indicating it is a common component in the autochthonous phytoplankton of the Mekong River, as it is in other large lowland rivers elsewhere in the world (Hötzel and Croome, 1996).

The relatively high sedimentation rates inferred from the radiocarbon chronology between 7000 and 5500 yr BP, and particularly between 7000 and 6300 BP (25 times the historic rate; Penny et al., 2005) suggest, *prima facie*, larger sediment volumes. However, Ta et al. (2002) have demonstrated that progradation rates of the Mekong Delta were not markedly higher in the early Holocene, and in fact much lower than the period ca. 5–6000 BP where sedimentation rates reached as much as 64 mm a^{-1}. If sediment flux from the Mekong River was controlling sedimentation in the Tonle Sap lake, an *increase* in sedimentation would be expected in the middle Holocene, rather than a clear and consistent decrease.

It has been shown that, despite recent sedimentation rates in the Tonle Sap being less than 1 mm a^{-1} (Penny et al., 2005), the lake and surrounding wetlands retain more than 80% of the ca. 5.7 M tons of annual suspended sediment flux from the Mekong River (MRCS/WUP-FIN, 2003a), indicating that the bulk of sediment carried into the lake from the Mekong settles out in the sheltered littoral areas and in extensive riparian floodplains, and that the net sedimentation rate within the lake basins is controlled more by the re-entrainment of particles during the flood-recession phase than by changes in sediment volume. Given this, and the evidence for relatively stable sediment flux from the Mekong River during the Holocene (Ta et al., 2002), it is probable that the falling rates of sediment accumulation in the lake basin from the middle Holocene indicate higher rates of sediment re-suspension from the lake bed during the dry season recession phase, and thus lower *net* sedimentation. This, in turn, suggests changes in the depth of mixing in the water column driven by changes in wind strength, a fall in lake levels or an increase in the amplitude of seasonal variation in lake levels.

Dramatic changes are apparent in both the pollen record and particle size data at and above 1.0 m depth in the core, from an interpolated age of approximately 5200 BP. Pollen of *Macaranga*, a well-known indicator of disturbance in terrestrial environments (Kuusipalo et al., 1996), increases markedly, while increases in corrected charcoal particle concentrations infer changes in the regional fire regime. The increased relative abundance of Poaceae pollen from 1.0 m depth may be, in part, driven by this change in fire regime. Almost identical evidence is apparent in the northeast of Cambodia (Maxwell, 2004, 2001), and northeast Thailand (White et al., 2004; Kealhofer and Penny, 1998), where increases in secondary forest taxa, grasses, and burning occur from ca. 5300 and 5500 BP, respectively. This is interpreted by Maxwell (2004, 2001) as evidence of a shift toward a more seasonal and seasonally drier environment as the relative influence of the southwest (wet) monsoon weakened, a claim supported by increasing seasonality of sea surface temperatures in the South China Sea after ca. 5000 BP (Huang et al., 1997).

Marked changes in the composition of the floodplain vegetation are also apparent from the middle Holocene. *Rhizophora* begins to decline from ca. 5600 BP (140 cm depth), while successional changes in the herbaceous floodplain vegetation are implied by a sharp increase in Cyperaceae pollen and the disappearance of several aquatic types (*Ipomea*, *Hydrocharis dubia*, *Hydrocera trifolia*, *Nepenthes* and *Nymphoides indica*). The gradual decline of the climbing fern *Stenochlaena palustris* and the disappearance from the record of *Ilex cymosa* are particularly noteworthy. These plants do not exist in the modern 'flooded forest' due to the amplitude of seasonal inundation, which can be as large as 8 m, and completely submerges the canopy for several weeks to months (McDonald et al., 1997). Successional change in floodplain vegetation around the lake from ca. 5600 BP (140 cm depth) is strong evidence of a shift in the lake's flooding regime toward larger seasonal contrasts in lake levels driven by a decline in the relative influence of the southwest monsoon.

Mean mineral particle size of core S2C1 increases coincidently with the onset of this period of relatively weak southwest monsoon influence and increased seasonality, reflecting a greater proportion of coarse-silt to fine-sand sized clasts deposited at the core site. This is consistent with deeper and more energetic mixing of sediments associated with the development of more variable lake levels from the mid Holocene under a drier and more seasonal climate. Carbonnel and Guiscafré (1965) documented identical particle size profiles from their cores GC8 and GC1 (Fig. 2), indicating this phenomenon was contiguous across the two lake basins.

Peaks in *Quercus* and *Trema* at 70 (interpolated age of ca. 4900 BP) and 50 cm depth (interpolated age of ca. 3800 BP), respectively, suggest continued successional changes in the dryland flora in central Cambodia into the late Holocene. The dramatic increase in the relative abundance of *Pinus merkusii* pollen from ca. 3300 BP (40 cm depth), almost certainly a reflection of vegetation change in regional uplands around the lake, is noteworthy. Of the four pine species known to occur in Southeast Asia, *P. keysia* and *P. merkusii* are the most common, while *P. dalatensis* and *P. krempfi*, both endemic to the highlands of southern Vietnam, have a highly restricted distribution (Richardson and Rundel, 1998). In Cambodia, only *P. merkusii* is widespread, and is best represented to the west of the Mekong River, in uplands around the Tonle Sap (Rollet, 1972). In mainland Southeast Asia, *P. merkusii* is fire-tolerant plant, capable of colonizing exposed, nutrient poor soils in markedly seasonal environments, and in some instances is known to have aggressively expanded its range as a result of anthropogenic burning (Goldammer and Peñafiel, 1990; Stott, 1976). *Pinus* is also known to have been distributed more widely throughout Indochina in the past, under markedly cooler and drier climates when wildfires were common (Penny, 2001; Werner, 1997). The increase in *Pinus* pollen from ca. 3300 BP probably reflects an expansion of its range under seasonal climates and increasingly widespread fires. The increasing concentration of microscopic charcoal particles through the late Holocene, which derive predominantly from regional sources, is consistent with this.

4.2. Development of the lake and wetlands

Tsukawaki and co-workers (Tsukawaki et al., 1997; Tsukawaki, 1997, 1998, 2000, 2002) have proposed a model for the development of the Tonle Sap system during the Holocene, based on numerous sediment cores across the two lake basins. They claim that changes in stratigraphy (colour and compactness), clay mineralogy (increased proportion of illite) and sedimentation rates (falling) from ca. 5500–5000 BP represent the formation of a single, large fluvial lake within the Tonle Sap basin, triggered by the establishment of a connection between the Tonle Sap and Mekong Rivers as the Mekong River migrated westward under the influence of the Holocene sea level maximum. Prior to this substantial geomorphic and hydrological rearrangement, a chain of smaller lakes, presumably linked by extensive wetlands, filled the basin. Under this model, the highly interdependent relationship between the Mekong River and the Tonle Sap lake began in the mid-Holocene, and its unusual flooded forest ecosystems are presumably of the same antiquity.

The data presented here, and careful consideration of the existing data, refute this model. The presence of *Rhizophora* pollen in the sediments of the Tonle Sap is significant. The identification of this pollen type as *Rhizophora* rather than Rhizophoraceae (including similar forms from *Bruguiera*, *Ceriops* and *Carallia*) is confidently made, and detailed comparison with pollen reference samples from the terrestrial/freshwater genus *Carallia* (*C. brachiata*, *C. borneensis*, *C. calophylloidea*, *C. eugenioidea*) indicate the two are unlikely to be confused (see also Muller, 1964). *Rhizophora* has a relatively narrow ecological tolerance in terms of salinity, temperature and period of inundation, and is therefore closely tethered to the coastal front (Blasco et al., 1996), and those inland rivers influenced by the intrusion of saline and tidal waters. If its presence in the lake, or as a riparian fringe along tidal rivers feeding the lake, under higher-than-present sea levels is to be inferred from the pollen data, then a permanent connection to the South China Sea via the Mekong Rivers must have been apparent from the early Holocene.

It is possible that the *Rhizophora* pollen in the Tonle Sap sediments is indicative of long distance wind transport from the Mekong River delta prior to and during the Holocene high sea level. However, *Rhizophora* does not contribute significantly to regional pollen rain (Blasco et al., 1996), and maintains a close relationship between pollen abundance and source vegetation (Crowley et al., 1994). Species of *Rhizophora* occurring in Singapore are given low (*R. apiculata*) to medium (*R. mucronata*) relative pollen 'export ability' (Taylor et al., 2001), reflecting predominantly local or near-local deposition. Van der Kaars (2001) reports that ''mangrove pollen grains are not exported widely from their source area'' (p. 344) based on analysis of surface marine sediments in eastern Indonesian waters.

Crowley et al. (1994) suggest that the local (i.e. on site) occurrence of mangrove forest is indicated by values of its pollen exceeding 50% of the pollen sum, and that these values fall with distance from the mangrove communities. However, *Rhizophora* pollen can be under-represented even within *Rhizophora* communities (ca. 9%; Phillips et al., 1997). In the Tonle Sap pollen record, *Rhizophora* reaches a maximum representation of 20.8% of the arboreal pollen assemblage, and averages 14.2% between 370 and 240 cm depth, ca. 7900–7300 yr BP (an average of 866 individuals per cm^3). Clearly, these values are not sufficient to indicate the growth of *Rhizophora*-dominated communities on or near the core site, though the apparent localised pollen distribution of the genus and the current distance of the core site to the nearest shore (19–20 km) is suggestive of mangroves if not in the margins of the lake itself, then certainly within the Tonle Sap/Mekong Rivers. In concert with diatom evidence for higher salinities in the lake in the early Holocene, the presence of mangrove pollen in the sediments of the Tonle Sap indicate conclusively a connection with the Mekong River and the South China Sea during the early Holocene. Indeed, McDonald et al. (1997) observe that, in terms of its structure and composition, the modern flooded forest of the Tonle Sap retain "a decided feel and look of a marine system" (p. 14).

Many shells of the Asiatic clam *Corbicula fluminaea* were apparent in the sediment of the Tonle Sap. Most of these individuals were in excellent state of preservation, fully articulated (see the individual at ca. 0.04 m depth in S2C1 X-radiograph, Fig. 3), and with the periostracum intact. *C. fluminaea*, which has a motile larva that allows the species to migrate rapidly upstream along water-courses (Britton and Morton, 1986), is recognised an aggressive colonial organism outside of Asia. The biogeography of *C. fluminaea* in the Tonle Sap, then, might be instructive in terms of the timing of regional hydraulic connections that would have acted as a pathway for migration from the Mekong River. The earliest appearance of *C. fluminaea* is at 0.94–0.95 m depth in S1C3, very close to the Tonle Sap River mouth (Figs. 2 and 3), which dates to ca. 6100 BP (this age estimate is interpolated between peaks in magnetic susceptibility that can be correlated to the directly dated S2C1 core). It appears somewhat later in S2C1, after 2100 BP (CAM66653; Table 1), and not until 1400 BP at S3C1 (interpolated age). This pattern of occurrence across the Tonle Sap basins may reflect the migration of *C. fluminaea* into the lake from Mekong River from the middle Holocene, which necessitates a permanent connection between the lake and the Mekong River that predates the mid-Holocene sea level maximum. Whether the timing of this migration represents the first establishment of this connection, is a response to falling salinities in the Tonle Sap (Morton and Tong, 1985), or is merely the natural spread of this species from northern Asia along pre-existing hydrological networks, is unknown.

The relative uniformity of sediment type and the consistent stratigraphy across the lake basins (Carbonnel and Guiscafré, 1965; Tsukawaki et al., 1997; Tsukawaki, 2002; Penny et al., 2005) strongly suggest a single contiguous water body throughout the Holocene, rather than a chain of smaller lakes surrounded by extensive wetlands. Despite more than 30 cores taken from the lake basin (Tsukawaki, 2002; Carbonnel and Guiscafré, 1965; this study; Fig. 2), there is no evidence of pedogenesis, redox features, or the deposition or organic sediments that would be consistent with a floodplain in a seasonal tropical environment. There is certainly no evidence in the pollen data to indicate a period of extensive freshwater marsh in the early Holocene. Moreover, the dominance of the diatom *Aulacoseira* in early Holocene sediments indicates very turbid conditions, indicative of either a large lake with sufficient fetch to generate the turbulence, or a allocthonous source, which also necessitates a connection to the Mekong River.

Tsukawaki (1998) describes an increase in illite in the sediments of the lake from the middle Holocene. Illite, a common component of the suspended load of Asian rivers, including the Mekong (Heroy et al., 2003; Tamburini et al., 2003), is abundant in the lake and the Tonle Sap River, but was absent from terrestrial alluvial deposits around the lake, and in a local river. Illite, then, is thought to derive exclusively from the Mekong River basin. Tsukawaki (1998) claims that the absence of illite in the "lower halves of two cored sediments" (p. 57), is evidence of local rather than regional sediment sources prior to the middle Holocene. It is difficult to assess these claims, however, as the spectra from the cores have not been published fully, and are described vaguely. Increases in illite sedimentation from the middle Holocene might be equally well explained by a change in the intensity of hydrolysis associated with changes in lake water chemistry (particularly salinity) in the wake of regressing sea levels and a lower and more seasonal distribution of annual rainfall.

5. Conclusions

The data presented here demonstrate substantial change in the hydrodynamics of the Tonle Sap lake and the vegetation of its catchment as a result of monsoon variability and sea-level fluctuations during the Holocene. During the period >7000 to ca. 5500 ^{14}C yr BP the Tonle Sap exhibited less seasonal variation in depth, and supported littoral swamp-forest communities that were subtly different from their modern equivalents. The lake was clearly influenced by tidal and saline waters in the early to middle Holocene, coinciding with the sea level transgression of >2.5 m that inundated southern Vietnam and parts of southern Cambodia (Nguyen et al., 2000). Despite this sensitivity, the projected rise in global mean sea level of 0.09–0.88 m (Houghton et al., 2001) is unlikely to directly affect the ecology of the Tonle Sap to the extent apparent in the middle Holocene, but even relatively minor increases in mean sea level are likely to change the extent of flooding in southern Cambodia and extend tidal influence further inland from the Mekong Delta, particularly in the dry season. The data presented here indicate that lake levels became more variable as a result of decreased rainfall and increased seasonality from the middle Holocene. Predicted increases in early monsoonal rainfall (Nijssen et al., 2001) are likely to result in more rapid, and possibly more extensive flooding in the lower Mekong Basin. If seasonality becomes more marked then the amplitude of lake level fluctuation is likely to be more pronounced, possibly triggering the readjustment of floodplain vegetation to a new inundation regime. This is of particular significance if the *Barringtonia acutangu-*

la/*Diospyros cambodiana* 'flooded forest' is forced to migrate landward where it will come into conflict with increasing land use pressure. The possibility that changes in flood magnitude and duration may encourage the growth weed species (*Mimosa pigra*, *Pistia stratiotes*, *Salvinia molesta*, *Eichhornia crassipes*) has already been noted (MRCS/WUP-FIN, 2003b). The flooded forests are of enormous conservation value, particularly in terms of the rejuvenation of fish stock within the lake and the Mekong River (Bonheu and Lane, 2002), and possible changes in the distribution or composition of these riparian forests as a result of climate change requires careful consideration.

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