

THE IMPACT OF GRAZING BY *NEOTRICULA APERTA* (GASTROPODA: POMATIOPSIDAE) ON POST-SPATE RECOVERY OF THE ALGAL AUFWUCHS IN THE LOWER MEKONG RIVER: CHANGES IN STANDING CROP AND SPECIES DIVERSITY

*Stephen W. Attwood*¹

ABSTRACT

Field work was carried out in habitats of the epilithic schistosome-transmitting snail *Neotricula aperta* (gamma race) along the Mekong River in Northeast Thailand and southern Laos.

Changes in algal standing crop and species diversity were followed for the epilithic aufwuchs community throughout the annual flood-drought cycle of the Mekong River. The impact of grazing by *N. aperta* (gamma race) on the algal aufwuchs was also assessed. Comparisons were made between habitats at Ban-Khi-Lek (Thailand), an area free of human schistosomiasis, and at Ban-Xieng-Wang, a site of endemic transmission of schistosomiasis *mekongi* in southern Laos.

The aufwuchs at Ban-Xieng-Wang appeared less diverse than that at Ban-Khi-Lek, however, a greater biomass was achieved at Ban-Xieng-Wang. The greater availability of algal food in southern Laos may explain the greater *N. aperta* population densities there and possibly the transmission of schistosomiasis in that region.

At Ban-Khi-Lek, a marked reduction in (epilithic) algal biomass was observed during the high water (spate) period, with rapid recovery of biomass and diversity in the early low water period.

Species diversity of the algal aufwuchs appeared to be higher in *N. aperta* microhabitats than elsewhere along the river bed; however, the converse was true during the spathe period.

INTRODUCTION

Spate (flood) events can be important in regulating biomass (or standing crop) and composition of the algal aufwuchs in lotic systems (DOUGLAS, 1958; FISHER & GRIMM, 1988; ELBER & SCHANZ, 1990) and can effect marked reductions in cell densities. However, these communities appear to be highly resilient and can recover rapidly from such disturbance (HOAGLAND ET AL., 1982; GRIMM & FISHER, 1989). Many studies have examined benthic algal recovery following spates (eg. POWER & STEWART, 1987; BIGGS & CLOSE, 1989; GRIMM & FISHER, 1989; PETERSON & STEVENSON, 1990); however, few have examined

¹ School of Biological Sciences, Queen Mary & Westfield College (University of London), Mile End Road, London E1 4NS.

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the impact of grazing on this recovery. The almost exclusively epilithic, tropical freshwater snail *Neotricula aperta* (TEMCHAROEN, 1971) inhabiting the lower Mekong River provides a useful model for study in this context. The stream flow of the Mekong River shows marked seasonal variations (Fig. 1). Generally, the river rises following the onset of the southwest monsoon in mid-May and the maximum level is achieved in September or October (DAVIS ET AL., 1976; KITIKOON & SCHNEIDER, 1976; DAVIS, 1979; ATTWOOD, 1995). The onset of the spate in the lower Mekong is predictable, allowing severe flood conditions to be foreseen; this is rarely the case in temperate climates (ELBER & SCHANZ, 1990). In addition, *N. aperta* is annual and semelparous (ATTWOOD, 1995), with new snails hatching in March (early low water). This situation allows the simultaneous development of a herbivorous fauna and an epilithic algal flora to be observed following a major spate event.

N. aperta, gamma race, is the natural snail host of *Schistosoma mekongi* Voge, Bruckner & Bruce 1978 (Trematoda: Schistosomatidae), responsible for human schistosomiasis in the Lower Mekong Basin. *N. aperta*, gamma race, is found along the Mekong river in Northeast Thailand, southern Laos, Kampuchea and (probably) Vietnam. In spite of the wide geographical range of the gamma race of *N. aperta*, a site at Ban-Xieng-Wang (BXW), Khong Island in southern Laos, remains the only documented endemic focus of human schistosomiasis *mekongi* (see SORNMANI ET AL., 1971). Consequently, it was felt that an investigation of the habitat conditions in Northeast Thailand and in southern Laos might reveal factors explaining schistosomiasis endemicity in southern Laos.

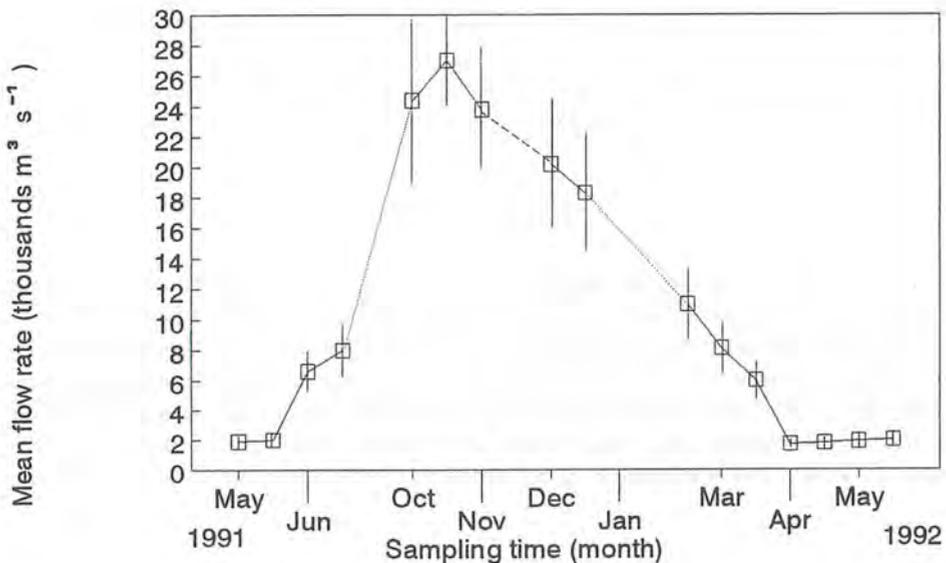


Figure 1. Semi-monthly measurements of flow rate for the Mekong River at Ban-Khi-Lek, Thailand. Data are mean \pm S.D., $n = 6$. Missing data = (...). After Attwood (1995).

METHODS

Study Localities and Sampling Techniques

Field work was carried out on the Lao-Thai border at Ban-Khi-Lek (BKL) (16°2'33"N; 105°18'27"E), a series of rock islands in the Mekong River about 8 km downstream of Khemmarat, Ubon Ratchathani Province, Northeast Thailand. The second site lay 270 km down river, south of Khemmarat, on Khong Island, Champassac Province, southern Laos. The samples were taken from the southeastern limit of the island at BXW (14°6'30"N; 105°51'45"E). Factors of inaccessibility, difficulty in obtaining travel permits and a lack of security limited the number of samples taken in Laos. Samples were taken at intervals (roughly semi-monthly during low water periods and bi-monthly at other times) over the period May 1991 to May 1992. The aufwuchs was sampled from the upper peripheral surfaces of stones collected at random from the 0.1 to 0.7 m water layer. Stones bearing *N. aperta* at densities > 10 m⁻² were denoted as SN+ stones, whilst those bearing no *N. aperta* (and few snails of other species) were denoted as SN- stones. *N. aperta* tended to dominate the invertebrate fauna of those stones upon which it occurred.

A disposable apparatus was constructed to remove the algae (aufwuchs) from a known constant area (approx. 4 cm²) on the upstream periphery of the upper surface of each stone collected. The apparatus consisted of a 20-ml (disposable) syringe the nozzle of which had been cut off and replaced by a rubber ring to form a seal with the substratum. The head of a small toothbrush was attached to the end of the syringe plunger, so that the brush could abrade the substratum through the opening of the decollated syringe. The apparatus was replaced between each stone collected. To obtain a sample, a stone was lifted from the habitat and immediately transferred (still submerged) into a tray. The tray was gently lifted from the water and the rubber ring of the sampler placed hard against the stone, whilst the plunger was rotated three times to dislodge the aufwuchs. The plunger was then withdrawn to fill the syringe with ca. 1 ml of water from the tray. The syringe and stone were then removed from the tray and both inverted with the syringe still *in situ*. The stone was removed and the particles of epilithic material allowed to settle in the syringe for 5 min after which the plunger was depressed expelling the supernatant. The aufwuchs sample was then carefully washed into a glass vial of 1 ml FAA (formalin-acetic acid: 50% 95%-ethanol, 35% distilled water, 10% formalin and 5% glacial acetic acid; after PRESCOTT, 1954). As the phytoplankton density in the river was not high, its contribution to the sample, from the small volume of water in the syringe, was judged to be negligible; this judgement was based upon controls in which 20 ml of river water was filtered and the chlorophyll content of the filtrate found to be below the sensitivity of the assay procedure given below.

Additional aufwuchs samples, taken following the above method, were also suspended in 15 ml of sterile dilution water (APHA, 1980) (see Table 1 for composition). A 25-mm syringe filter holder (Gelman Type 316 with Delrin-acetal resin body, stainless steel support screen and Viton O-ring) containing a 0.2 µm Whatman (WCN) membrane filter was used to filter 10 ml of the aufwuchs suspension. On the rare occasions where samples contained much coarse material, a 2.7 µm GF/D membrane pre-filter was also used. The filter(s) bearing the samples were placed in small vials containing 0.2 ml magnesium carbonate suspension (1.0 g in 100 ml distilled water) and frozen ready for transport to Bangkok.

Table 1. The composition of the "cell dilution water" (following APHA., 1980).

Component	Quantity
Phosphate buffer:	
KH ₂ PO ₄	34.0 g / 500 ml distilled water (adj. to pH 7.2 with 1N NaOH), diluted to 1 l, then diluted 1:25
Final solution (l ⁻¹):	
Phosphate buffer	1.25 ml
MgSO ₄ .7H ₂ O (50 g l ⁻¹)	5.00 ml

Estimation of Chlorophyll Concentration

As an indicator of algal biomass (excluding necromass) the chlorophyll a content was determined spectrophotometrically after extraction with 90% acetone ("Trichromatic" method), following STRICKLAND & PARSONS, (1968) except that the remains of the WCN filter were removed soon after addition of the acetone. The samples frozen in magnesium carbonate (see above) were used for the estimation of chlorophyll a. On arrival in the laboratory, and immediately prior to the assay, the filter and filtrate were macerated in 90% acetone. The reliability of the extraction was monitored by extraction of 2.4 mg l⁻¹ control suspensions of the blue-green alga *Spirulina*. The controls gave a mean chlorophyll a concentration of 1.6 ± 0.1 % (\pm S.D., n=7) of the dry weight including ash for *Spirulina*, which compares well with reported values of around 1.7% for blue-green algae (MCCONNELL & SIGLER, 1959).

Sample Transport

After collection the samples were stored in a refrigerator. All samples were transported to the laboratory in Bangkok by road, in insulated boxes containing ice, within five days of collection. On reaching the laboratory all samples were stored in a refrigerator at 4 °C (except for the chlorophyll samples which were kept frozen). The maximum storage period was 30 days.

Counting Technique

In order to minimise errors a standard counting procedure was followed throughout the study. Estimates of algal cell densities were made by means of haemocytometer counts. The counts were made for aliquots of the 1 ml suspensions of aufwuchs material in FAA. Each aliquot was withdrawn into a glass pipette after the sample had been mixed by inverting the vial 15 times. The ca. 0.1 ml aliquot was pipetted under one corner of the coverslip on the (tilted) haemocytometer. The graduated centre of the haemocytometer chamber formed a counting field volume of 0.1 µl. The entire counting field was examined at x400 and a single scan covering the entire counting field is here called a "run". The samples were examined using an Olympus BH-2 light microscope with WHK 10x/20L

eye-pieces and (for high power) a D-plan 40 objective (0.65, 160/0.17). The chamber was refilled with a fresh aliquot between each run. The natural cell density in the samples was found to be acceptable and concentration techniques were not required. The count for each taxon was taken as the number of squares in which it was present during each run (the counting field was divided into 25 smaller squares) and so the counts may be regarded as estimates of bio-volume. The counting unit used was the natural unit or "clump" count (APHA 1980); that is any unicellular organism, natural colony or filament represented a single count where it occupied only one square.

In order to balance accuracy with economy, 30 runs were counted per sample stone. Studies of the accuracy of sampling with the Sedgwick-Rafter counting cell indicated that this level of replication should reveal 90–95% of the species present (MCALICE, 1971). In general, on each sample date, five SN+ stones and five SN- stones were sampled. Each set of five stones, and the associated 150 runs, were taken as five observations and converted to an estimate of mean bio-volume as number of natural units μl^{-1} ($n=5$).

Identification of the algae followed MIZUNO (1981) for the Chrysophyta and SMITH (1933) for the Chlorophyta and Cyanophyta.

Sources of Error

The above procedure clearly constitutes a 2-stage sampling technique (COCHRAN, 1963). Accordingly, the sampling procedure sought to achieve uniformity in terms of stone type (size and texture) and number of twists of the sampling brush etc. Sources of error at the secondary level include failure to achieve random suspension within the sample vial (eg. filamentous members of the Ulotrichales and Zygnematales were more difficult to suspend than the diatoms) and losses during transfer of the material to the chamber. As the grade of the epilithic deposit varied over the year, on a small number of occasions (when large particles were common) there were problems filling the pipette and counting chamber.

RESULTS

The data for BKL (Thailand) show a marked decrease in algal standing crop (bio-volume or biomass) at the onset of spate conditions in mid- to late June (see Fig. 2). The fall in biomass in the mid-April (1992) sample was probably due to a general reduction in the haptobenthos following a severe storm on 4 April 1992. The rapid recovery of the algal populations following the main annual spate (July–January) and the storm in April (Fig. 2) demonstrates the considerable potential for algal colonisation/recruitment in these habitats. Figure 3 shows that during the low water period (mid-April to late May) SN+ stones supported a greater algal standing crop than did stones bearing no *N. aperta*, however, during the late spate period (December–January) this relationship was reversed. The biomass data for BXW, although limited, did not show any significant difference from those for Thailand.

The chlorophyll content of algal species is reported to be fairly constant (SLÁDECEK & SLÁDECKOVÁ, 1964) and does not differ markedly between the various algal groups involved here (range 1–2% for green and blue-green algae, MCCONNELL & SIGLER, 1959),

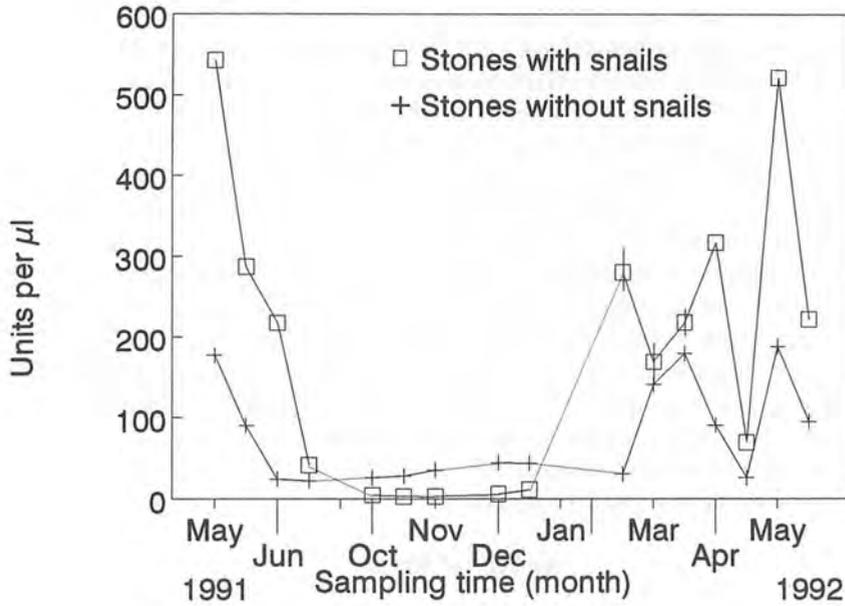


Figure 2. Seasonal variation in the standing crop (based upon algal cell counts of a 1 ml suspension of aufwuchs removed from a 4 cm² area of stone surface) of algae on stones collected from the Mekong River at Ban-Khi-Lek, Thailand. Data are mean \pm S.D., n=5 (stones). Missing data = (...).

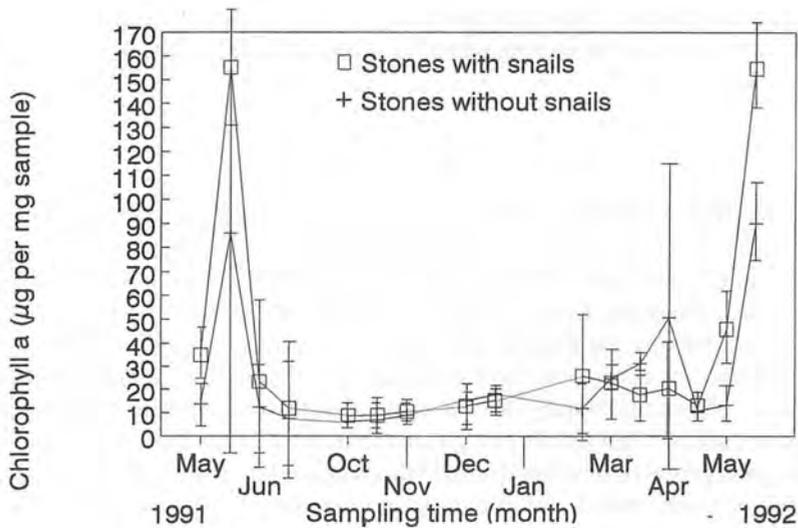


Figure 3. Seasonal variation in the algal standing crop (as μg chlorophyll a per mg of aufwuchs sample) on stones collected from the Mekong River at Ban-Khi-Lek, Thailand. Data are mean \pm S.D., n=5 (stones). Missing data = (...).

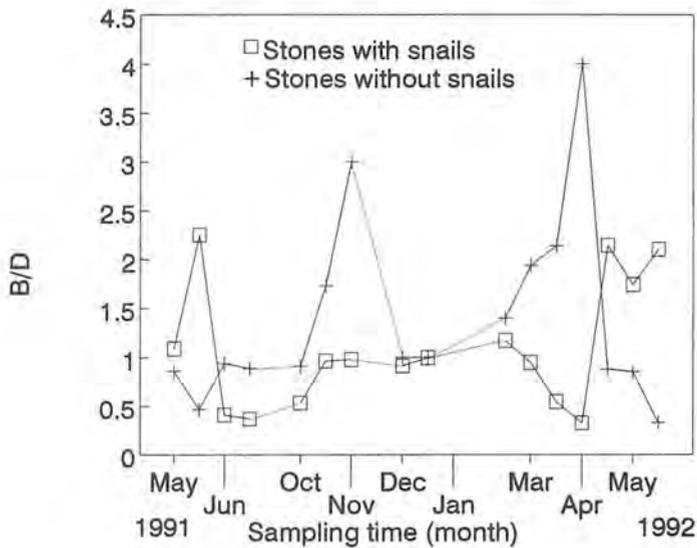


Figure 4. Variation in the Blue-green algae/Diatom (B/D) quotient for aufwuchs samples taken from stones in the Mekong River at Ban-Khi-Lek, Thailand. Missing data = (...).

as such it is considered to be a better indicator of (viable) algal biomass than are cell counts or bio-volume estimations (SLÁDECKOVÁ, 1962). However, in the present study seasonal variations in chlorophyll content (Fig. 3), for both SN+ and SN- stones, generally reinforced those trends evidenced by the direct counts data. Chlorophyll concentrations at BXW in late March 1992 (Table 2) indicated that the algal biomass might be significantly less than that at BKL at the same time of year (and for both stone types); however, this difference might have been due to a loss of chlorophyll during sample transport from the more remote site BXW, especially as the corresponding direct counts were less distinct.

The most obvious seasonal change in the epilithic aufwuchs of the Mekong River was the physiognomic succession. The succession began in early January with almost bare rock, however, the stones were soon colonised by a mixture of *Phormidium* and *Oscillatoria* species (Cyanophyta) which formed a thin but resilient dark green coating over the stones (February to March). In early May short tufts of *Cladophora* and *Spirogyra* were found on the peripheries of the stones that faced into the current. The succession was terminated in late May by the onset of high water but by that time stands of long, stringy filaments of *Rhizoclonium* (often up to 1 m in length) had developed on the stones.

The relative proportions of the two main algal groups present, the blue-green algae (Cyanophyta: Myxophyceae: Hormogonales) and the pennate diatoms (Chrysophyta: Bacillariophyceae: Pennales), were investigated as the quotient of their respective bio-volumes (B/D-quotient, blue-greens/diatoms). The results indicated a marked difference between SN+ and SN- stones in terms of B/D-quotient. The data (Fig. 4) revealed that the

Table 2. Summary parameters describing the algal epilithon from *Neotricula aperta* microhabitats (SN+) and from relatively snail-free substrata (SN-). All samples were taken from the Mekong River at Ban-Xieng-Wang, southern Laos. Where appropriate the associated standard deviations accompany the data (Chla = Chlorophyll a; H = Shannon-Weaver diversity). The data are reported to 3 significant figures.

Parameter	7 January 1992		28 March 1992	
	SN+	SN-	SN+	SN-
Cell density (units μl^{-1})	59.4 \pm 0.96	44.6 \pm 2.67	140 \pm 3.67	190 \pm 5.61
B/D-quotient	0.95	1.00	2.10	1.95
Chla content ($\mu\text{g mg}^{-1}$)	19.0 \pm 21.6	32.2 \pm 31.8	15.7 \pm 14.5	6.84 \pm 5.02
H	4.02	1.98	3.13	4.23
Species richness	26	12	78	29
SIMI (SN+ <i>cp.</i> SN-)	-0.13-		-0.50-	

early low water aufwuchs of SN+ stones was dominated by diatoms (low B/D-quotient), however, as low water conditions continued the cyanophytes became increasingly dominant. Throughout the spate the SN+ aufwuchs was dominated by diatoms and Cyanophyta were relatively scarce. The seasonal variation in B/D-quotient for SN- stones was the converse of that for SN+ stones. SN- stones appeared to be dominated by cyanophytes during spate periods and by diatoms during late low water. The data for BXW (Table 2) showed less marked differences in B/D-quotient between stone types than did those for BKL. In addition, throughout the high water to low water transition at BXW, B/D-quotient values remained close to unity whilst those at BXW showed considerable variation. These observations might be the result of less marked fluctuations in hydrological conditions at BXW, although the data set at BXW was much smaller than that at BKL and trends were difficult to discern.

Algal species richness (number of different taxa present) for habitats at BKL (Fig. 5), like algal biomass, fell markedly during the spate and recovered rapidly after the return of low water conditions. Species diversity (as the Shannon-Weaver diversity index (H), described by MARGALEF, 1969; Fig. 6), species richness and biomass data for BKL all showed higher values for SN+ stones during the post-spate recovery and early low water periods and relatively higher values for SN- stones at the height of the spate (October–November). Minor fluctuations in species diversity (probably due to storms) occurring outside the main annual spate appeared to be less marked on SN+ stones than on SN- stones (Fig. 6). The attenuation of these fluctuations in species diversity on SN+ stones

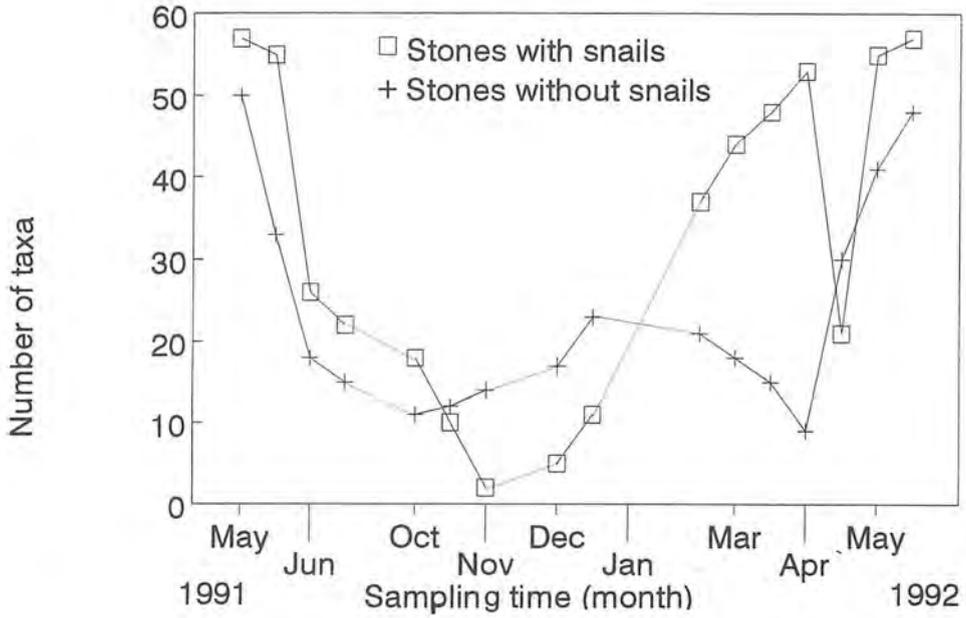


Figure 5. Seasonal variation in algal species richness for the epilithic aufwuchs in the Mekong River at Ban-Khi-Lek, Thailand. Missing data = (...).

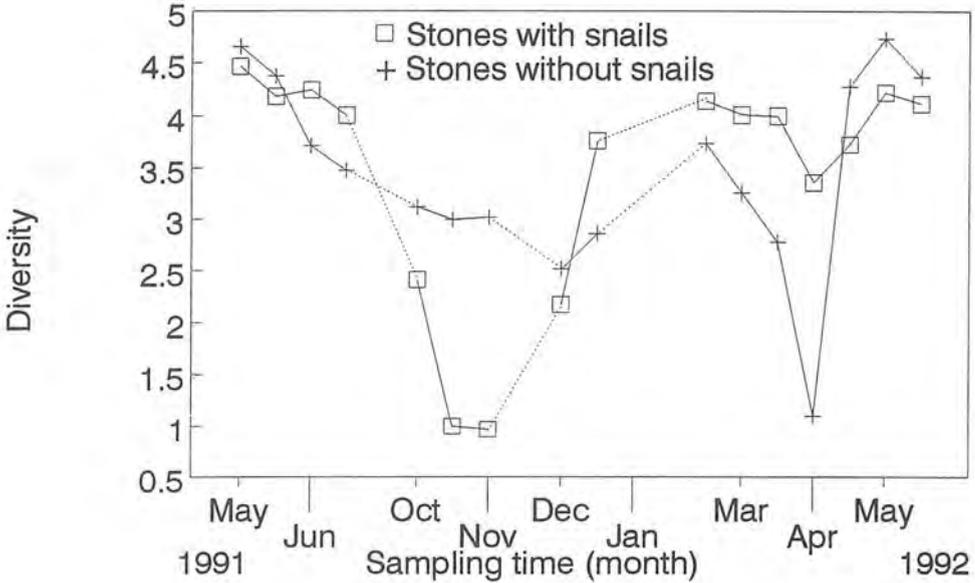


Figure 6. Seasonal variation in algal species diversity index for the epilithic aufwuchs in the Mekong River at Ban-Khi-Lek, Thailand. Missing data = (...).

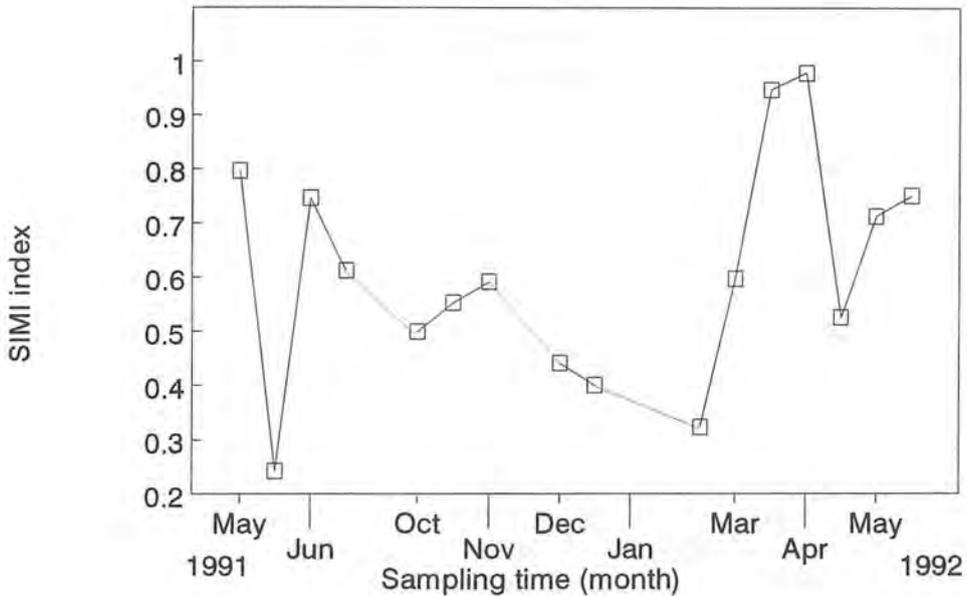


Figure 7. A comparison (using Stander's Similarity Index, SIMI) of the specific composition of the epilithic algal aufwuchs between stones bearing high densities of snails and those bearing few or no snails, for stones collected from the Mekong River at Ban-Khi-Lek, Thailand. Missing data = (...).

resulted in lower SIMI values (STANDER'S (1970) similarity index SIMI; 0 = no similarity, 1 = identical communities in terms of species composition and relative abundance), comparing SN+ with SN- substrata, at times of hydrological change (ie. in February or in late May or after freak storms; Fig. 7). There was little difference between the BKL and BXW samples in terms of species diversity; however, there was some discrepancy in the species richness data. The species richness for SN+ stones at BXW in early January (Table 2), whilst agreeing with the SN+ data from BKL, greatly exceeded that of the SN- stones; the values for the SN- stones at BXW were much lower than those for the same stone type at BKL.

DISCUSSION

The algal diversity and biomass of the Mekong River aufwuchs was high. Some of the algal richness is attributable to the effect of high insolation. Frequent habitat disturbance, through interruption of the process of competitive exclusion, is also likely to have been responsible for the species diversity observed. The annual spate, as well as minor spate events in the intervening period, may have been sufficient to significantly disrupt the algal community.

A marked reduction in algal biomass was observed during the spate period. The effects of current aside (which probably led to severe degradation of the epilithon), the most obvious cause of this fall in biomass was the decrease in light penetration following the introduction of large amounts of suspended solids to the water body (TILZER ET AL., 1976). In an oligotrophic river such as the Mekong, the introduction of nutrients (as run-off material) might be expected to stimulate productivity. However, run-off material rich in iron or aluminium may remove nutrients from solution through precipitation and/or sorption (ELBER & SCHANZ, 1990).

The results indicated a decline in diatom diversity, relative to that of blue-green algae, throughout the low water period on SN+ stones. The reason for this was probably community succession, the dominance of filamentous algal mats later in the low water period probably accelerated the decline of the diatom populations, especially those of *Achnanthes*, *Cocconeis*, *Nitzschia* and other adnate or nitrogen-heterotrophic diatoms. KORTE & BLINN (1983) described the involvement of diatoms in the primary successional (colonisation) process. Other authors have cited diatoms as the primary colonists of newly immersed surfaces (O' NEILL & WILCOX, 1971; HOAGLAND ET AL., 1982; ROEMER ET AL., 1984). Many diatom species are short lived, grow well at high levels of resource availability (ie. are *r*-selected strategists) and, therefore, would be expected to dominate the aufwuchs early in its recovery after the spate.

ATTWOOD (1993) demonstrated that the radular morphology of *N. aperta* restricts grazing to no closer than 4 μm to the stone or substratum, which would make algae with overstorey (upper layer) growth habits more susceptible to grazing. It is likely that grazing of the pedunculate diatoms of the overstorey conferred an advantage, in terms of light and other resource availabilities, on the blue-green algae of the understorey. Blue-green algal mats are reportedly able to consume 35–48% of the available nitrogen at the stone's surface as well as competing successfully for light (POWER & STEWART, 1987). Accordingly, once the blue-greens gain an advantage many diatom taxa are likely to be excluded. During late low water, when *N. aperta* population densities peaked, diatoms were more common (relative to blue-greens) on SN- stones than on SN+ stones; therefore it appears that grazing did have a deleterious effect on the growth of some diatom species, especially of prostrate and adnate forms.

During the main spate period the SN+ aufwuchs was dominated by diatoms rather than blue-green algae. The SN- stones, in contrast, bore mainly blue-green algae during the spate and so the relative paucity of Cyanophyta on SN+ stones may be an effect of grazing. Although the snails did not appear to graze cyanophytes during low water, the grazing pressure was probably greatest during the spate and blue-greens may also have been taken at that time. DENICOLA & MCINTIRE (1990b) also found that high grazing pressure reduced the epilithon to a thin mat of adnate diatoms such as *Achnanthes lanceolata* and *Cocconeis placentula*. Such non-motile, prostrate growth forms appeared to be more abundant under conditions of low irradiance and/or intense herbivory as both these effects reduce the degree to which these diatoms are buried beneath the overstorey.

The rate of succession at BXW appeared somewhat slower than that at BKL and the B/D-quotient remained close to unity throughout post-spate recovery and on into early low water. In addition, the biomass at BXW was found to be significantly greater than at BKL between late March and early April. These differences were probably the result of the more

severe spate at BKL during 1991/1992. Accrual processes are largely regulated by species specific interactions within the microhydraulic environment of the substratum-water interface. Increased stream flow enhances the impingement rate of algal propagules onto the substratum, but the concomitant increase in shear stress on the surface results in preferential attachment by forms which are small, adnate and/or mucilaginous and thereby restricts the progress of the succession (CHOW, 1959; VOGEL, 1981; KORTE & BLINN, 1983; STEVENSON, 1983). Under these hydraulic constraints generally more algal cells accrue in lower velocity habitats (REISEN & SPENCER, 1970; LAMB & LOWE, 1987; DENICOLA & MCINTIRE, 1990a) and this is probably the reason for the higher biomass at BXW. The earlier accumulation of algal biomass at BXW might have facilitated the more rapid growth of *N. aperta* populations there (by providing food) and thereby supported the transmission of schistosomiasis.

It was apparent that, despite being subjected to considerable grazing pressure, stones bearing very high densities of *N. aperta*, gamma race, during the low water period developed more diverse algal communities than did SN- stones. The high diversity on SN+ stones may have been a result of what is commonly called "exploiter mediated coexistence" (TANSLEY & ADAMSON, 1925); this occurs where the densities of the species present in a community are reduced (by predation) to levels where competition is no longer important and/or where competitively dominant species (in this case overstorey diatoms) are selectively grazed (JONES, 1933). In the highly fluvial Mekong River colonisation rates of most species (algae, snails and other invertebrates) onto stones are quite low and therefore each stone might be regarded as an ecological "island". During low water, as the numbers of rock pools and stable stones (in the current) increase, the effect is equivalent to an increase in island size and offers greater opportunity for island colonisation by new algal species with lower fecundities and growth rates. The colonisation of stones by such *K*-strategists may explain the observed increases in species diversity on both SN+ and SN- stones during low water. On the other hand, the colonisation rate of *N. aperta* during low water, although still relatively low, is at its highest (ATTWOOD, 1994) and it is possible that the snails selected substrata bearing more diverse algal communities; this selection might have led to the higher algal diversities observed on SN+ stones. However, the above is unlikely as the time taken for the snails to colonise a stone is probably still greater than that taken for recovery of the aufwuchs, which is less than one week (ATTWOOD, 1993). Alternatively, the snails might have been most common on stones which were most stable in the current and which also happened to bear the more diverse algal communities.

During the main spate period the values of algal biomass, diversity and richness for SN+ stones actually fell below those of SN- stones. SIMI values indicated that the algal communities of the SN+ and SN- stones differed most during the early spate. As rates of between-stone snail migration were low during the early spate, marginal value theorem may explain the changes in the SN+ community at that time. The theorem suggests that a snail would leave a stone once its energy extraction rate fell below some critical value, however, this critical value may be quite low (and therefore stay times quite long) in an environment where the travelling time between stones is long (CHARNOV, 1976; PARKER & STUART, 1976). Consequently, during the spate, there is some advantage to a snail in remaining on a stone until the periphyton is almost completely exhausted.

In summary, it appears that the annual spate of the Mekong River greatly reduces

(epilithic) algal populations and initiates a rapid recovery during the subsequent low water period. Grazing by *N. aperta* apparently accelerated the algal succession and effected a greater species diversity in the algal community. In a subsequent report the analysis of the algal aufwuchs will be extended to include an examination of changes in species abundance in the community.

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