NAT. HIST. BULL. SIAM SOC. 43: 171–197, 1996

THE IMPACT OF GRAZING BY NEOTRICULA APERTA (GASTROPODA: POMATIOPSIDAE) ON POST-SPATE RECOVERY OF THE ALGAL AUFWUCHS IN THE LOWER MEKONG RIVER: CHANGES IN SUCCESSIONAL PATTERNS AND RELATIVE ABUNDANCE OF SPECIES

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

In May 1991 (late low water period) overstorey diatoms dominated the diatom fraction of the aufwuchs on stones bearing snails, with the blue-green algae dominant overall. Snail-free stones were characterised by a predominance of *Rhizoclonium* (Ulotrichales). In June (early spate period) the aufwuchs reverted to a community of mainly pioneer diatoms. Immediately after the end of the annual spate, 18 February 1992, chlorophycean algae were scarce and a two-dimensional community consisting of 53% blue-green algae and 45% adnate diatoms was found. During the high to low-water transition (April, 1992) observations of stones bearing many snails indicated that Ulotrichales, Hormogonales and Pennales were preserved, with Ulotrichales dominant. In contrast, stones bearing few or no snails showed a paucity of Cyanophyta and a low diatom diversity. The ecological significance of these observations is discussed.

Grazing by *N. aperta* accelerated the successional process and post-spate recovery of the aufwuchs. Filamentous Cyanophyta and overstorey diatom species were encouraged by grazing. Grazing appeared to inhibit the later stages of the succession.

Key words: Algal succession, Grazer-periphyton interactions, Mekong River algalflora, Molluscs, Schistosomiasis mekongi, Flood recovery.

INTRODUCTION

Many studies have examined benthic algal recovery following spates (e.g. POWER & STEWART, 1987; BIGGS & CLOSE, 1989; GRIMM & FISHER, 1989; PETERSON & STEVENSON, 1990); however few studies have examined the impact of grazing on this recovery. Where

[1] School of Biological Sciences, Queen Mary & Westfield College (University of London), Mile End Road, London E1 4NS
Received 26 April 1996; accepted 15 November 1996

grazer-periphyton interactions have been studied the emphasis is often on some other factor such as substratum texture (DUDLEY & D'ANTONIO, 1991), resource partitioning (HILL & KNIGHT, 1988) or the effects of irradiance (STEINMAN ET AL., 1989). The above are of course all worthy investigations and no biocoenosis should be studied in isolation, without regard to other external parameters. However, there has yet been no comprehensive demonstration of the ways in which grazing can influence the direction and progress of algal succession. Accordingly, the aim of the present study was to fill this gap in the literature.

All of the most commonly occurring (in the Mekong River) algal species were followed and no attempt was made to group these taxa into a limited number of categories. Information regarding species composition is essential to enquiries about community structure and succession (MCALICE, 1971). Nevertheless, many reports fail to note the contribution of individual algal species and either report on certain indicator species (often restricted to a single family) or describe changes in one or more algal groups. Part I of this study (ATTWOOD, 1996) demonstrated, using biomass data and species diversity and richness indices, that grazing by the gamma race of *Neotricula aperta* (TEMCHAROEN, 1971) has an effect on the recovery of the (epilithic) algal aufwuchs in the Mekong river following the annual spate (of June–November). ATTWOOD (1996) suggested that grazing by *N. aperta* increased species diversity and accelerated the normal algal succession on stones in the river. However, grazing appeared to inhibit later successional stages and the algal diversity on stones bearing *N. aperta* (gamma race) fell during the spate period relative to stones bearing few or no snails.

N. aperta an almost exclusively epilithic, tropical, freshwater snail inhabiting the lower Mekong River, provides a useful model for the study of grazer-periphyton interactions and post-spate algal recovery. The stream flow of the Mekong River shows marked seasonal variations. 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, KITIKOON & TEMCHAROEN, 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 (onset of low water). This situation allows the simultaneous development of a herbivorous invertebrate fauna and an epilithic algal flora to be observed following a major spate event.

N. aperta, gamma race, is also the natural snail host of *Schistosoma mekongi* VOGE, BRUCKNER & BRUCE, 1978 (Trematoda: Schistosomatidae), responsible for human schistosomiasis in the Lower Mekong Basin. The gamma race of *N. aperta* is found along the Mekong River in Northeast Thailand, southern Laos, Kampuchea and (probably) Vietnam. In spite of the wide geographical range of *N. aperta,* a site at Ban-Xieng-Wang (BXW), Khong Island, 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 conditions in Northeast Thailand and southern Laos might reveal factors explaining endemicity on Khong Island.

MATERIALS AND METHODS

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 near Khemmarat, Ubon-Ratchathani Province, Northeast Thailand. The second study 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). Samples were taken at intervals (roughly twice monthly during low water periods and bimonthly at other times) over the period May 1991 to May 1992. The aufwuchs was sampled from the upstream edges of the upper surfaces of stones collected at random at depths ranging from 0.1 to 0.7 m. Stones bearing *N. aperta,* gamma race, (at densities>10 m^{-2}) were denoted as SN+, whilst those bearing no *N. aperta* (and usually no snails of any other species) were denoted as SN– stones. *N. aperta* tended to dominate the invertebrate fauna of those stones upon which it occurred. An aufwuchs sample from a consistent (approx. 4 cm^2) area was taken from each stone (for details of apparatus and procedure used see ATTWOOD, 1996). The aufwuchs samples were placed into separate glass vials containing 1 ml FAA (50% ethanol (95%), 35% distilled water, 10% formalin and 5% glacial acetic acid; after PRESCOTT, 1954). All samples were transferred to the laboratory in Bangkok by road in insulated boxes containing ice and within five days of collection.

In order to minimise errors a standard counting procedure was followed throughout the study (ATTWOOD, 1996). For each stone sampled 30 separate aliquots (of the 1 ml sample in FAA) were examined and the numbers of each taxon present were counted). The results were then averaged to give the count for each stone (sample). Tables and figures present average values for five stones sampled on each date. The species list for all taxa identified in the aufwuchs samples throughout the study is given in Table 1. All diatoms were identified to species; however, some of the Botrydiaceae, Oedogoniaceae and Zygnemataceae (with which the author was unfamiliar) were only identified to genus. Identifications of the Chrysophyta were made with MIZUNO (1981) and those for the other algae with SMITH (1933) and PRESCOTT (1954). Reference slides were made for those diatom species which could not be indentified from the uncleared samples; the method used followed MCBRIDE (1988).

RESULTS

Figures 1–4 and Table 2 give the relative (percentage) contributions of dominant algal groups and the individual taxa, respectively, present in the aufwuchs samples taken at BKL throughout the study (data for SN+ and SN– stones are given separately). The seasonal flood cycle of the river not only affected species richness and biomass (see ATTWOOD, 1996), but also the structure of the epilithic algal community itself.

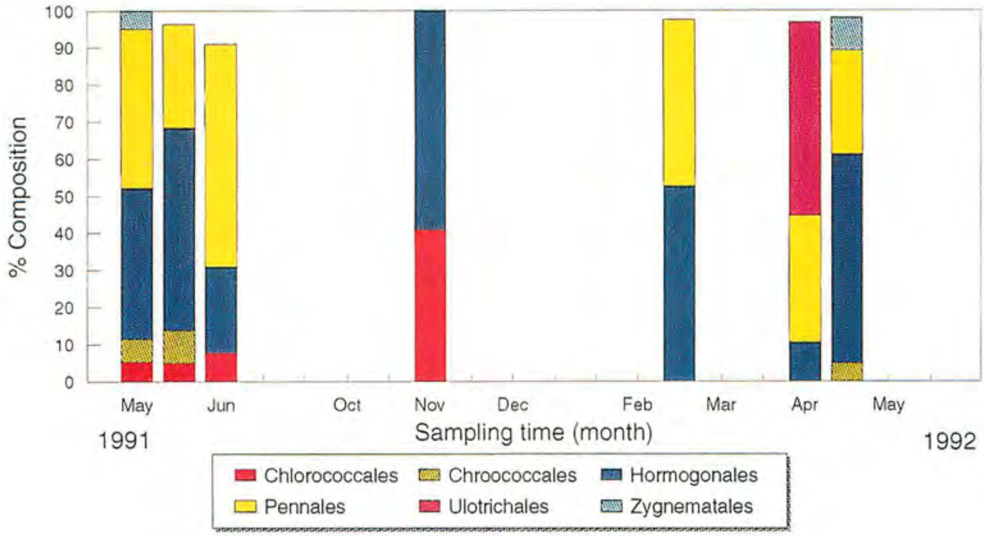
Aufwuchs samples taken from SN+ stones during the mid low-water period of 1991 (2 May) revealed an algal community dominated by diatoms and blue-green algae (Hormogonales) with minor contributions from chlorococcalean, chroococcalean and zygnematalean algae. The diatom fraction was dominated by *Cymbella ventricosa* and

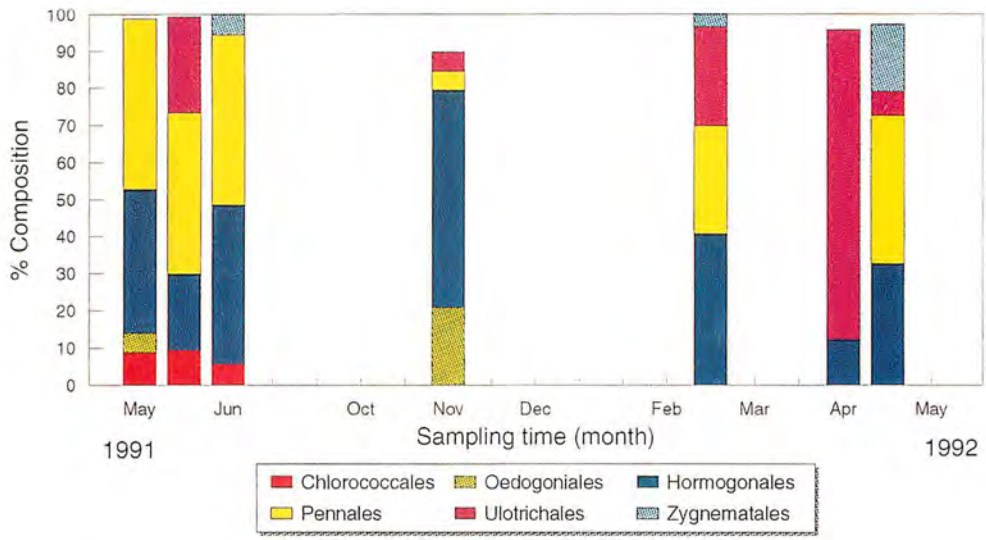
Navicula cryptocephala var. *veneta* (both were quite large, with mean valve–face dimensions of 31.7x8.7 and 29.8x6.7 µm, respectively) and smaller diatoms such as *Frustulia rhomboides* (14.4x3.8 µm). Genera with typically large species were also common, for example *Navicula (N. cantonensis,* 36.5x18.5 µm; *N. pupula* var. *rectangularis,* 53.8x14 µm; *N. pupula* var. *elongata* and *N. gracilis,* 36.5x9.6 µm). Large tychoplanktonic forms (e.g. *Synedra ulna,* 73.1x6.7 µm) and small periphyta (e.g. *Cymbella cistula* and *C. cupsidata* (20.2x6.7 µm)) were less common. The Cyanophyta were dominated by *Phormidium spp. (P. mucicola* and *P. tenue)* which formed a thin (trichome dimensions typically 300–10x7.7 µm and 10x2.9 µm, respectively) resilient dark green coating on the stones during low water (2 May, 1991), as well as by some interwoven *Oscillatoria* trichomes (*O. tenuis* and *O. formosa,* typically 120x4 µm). The Chlorophyta were represented by Chlorococcales (mostly small, spherical, unicellular chlorophytes), such as *Palmellococcus miniatus* (3.8 µm dia.), and by the larger zygnematale *Spirogyra* (234.6x53.8 µm) which, constituting 5% of the total algal bio-volume (Table 2), formed tufts of short filaments around the edges of stones exposed to the current. Samples taken from SN– stones on 2 May 1991 also revealed an aufwuchs dominated by Pennales and Hormogonales. However, Zygnematales were rare whilst members of the Oedogoniales were more common and their dried remains formed a "white" coating over the recently exposed stones of the late low water period.

With the continuation of relatively stable low water conditions a second sample was taken on 18 May 1991 (Table 2). The SN+ stones again appeared to be dominated by diatoms and blue-green algae but more so by the latter. The main chlorophycean dominant was again *P.miniatus* followed by *Chlorococcum infusionum* (7.7x3.9 µm). The appearance of desmids such as *Cosmarium circulare* may have been a consequence of river *p*H which fell from 8.4 in early May to 7.9 by mid-May. Diatom diversity decreased slightly (from 2 May) and the dominant taxa were smaller algae such as *Frustulia.* Tychoplanktonic diatoms were more common than in early May. Figure 2 indicates that during mid-May SN– stones bore a significant proportion of Ulotrichales, however, this was not the case on SN+ stones (see Fig. 1). Indeed, the main chlorophycean dominant of SN– stones was *Rhizoclonium crispum,* which formed long trailing strands in the water.

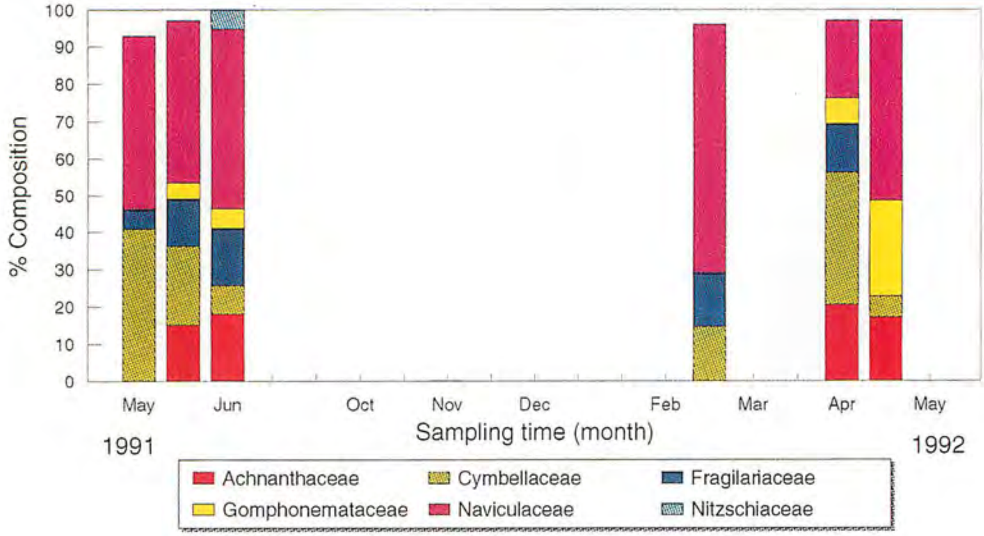
Samples taken off SN+ stones in early June (1991), that is at the onset of the main spate, revealed a predominance of diatoms followed by blue-green algae with a modest presence of Chlorococcales. The diatom fraction was dominated by relatively small specimens (e.g. *Navicula cryptocephala* var. *veneta*) and *Achnanthes crenulata,* an uncommon diatom during the May (1991) collections, was also prevalent. The main cyanophycean dominant was *Oscillatoria tenuis,* which made up nearly 20% of the total algal epilithon. The specific composition of the SN– aufwuchs was little different from that of the SN+ stones (Stander's (1970) similarity index, SIMI = 0.76); however, small *Nitzschia spp.* (e.g. *N. capitellata,* 19.2x5.8 µm) were more common.

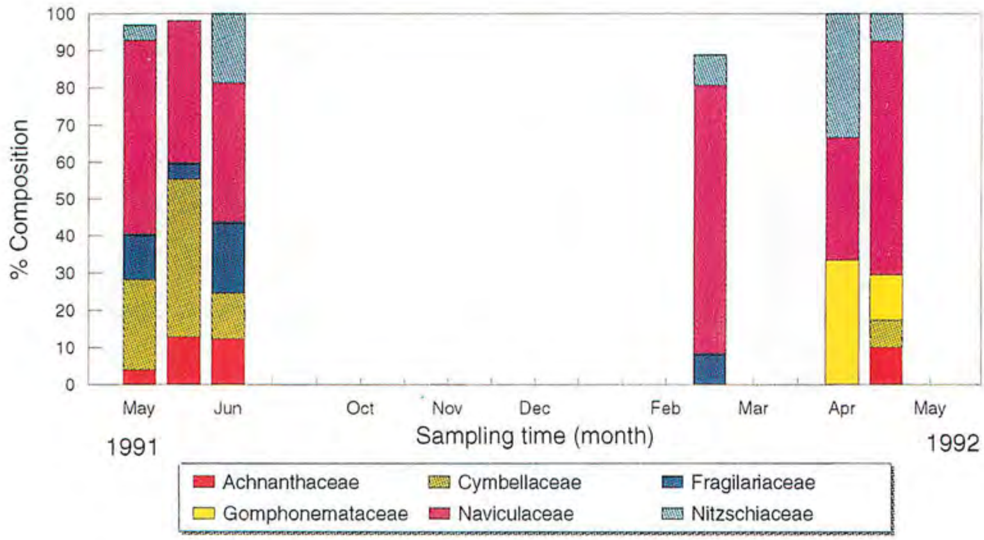
Samples taken from SN+ stones during the latter stages of the spate (10 November 1991) served to demonstrate the impact of the spate on algal community composition. The samples consisted of almost exclusively *Palmellococcus miniatus* (Chlorococcales = 42% of total sample) and of *O. tenuis* (Hormogonales = 58%). A greater species richness and diversity was found on SN– stones (see ATTWOOD, 1996), with the aufwuchs dominated by Hormogonales (58.5% of sample total), Oedogoniales (20.8%) and Ulotrichales (5.3%).





Figures 1 (upper) and 2 (lower). Percent composition of the algal aufwuchs, showing the occurrence of dominant (i.e. 5% of total sample bio–volume) groups in samples (each based on 5 stones) taken from the Mekong River at Ban-Khi-Lek, Thailand. Figure 1: samples from stones supporting a high density of *Neotricula aperta* snails; Figure 2: samples from stones supporting no *N. aperta*.





Figures 3 (upper) and 4 (lower). Percent composition of the diatom fraction of the aufwuchs, showing the occurrence of dominant (i.e. 5% of total sample bio-volume) families in samples (each based on 5 stones) taken from the Mekong River at Ban-Khi-Lek, Thailand. Figure 3: samples from stones supporting a high density of *Neotricula aperta* snails; Figure 4: samples from stones supporting no *N. aperta*.

Small species dominated the diatom fraction (eg. *Navicula medisculus,* 15.4x5.8 µm), however, the Pennales accounted for only 3.5% of the total collection.

A recovery of the aufwuchs, in terms of algal species richness and diversity, was observed on SN+ stones during the post-spate recovery period (Table 2: mid-February, 1992). Cyanophyta dominated these samples (53% of the total sample; Fig. 1 and Table 2) with a species composition similar to that of the pre-spate samples. The remainder of the sample was made up of diatoms (45%, see Fig. 1) and these were mostly *Navicula spp.*, some of which were species with characteristically large frustules; for example, *N. cupsidata* var. *ambigua* (28.8 x 10.7 µm) and *N. pupula* var. *rectangularis* (30.8 x 8.7 µm). The aufwuchs of SN– stones appeared less diverse, however, a significant presence of Ulotrichales and Zygnematales was recorded; their predominance appeared to be at the expense of diatoms. The Ulotrichales and Zygnematales were mainly represented by *Cladophora glomerata* and *Spirogyra* respectively. The SN– stones also bore many small diatoms including smaller representatives of many of the *Navicula spp.* listed above for SN+ stones, however, the SN– samples contained *Nitzschia capitellata* (13.5x3.8 µm) which represents a genus not found on the SN+ stones.

SN+ samples taken during the high-low-water transition period on 1 April 1992 revealed an epilithon dominated almost equally by Ulotrichales and Pennales with relatively few Hormogonales (Fig. 1). The long, wiry, green-filaments of *Cladophora glomerata* and *Rhizoclonium crispum* dominated the aufwuchs to form a green carpet over the stones; the remainder of the chlorophycean fraction consisted of small Chlorococcales (e.g. *C. infusionum* and *P. miniatus;* Table 2). The diatom diversity was high and chain–forming species were common (e.g. *Cymbella sinuata, C. graciles* (17.3 x 7.7 µm), *C. ventricosa* and *Gomphonema gracile* (17.3 x 5.3 µm)) as well as tychoplankton (e.g. *Tabellaria,* 481 x 32.5 µm) and euperiphyta e.g. *Cocconeis pediculus, C. placentula* var. *euglypta, Mastogloia smithii, Navicula cryptocephala* var. *veneta* and *Navicula radiosa*). The SN– samples were again dominated by *Cladophora glomerata* and the Cyanophyta present differed little (in species and proportion) from the SN+ aufwuchs. The SN– diatom diversity was, however, lower and included *Nitzschia palea* (27.9 x 5.8 µm), and *Gomphonema* and *Gyrosigma spp.*

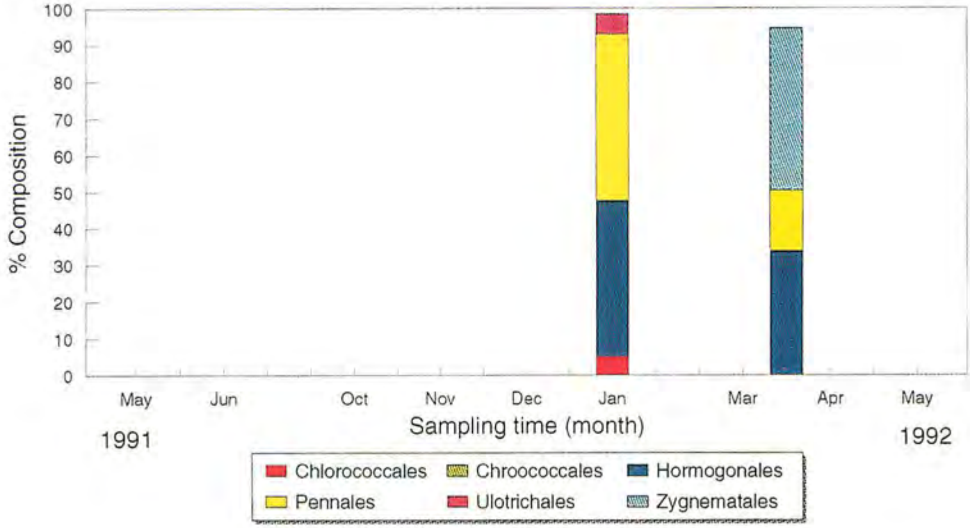
The final samples were taken later in the low water period on 19 April 1992. The SN+ aufwuchs was similar to that of early May (1991), especially with regard to the Chlorophyta fraction (which contained much *Spirogyra*) and to the cyanophyte fraction. The particularly high species diversity for these samples (see ATTWOOD 1996) was mostly attributable to the diversity of the diatom fraction. The diatom species found were little different from those present at the start of April, however, *Achnanthes brevipes* (35.6 x 13.5 µm) and *Frustulia viridula* were found in the 19 April samples. In the SN– samples, again, the Chlorococcales were not well represented and the main chlorophycean dominants were Zygnematales (*Spirogyra* and *Zygnema*). However, in the SN– aufwuchs filamentous Zygnematales and Ulotrichales together made up 25% of the total sample (Table 2), rivalling the diatoms in terms of bio-volume.

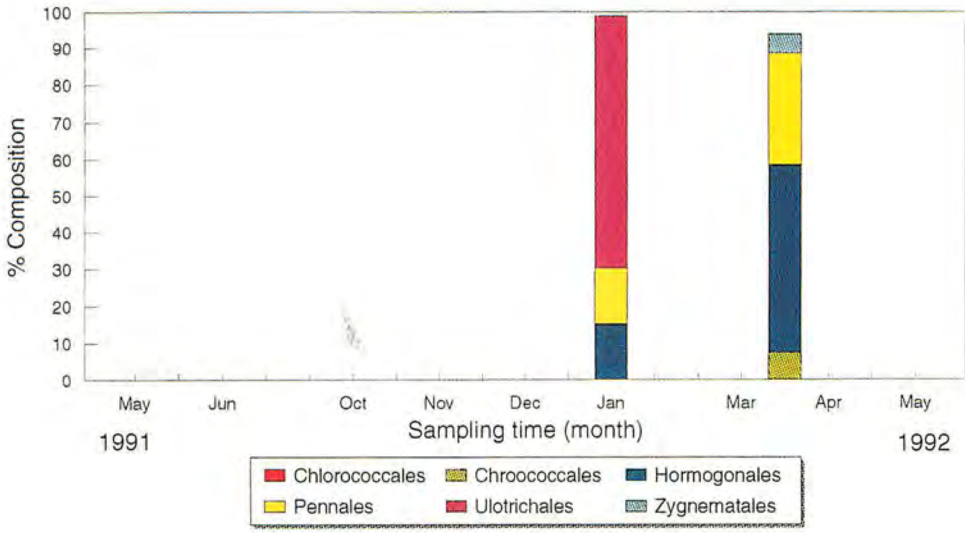
The stones at BXW (Laos) were also examined for aufwuchs composition (see Figs 5–8, Table 3). The first samples were taken on 7 January (1992) and compared well with those taken later (18 February 1992) at BKL (SIMI = 0.71); however, the diatom fraction of SN+ stones at BXW showed some unique features. Those *Cymbella spp.* found at BKL were not so common in the Lao samples. The tychoplanktonic *Synedra ulna* was also less common in Laos and the periphytic *Achnanthes brevipes* (25 x 7.7 μm) was found at BXW, but not at BKL in February. The absence of *S. ulna* at BXW may have been due to the fact that the current at BXW had not yet completely subsided following the spate. The ulotrichale *Cladophora* was relatively rare at BXW apparently being replaced by *Rhizoclonium hieroglyphicum.* The second sample (28 March, 1992) taken at BXW did not compare as favourably with samples taken from BKL on 1 April 1992 (SIMI = 0.53). Ulotrichales were virtually absent from the SN+ aufwuchs at BXW and the only filamentous green–algae were Zygnematales. The diatoms sampled at BXW included many species that were rare or absent at BKL (eg. *Fragilaria construens* (315 x 32.5 μm), *Gyrosigma spenceri* (71.2 x 10.6 μm) and *Rhoicosphaenia curvata*). On the SN– stones the chlorophycean diversity was much greater and (unlike the BKL samples) *Cladophora* was not found. The SN– aufwuchs also showed greater diversity, relative to corresponding samples from BKL, and *Achnanthes, Cocconeis, Cymbella* and *Fragilaria spp.* were common. However, *Nitzschia spp.* relatively common at BKL were scarce at BXW.

The mean algal cell sizes for algal dominants were recorded for aufwuchs samples from *N. aperta* (gamma race) habitats at BKL and BXW on various dates throughout the study; these data are summarised in Table 4. In order to eliminate the effects of species composition on mean cell size for the aufwuchs, the algae were divided into a number of categories on the basis of morphological characteristics and taxonomic affinity (see Table 4).

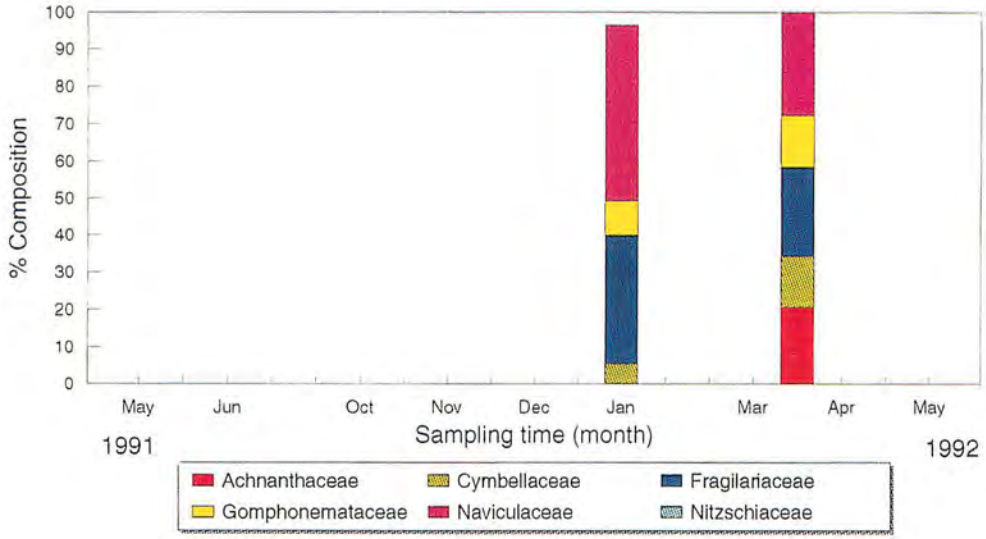
For all sample dates (for which sufficient data were available) and at both BKL and BXW no significant difference was detected, in terms of mean cell size, between SN+ and SN– samples for any of the following groups: Achnanthaceae, Cymbellaceae, Fragilariaceae, Naviculaceae and Myxophyceae (Mann–Whitney U–tests; $P>0.05$). At BXW the mean size (filament length) for the pooled ulotrichale and zygnematale fraction was greater in the SN+ samples than in the SN– samples (638.9 ± 88.5 μm and 477.8 ± 165 μm, respectively; $P<0.01$, $U'=20$, n=12, 14). However, no significant difference was detected between the pooled fraction on SN+ stones and on SN– stones at BKL during any sample period. At BKL the mean cell size for the Chlorococcales was significantly greater on SN+ stones during the *N. aperta* population density peak on 18 May 1991 ($P<0.05$, $U'=1$, n=4, 4).

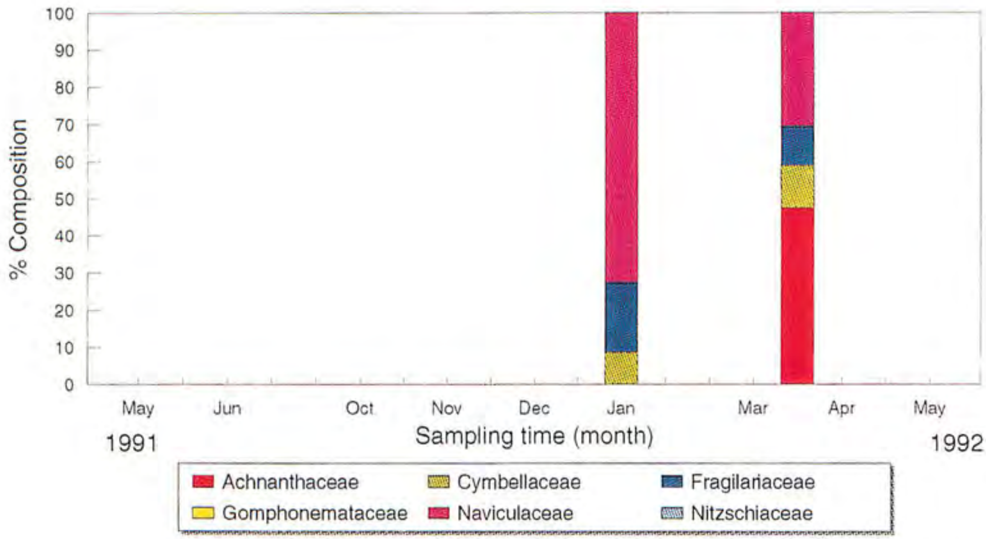
No significant seasonal variation (for either stone type) was detected for the Achnanthaceae, Fragilariaceae, Naviculaceae and Nitzschiaceae at either BKL or BXW (Kruskal–Wallis ANOVA tests; $P>0.05$). At BKL the cell size for the cymbellacean fraction remained relatively constant throughout the study except during the *N. aperta* peak (18 May 1991) when the cell size was significantly reduced (ANOVA; $P=0.01$, n=62). The cymbellacean fraction at BKL did not differ significantly from that at BKL. ANOVA indicated that (for both SN+ and SN– stones) the mean cell size for the pooled ulotrichale and zygnematale fraction did not vary significantly over the study. However, SN– data gathered at BXW on 28 March (1992) suggested that the mean cell size of the pooled fraction was significantly greater than in the first BXW sample and in any of the BKL samples.





Figures 5 (upper) and 6 (lower). Percent composition of the algal aufwuchs, showing the occurrence of dominant (i.e. 5% of total sample bio-volume) groups in samples (each based on 5 stones) taken from the Mekong River at Ban-Xieng-Wang, Laos. Figure 5: samples from stones supporting a high density of *Neotricula aperta* snails; Figure 6: samples from stones supporting no *N. aperta*.





Figures 7 (upper) and 8 (lower). Percent composition of the diatom fraction of the aufwuchs, showing the occurrence of dominant (i.e. 5% of total sample bio-volume) families in samples (each based on 5 stones) taken from the Mekong River at Ban-Xieng-Wang, Laos. Figure 7: samples from stones supporting a high density of *Neotricula aperta* snails; Figure 8: samples from stones supporting no *N. aperta*.

DISCUSSION

A number of cooperating processes may have been responsible for the rapid post-spate recovery of the aufwuchs. According to PETERSON & STEVENSON (1990) the initial recovery of lotic benthic algal communities is influenced by both direct encroachment, from foci of persistent cells, and impingement and subsequent proliferation of new colonists. However, HOAGLAND, ZLOTSKY & PETERSON (1986) reported that the colonisation of denuded rock surfaces was brought about almost exclusively by impingement. The development of filamentous algal mats has been cited as important in the process of recolonisation. PETERSON & STEVENSON (1990) suggested that diatom accrual probably benefits from current modification by filamentous algal mats. It was also possible that stones swept downstream introduced viable algal material into *N. aperta* habitats. DOUGLAS (1958) demonstrated that epiphytic algae such as *Achnanthes minutissima* accumulate downstream in small streams; this suggests that washing off and subsequent deposition and establishment of such diatoms is possible. Finally, diatom dispersal may be facilitated by the snails themselves, especially as apparently viable cells may be passed in the faeces (ATTWOOD, 1993).

KORTE & BLINN (1993) described the process of primary succession on severely denuded substrata. They suggested that colonisation began when an initial film of detrital mucilage, bacteria and fungi develops and conditions the substratum, the process taking only a few hours. Within 5 to 7 days a two-dimensional matrix of adnate diatoms develops, followed by an accretion of vertically oriented species called the "overstorey". In support of this model several authors have reported diatoms as the primary algal colonists (O' NEILL & WILCOX, 1971; HOAGLAND, ROEMER & ROSOWSKI, 1982; ROEMER, HOAGLAND & ROSOWSKI, 1984). Diatoms such as *A. minutissima* and *Achnanthes longipes* are anchored by only a short apical stalk (HASLE, 1974; ROEMER ET AL., 1984), whilst those such as *Cymbella affinis* and *Gomphonema olivaceum* produce long stalks (often>100 µm in length) which adhere to the substratum (ROEMER ET AL., 1984). The ability of certain diatoms to raise themselves above the substratum, to form a canopy blanketing the lower tier of algae, has obvious implications for light and nutrient competition (HUDON & BOURGET, 1981). These pedunculate diatoms will, in the subsequent discussion, be seen to be important to grazer-periphyton interactions in *N. aperta.*

The buccal apparatus of *N. aperta,* which limits grazing to not within 4 µm of the stone surface, may optimise feeding on overstorey growth forms whilst limiting feeding on understorey and prostrate algae. Clearly one method of grazer avoidance lies in the structural and functional heteromorphy of periphytic diatoms; for example, *Achnanthes lanceolata* being small, prostrate and well adhered to the substratum would be difficult to graze. In support of this the present results indicated that small *Achnanthes spp.* formed a greater proportion of the total diatom fraction (from early low water to early high water) on SN+ stones than on SN– stones. In addition, during the spate Chlorococcales (e.g. *Chlorococcum infusionum* and *Palmellococcus miniatus*) were more common on SN+ stones than on SN–; this may again be attributed to their small average cell size.

During the post-spate recovery period the rectum of *N. aperta* (gamma race) contained mostly *Navicula radiosa* and *Cymbella cupsidata* (see ATTWOOD, 1993); it is likely that viable cells of these species were scattered into the interstices of the two-dimensional community already established, so as to facilitate overstorey development on SN+ stones. The overstorey diatoms may compete successfully for light with filamentous algae (but not Cyanophyta); the relative predominance of Ulotrichales on SN– stones might therefore be attributable to the smaller community of overstorey diatoms. As already mentioned, the overstorey diatoms on SN+ stones would be preferentially grazed; however, as the bulk of these (ingested) algae may be passed into the faeces and remain viable, grazing need not effect a decline in their numbers. Indeed, grazed diatoms may benefit from being deposited in the faeces on top of the overstorey rather than becoming buried within it.

Tychoplanktonic diatoms were common on SN+ stones during the post–spate recovery period but were rarely found on SN– stones. This predominance on SN+ substrata requires explanation as tychoplankton impingement rates would have been high on both stone types, as the coagulation of suspended particles following the end of the spate led to an increased sedimentation rate for plankton (OSMANN–SIGG & STUMM, 1982). Araphid tychoplankton, such as *Synedra ulna* (a heavily silicified species expected to occur early in the tychoplankton succession), may have established better on SN+ stones as these bore a more extensive network of cyanophycean and zygnematalean algae which could trap tychoplankton.

By early April (1992) the Chroococcales were more common in the SN– aufwuchs than in the SN+. The SN+ stones bore quite high proportions of Cyanophyta which are normally associated with the earlier successional stages (e.g. *Phormidium mucicola, P. tenue* and *Oscillatoria spp.*). DENICOLA & MCINTIRE (1991) suggested that, where insolation is high, pioneer species may reestablish in the gaps opened up by grazing. The diatom fraction of SN+ stones in April (1992) contained a greater proportion of large, stalk forming, species than did that of the previous (i.e. post-spate recovery) sample. Larger naviculacean diatoms have often been found embedded in detritus particles (ROSOWSKI, HOAGLAND & ALOI, 1986) so may have settled out with the tychoplankton at the onset of less severe stream flow conditions. The success of these diatoms probably also lay in their ability to raise themselves into the overstorey. SLÁDECKOVÁ (1962) used the term " pseudoperiphyton" to describe those algae accreted into the aufwuchs through attachment to the forest of attachment stalks produced by overstorey diatoms such as *Cymbella; Achnanthes minutissima* is an example of the pseudoperiphyton and is strictly an epiphyte. Unlike the SN+ stones, the SN– aufwuchs of early April bore few pseudoperiphyta presumably because, in the absence of grazing, pedunculate diatoms providing for their attachment were scarce.

The species diversity during the early spate (June, 1991) was low (see ATTWOOD, 1996) and the diatom fraction comprised mostly *Achnanthes spp.* and small *Navicula.* Nevertheless, diatoms dominated the samples and this is typical of "pioneer" algal communities especially as the diatoms found were mostly of low stature. *Achnanthes spp.* are typically small diatoms that tend to dominate the epilithon under conditions of rapid flow and reduced grazing pressure (gamma-snail densities were low by this time) (ROUNICK & GREGORY, 1981; ROBINSON & RUSHFORTH, 1987).

Samples taken soon after restoration of low water conditions (1 April 1992) indicated rapid recovery of the aufwuchs. The SN+ aufwuchs still showed signs of the early colonists in that *Cocconeis* was still common. *Cocconeis* has a prostrate, adnate, growth habit and is mono-raphid (non-motile); therefore this diatom is well adapted to establishing in spate conditions but would not be expected to persist long after the development of the early overstorey. However, nutrient depletion in the vicinity of blue-green algal mats may have allowed *Cocconeis,* with its low phosphate requirement, to "hang on" into early low water. The presence of stalk forming diatoms such as *Cymbella, Gomphonema* and *Mastogloia* indicated that the overstorey was already developing and on SN+ stones was already sufficient to trap the large alga *Tabellaria fenestrata.*

In conclusion, the results of sampling the aufwuchs indicated that grazing initially enhanced the rate of cell replacement and altered the course of interspecific (algal) competition, thereby accelerating succession. However, the long term effect of grazing appeared to be inhibition of the later successional stages. The study also highlighted the resilience and rapid post-spate recovery of the epilithic aufwuchs and the high biomass and species diversity achieved. Further investigations are required in order to confirm the findings of the present study, particularly with respect to the effects of grazing on succession. Although *N. aperta* tends to dominate its habitats, it is possible that some other snail may have grazed the "SN–" substrata just prior to collection. Accordingly, laboratory studies are required so that reliable control (snail or grazer free) habitats may be established.

ACKNOWLEDGMENTS

Dr. W. Thamavit and Prof. E. S. Upatham (Mahidol University, Bangkok) for providing facilities and Prof. P. F. Newell for support in the UK. This work was supported by an SERC Studentship.

REFERENCES

ATTWOOD, S.W. 1993. *The Biology and Ecology of Neotricula aperta (Temcharoen), the Snail Intermediate Host of Human Schistosomiasis in the Lower Mekong Basin.* Ph.D. thesis, University of London.

ATTWOOD, S.W. 1995. A demographic analysis of *y-Neotricula aperta* (Gastropoda: Pomatiopsidae) populations in Thailand and southern Laos, in relation to the transmission of schistosomiasis. *J. Moll. Stud.* 61: 29–42.

ATTWOOD, S.W. 1996. 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. *Nat. Hist. Bull. Siam Soc.* 44: 61–74.

BIGGS, B.J.F. AND M.E. CLOSE. 1989. Periphyton biomass dynamics in gravel bed rivers: the relative effects of flow and nutrients. *Freshw. Biol.* 22: 209–231.

DAVIS, G.M. 1979. The origin and evolution of the Gastropod family Pomatiopsidae, with emphasis on the Mekong river Triculinae. *Acad. Nat. Sci. Philadelphia, Monogr.* 20: 1–120.

DAVIS, G.M., V. KITIKOON AND P. TEMCHAROEN. 1976. Monograph on *"Lithoglyphopsis" aperta,* the snail host of Mekong river schistosomiasis. *Malacologia* 15: 241–287.

DENICOLA, D.M. AND C.D. MCINTIRE. 1991. Effects of hydraulic refuge and irradiance on grazer periphyton interactions in laboratory streams. *J. Amer. Benth. Soc.* 10: 251–262.

DOUGLAS, B. 1958. The ecology of the attached diatoms and other algae in a small stony stream. *J. Ecol.* 46: 295–322.

DUDLEY, T.L. AND C.M. D'ANTONIO. 1991. The effects of substrate texture, grazing, and disturbance on macroalgal establishment in streams. *Ecology* 72: 297–309.

ELBER, F. AND F. SCHANZ. 1990. The influence of a flood event on phytoplankton succession. *Aqua. Sci.* 52: 330–344.

GRIMM, N.B. AND S.G. FISHER. 1989. Stability of periphyton and macro–invertebrates to disturbance by flash floods in a desert stream. *J. N. Amer. Benth. Soc.* 8: 293–307.

HASLE, G.R. 1974. The "mucilage pore" of pennate diatoms. *Nova Hedwigia* 45: 167–186.

HILL, W.R. AND A.W. KNIGHT. 1988. Concurrent grazing effects of two stream insects on periphyton. *Limnol. Oceanogr.* 33: 15–26.

HOAGLAND, K.D., S.C. ROEMER AND J.R. ROSOWSKI. 1982. Colonisation and community structure of two periphyton assemblages, with emphasis on the diatoms (Bacillariophyceae). *Amer. J. Bot.* 69: 188–213.

HOAGLAND, K.D., A. ZLOTSKY AND C.G. PETERSON. 1986. The source of algal colonisers on rock substrates in a freshwater impoundment. *Algal Biofouling, Studies in Environmental Science No.* 28. L.V. Evans & K.D. Hoagland (eds), pp. 21–40. Elsevier, New York.

HUDON, C. AND E. BOURGET. 1981. Initial colonisation of artificial substrates: community development and structure studied by scanning electron microscopy. *Can. J. Fish. Aqua. Sci.* 38: 1371–1384.

KITIKOON, V. AND C.R. SCHNEIDER. 1976. Notes on the aquatic ecology of *Lithoglyphopsis aperta*. *S. E. Asian J. Trop. Med. Publ. Hlth* 7: 238–243.

KORTE, V.L. AND D.W. BLINN. 1983. Diatom colonisation on artificial substrata in pool and riffle zones studied by light and scanning electron microscopy. *J. Phycol.* 19: 332–341.

MCALICE, B.J. 1971. Phytoplankton sampling with the Sedgwick–Rafter cell. *Limnol. Oceanogr.* 16: 19–28.

MCBRIDE, T.P. 1988. Preparing random distributions of diatom valves on microscope slides. *Limnol. Oceanogr.* 33: 1627–1629.

MIZUNO, T. 1981. *Illustrations of the Freshwater Plankton of Japan. 5th ed.* Hoikusha Publishing Company, Osaka, Japan.

O'NEILL. T.B. AND G.L. WILCOX. 1971. The formation of a "primary film" on materials submerged in the sea at Port Hueneme, California. *Pacific Sci.* 25: 1–12.

OSMANN–SIGG, G. AND W. STUMM. 1982. Partikelverteilung und natürliche koagulation im Zürichsee. *Schweiz. Z. Hydrol.* 44: 405–422.

PETERSON, C.G. AND R.J. STEVENSON. 1990. Post–spate development of epilithic algal communities in different current environments. *Can. J. Bot.* 68: 2092–2102.

POWER, M.E. AND A.J. STEWART. 1987. Disturbance and recovery of an algal assemblage following flooding in an Oklahoma stream. *Amer. Midl. Nat.* 117: 333–345.

PRESCOTT, G.W. 1954. *How to know the freshwater algae* W.M.C. Brown Company, Iowa.

ROBINSON, C.T. AND S.R. RUSHFORTH. 1987. Effects of physical disturbance and canopy cover on attached diatom community structure in a Idaho stream. *Hydrobiologia* 154: 49–59.

ROEMER, S.C., K.D. HOAGLAND AND J.R. ROSOWSKI. 1984. Development of a freshwater periphyton community as influenced by diatom mucilages. *Can. J. Bot.* 62: 1799–1813.

ROSOWSKI, J.R., K.D. HOAGLAND AND J.E. ALOI. 1986. Structural morphology of diatom–dominated stream biofilm communities under the impact of soil erosion. *Algal Biofouling, Studies in Environmental Science No.* 28 L.V. Evans & K.D. Hoagland (eds), pp. 247–299. Elsevier, New York.

ROUNICK, J.S. AND S.V. GREGORY. 1981. Temporal changes in periphyton standing crop during an unusually dry winter in streams of the western Cascades, Oregon. *Hydrobiologia* 83: 197–205.

SLÁDECKOVÁ, A. 1962. Limnological investigation methods for the periphyton ("Aufwuchs") community. *Bot. Rev.* 28: 286–350.

SMITH, G.M. 1933. *The Freshwater Algae of the United States, 1st ed.* McGraw–Hill, London.

SORNMANI, S., V. KITIKOON, C. HARINASUTA AND O. PATHAMMAVONG. 1971. Epidemiological study of schistosomiasis japonica on Khong Island, southern Laos. *S.E. Asian J. Trop. Med. Publ. Hlth* 2: 365–374.

STANDER, J.M. 1970. Diversity and similarity of benthic fauna of *Oregon*. M.S. thesis, Oregon State University, Corvallis.

STEINMAN, A.D., C.D. MCINTIRE, S.V. GREGORY AND G.A. LAMBERTI. 1989. Effects of irradiance and grazing on lotic algal assemblages. *J. Phycol.* 25: 478–485.

TEMCHAROEN, P. 1971. New aquatic mollusks from Laos. *Arch. Molluskenk.* 101: 91–109.

VOGE, M., D. BRUCKNER AND J.I. BRUCE. 1978. *Schistosoma mekongi* sp. n. from man and animals, compared with four geographic strains of *Schistosoma japonicum*. *J. Parasitol.* 64: 577–584.

Table 1. List of the algal species found in the Mekong River, within the range of *Neotricula aperta* (gamma race), of Thailand and Laos (May 1991–May 1992).

DIVISION (Sub–division)
ORDER
FAMILY:

CHLOROPHYTA (Chlorophyceae)

CHLOROCOCCALES

CHLOROCOCCACEAE:
Chlorococcum infusionum (Schrank) Meneghini

OOCYSTACEAE:
Ankistrodesmus falcatus (Corda) Ralfs
Oocystis borgei Snow
Palmellococcus miniatus (Kützing) Chodat

SCENEDESMACEAE:
Actinastrum gracillimum G.M. Smith
Scenedesmus armatus (Chodat) G.M. Smith
Scenedesmus bijuga Chodat

OEDOGONIALES

OEDGONIACEAE:
Bulbochaete Agardh

TETRASPORALES

PALMELLACEAE:
Gloeocystis gigas (Kützing)

ULOTRICHALES

CLADOPHORACEAE:
Cladophora glomerata Kützing
Rhizoclonium crispum Kützing
Rhizoclonium hieroglyphicum (Agardh) Kützing

COLEOCHAETACEAE:
Coleochaete divergens Pringsh

PROTOCOCCACEAE:
Pleurococcus vulgaris Meneghini (syn. *Phytoconis, Protococcus viridis*)

ULOTRICHACEAE:
Stichococcus bacillaris Näegeli

ZYGNEMATALES

DESMIDIACEAE:
Closterium acerosum (Schrank) Ehrenberg

Cosmarium circulare Reinsch
Penium minutum (Ralfs) Cleve
Tetmemorus Ralfs

MESOTAENIACEAE:
Cylindrocystis brebissonii Meneghini
Cylindrocystis diplospora Lund
Gonatozygon aculeatum Hastings
Netrium Näegeli

ZYGNEMATACEAE:
Pleurodiscus purpureus (Wolle) Lagerheim
Spirogyra Link
Zygnema Agardh

(Heterokontae)

HETEROSIPHONALES
BOTRYDIACEAE:
Botrydium Wallroth

CHRYSOPHYTA (Bacillariophyceae)

CENTRALES
COSCINODISCACEAE:
Cyclotella meneghiniana Kützing

PENNALES
ACHNANTHACEAE:
Achnanthes brevipes (Kützing) Cleve
Achnanthes crenulata Grunow
Achnanthes lanceolata (Brébisson) Grunow
Cocconeis pediculus Ehrenberg
Cocconeis placentula var. *euglypta* (Ehrenberg) Cleve
Cocconeis placentula var. *lineata* (Ehrenberg) Van Heurck
Rhoicosphenia curvata (Kützing) Grunow

CYMBELLACEAE:
Amphora ovalis Kützing
Cymbella cistula var. *maculata* (Ehrenberg) Kirchner
Cymbella cupsidata Kützing
Cymbella graciles Kützing
Cymbella lanceolata (Ehrenberg) Brun
Cymbella naviculiformis (Auerwald) Heib
Cymbella obtusiuscula (Kützing) Grunow [syn. *Encyonema* Kützing]
Cymbella sinuata var. *sinuata* Gregory
Cymbella tumida (Brébisson ex. Kützing) Van Heurck

Cymbella turgida (Gregory)
Cymbella ventricosa Kützing
Epithemia turgida (Ehrenberg) Kützing
Rhopalodia gibberula (Ehrenberg) O.F. Muller

DIATOMACEAE:
Diatoma elongatum (Lyngbye) Agardh
Diatoma vulgare var. *vulgare* Bory

EUNOTIACEAE:
Eunotia arcus Ehrenberg

FRAGILARIACEAE:
Fragilaria capucina Desmazières
Fragilaria construens (Ehrenberg) Grunow
Fragilaria crotonensis Kitten
Fragilaria intermedia Grunow
Fragilaria virescens Ralfs
Synedra affinis var. *affinis* Kützing
Synedra affinis var. *fascicultata* (Kützing) Grunow
Synedra pulchella var. *pulchella* (Kützing) Ralfs
Synedra rumpens var. *familiaris* (Kützing) Hustedt
Synedra tabulata Ehrenberg
Synedra ulna var. *oxyrhynchus* (Kützing) Van Heurck
Synedra ulna var. *ulna* (Nitzsch) Ehrenberg

GOMPHONEMATACEAE:
Gomphonema augur Ehrenberg
Gomphonema gracile Ehrenberg
Gomphonema olivaceum (Lyngbye) Kützing
Gomphonema parvulum Kützing

NAVICULACEAE:
Amphipleura pellucida Kützing [syn. *Frustulia pellucida* Kütz.]
Diploneis elliptica (Kützing) Cleve
Frustulia rhomboides var. *rhomboides* (Ehrenberg) De Toni
Frustulia viridula (Brébisson) De Toni
Gyrosigma obtusatum (Sullivan) [syn. *G. nodiferum* (Grun.)] Reim
Gyrosigma spenceri (Quekett) Cleve
Mastogloia smithii (Smith) Thwaites
Navicula anglica var. *subsalsa* Grunow
Navicula bacillum var. *bacillum* Ehrenberg
Navicula cantonensis Ehrenberg
Navicula cryptocephala var. *veneta* (Kützing) Grunow
Navicula cupsidata var. *ambigua* (Ehrenberg) Cleve
Navicula exigua var. *exigua* (Gregory) Grunow
Navicula gracilis Ehrenberg

Navicula lanceolata (Agardh) Kützing
Navicula medisculus Schumann
Navicula oppugnata Hustedt
Navicula placentula (Ehrenberg) Grunow
Navicula pupula var. *elongata* (Gregory) Grunow
Navicula pupula var. *rectangularis* (Gregory) Grunow
Navicula radiosa var. *radiosa* Kützing
Neidium affine var. *amphirhynchus* (Ehrenberg) Cleve
Pinnularia viridis (Nitzsch) Ehrenberg
Stauroneis anceps Ehrenberg
Stauroneis gracilis (Ehrenberg) W. Smith

NITZSCHIACEAE:
Denticula tenuis var. *crassula* (Naëg. ex. Kütz.) W & G.S. West
Nitzschia capitellata Hustedt
Nitzschia disspata (Kützing) Grunow
Nitzschia filiformis (W. Smith) Schütt [syn. H*omoeocladia* Agardh]
Nitzschia frustulum var. *frustulum* (Kützing) Grunow
Nitzschia kutzingiana Hilse
Nitzschia palea var. *palea* (Kützing) W. Smith
Nitzschia tryblionella Hantzsch

SURIRELLACEAE:
Surirella splendida (Ehrenberg) Kützing

TABELLARIACEAE:
Tabellaria fenestrata (Lyngbye) Kützing

(Chrysophyceae)

CHRYSOMONADALES
CHROMULINACEAE:
Chrysococcus Klebs

CYANOPHYTA (Myxophyceae)

CHROOCOCCALES
CHROOCOCCACEAE:
Coelosphaerium confertum W & G.S. West
Coelosphaerium kuetzingianum Näegeli
Chroococcus cohaerens (Brébisson) Näegeli
Microcystis marginata (Meneghini) Kützing
Synechococcus aeruginosus Näegeli [syn. *Coccochloris aeruginosa* (Näeg.)]
Synechocystis aquatilis Sauvagean [syn. *Chroococcus limneticus* Lemm.]

HORMOGONALES
OSCILLATORIACEAE:

Arthrospira Stizenberger
Lyngbya birgei G.M. Smith
Lyngbya ochracea (Kützing) Thuret
Lyngbya putealis Montagne
Oscillatoria agardhii Gomont
Oscillatoria amphibia Agardh
Oscillatoria chalybea Mertens
Oscillatoria formosa Bory
Oscillatoria limosa Agardh
Oscillatoria ornata Agardh
Oscillatoria splendida Greville
Oscillatoria tenuis Agardh
Phormidium ambiguum Kützing
Phormidium mucicola Naumann & Huber–Pestalozzi
Phormidium tenue (Meneghini) Gomont
Spirulina albida Turpin
Trichodesmium lacustre Klebahn

RIVULARIACEAE:
Calothrix braunii Barnet & Flahault

SCYTONEMATACEAE:
Plectonema tenue Thúret
Plectonema tomasiniana (Kützing)

(Rhodophyceae)

BANGIALES

ERYTHROTRICHIACEAE:
Compsopogon coeruleus (Balbis) Montagne

Table 2. Algal dominants of the epilithon within the microhabitat of *Neotricula aperta* in the Mekong river at Ban–Khi–Lek, Thailand. Separate entries are made for those substrata bearing large numbers of *N. aperta* snails (SN+) and for those bearing few or no snails (SN–). The 5 most common chlorophycean, 10 most common chrysophycean and 5 most common cyanophycean taxa are reported (algal diversity permitting) for samples collected between May 1991 and May 1992. Relative frequencies (as a proportion of the total cell count for the sample) are given for each algal dominant.

2 May 1991 (mid low water): SN+	SN–
Chlorophyta	
Spirogyra sp. (0.05)	*Palmellococcus miniatus* (0.07)
Palmellococcus miniatus (0.02)	*Bulbochaete sp.* (0.05)
Oocystis borgei (0.004)	*Oocystis borgei* (0.01)
Closterium acerosum (0.002)	*Coleochaete divergens* (0.005)
Tetmemorus sp. (0.002)	*Gloeocystis gigas* (0.005)
Chrysophyta	
Cymbella ventricosa (0.09)	*Navicula c. veneta* (0.08)
Frustulia r. rhomboides (0.04)	*Navicula r. radiosa* (0.05)
Navicula cantonensis (0.03)	*Cymbella ventricosa* (0.04)
Navicula c. veneta (0.03)	*Synedra affinis* (0.03)
Rhopalodia gibberula (0.03)	*Cymbella cistula* (0.02)
Cymbella cupsidata (0.02)	*Epithemia turgida* (0.02)
Navicula r. radiosa (0.02)	*Frustulia r. rhomboides* (0.02)
Cymbella cistula (0.01)	*Navicula gracilis* (0.02)
Navicula p. elongata (0.01)	*Gomphonema gracile* (0.01)
Navicula p. rectangularis (0.01)	*N. p. rectangularis* (0.01)
Synedra ulna var. *ulna* (0.01)	
Cyanophyta	
Phormidium mucicola (0.22)	*Phormidium mucicola* (0.14)
Oscillatoria tenuis (0.11)	*Oscillatoria tenuis* (0.10)
Synechococcus aeruginosus (0.06)	*Phormidium tenue* (0.08)
Oscillatoria formosa (0.02)	*Oscillatoria splendida* (0.03)
Phormidium tenue (0.01)	*Oscillatoria amphibia* (0.02)

Table 2 (continued)

18 May 1991 (late low water): SN+	SN–
Chlorophyta	
Palmellococcus miniatus (0.04) *Spirogyra spp.* (0.03) *Chlorococcum infusionum* (0.01) *Cosmarium circulare* (0.01) *Oocystis borgei* (0.01)	*Rhizoclonium crispum* (0.27) *Palmellococcus miniatus* (0.09) *Rhizoclonium hieroglyphicum* (0.04) *Oocystis borgei* (0.02)
Chrysophyta	
Frustulia r. rhomboides (0.04) *Navicula c. veneta* (0.03) *Synedra rumpens* (0.03) *Cocconeis pediculus* (0.02) *Cymbella cupsidata* (0.02) *Navicula cantonensis* (0.02)	*Epithemia turgida* (0.07) *Rhopalodia gibberula* (0.06) *Cymbella ventricosa* (0.04) *Frustulia r. rhomboides* (0.04) *Navicula c. veneta* (0.04) *Navicula lanceolata* (0.04)
Cyanophyta	
Phormidium tenue (0.29) *Oscillatoria tenuis* (0.23) *Synechococcus aeruginosus* (0.10) *Oscillatoria formosa* (0.06) *Oscillatoria amphibia* (0.03)	*Oscillatoria amphibia* (0.07) *Oscillatoria tenuis* (0.06) *Phormidium mucicola* (0.04) *Phormidium tenue* (0.02) *Oscillatoria chalybea* (0.01)
10 June 1991 (carly spate): SN+	SN–
Chlorophyta	
Bulbochaete sp. (0.08) *Chlorococcum infusionum* (0.04) *Oocystis borgei* (0.04) *Palmellococcus miniatus* (0.02) *Penium minutum* (0.02)	*Netrium sp.* (0.06) *Chlorococcum infusionum* (0.03) *Palmellococcus miniatus* (0.03) *Coleochaete divergens* (0.03)
Chrysophyta	
Navicula c. veneta (0.12) *Achnanathes crenulata* (0.08)	*Navicula c. veneta* (0.11) *Achnanthes crenulata* (0.06)

Table 2 (continued)

Gyrosigma spenceri (0.06) *Navicula r. radiosa* (0.05) *Synedra affinis* (0.05)	*Nitzschia capitellata* (0.06) *Synedra ulna* var. *ulna* (0.06)
Cyanophyta	
Oscillatoria tenuis (0.17) *Phormidium mucicola* (0.03) *Oscillatoria formosa* (0.02) *Spirulina albida* (0.02) *Synechococcus aeruginosus* (0.02)	*Oscillatoria tenuis* (0.25) *Phormidium mucicola* (0.11) *Oscillatoria amphibia* (0.03) *Phormidium tenue* (0.03)
10 November 1991 (late spate)	
SN+	SN–
Chlorophyta	
Palmellococcus miniatus (0.40)	*Bulbochaete sp.* (0.20) *Pleurococcus vulgaris* (0.05) *Gonatozygon aculeatum* (0.02)
Chrysophyta	
	Chrysococcus sp. (0.02) *Navicula mediscu1us* (0.02) *Stauroneis gracilis* (0.02)
Cyanophyta	
Oscillatoria tenuis (0.60)	*Oscillatoria tenuis* (0.27) *Phormidium tenue* (0.13) *Oscillatoria formosa* (0.10) *Coelosphaerium kuetzingianum* (0.08) *Oscillatoria splendida* (0.05)
18 February 1992 (post spate recovery)	
SN+	SN–
Chlorophyta	
Chlorococcum infusionum (0.01) *Cosmarium circulare* (0.01)	*Cladophora glomerata* (0.23) *Pleurococcus vulgaris* (0.03)

Table 2 (continued)

Pleurococcus vulgaris (0.01)	*Spirogyra sp.* (0.02) *Cosmarium circulare* (0.01)
Chrysophyta	
Navicula r. radiosa (0.07) *Navicula medisculus* (0.06) *Navicula cupsidata ambigua* (0.05) *Navicula p. rectangularis* (0.05) *Fragilaria construens* (0.04) *Navicula c. veneta* (0.04) *Cymbella cupsidata* (0.03) *Cymbella obtusiuscula* (0.02) *Stauroneis gracilis* (0.01)	*Frustulia r. rhomboides* (0.13) *Navicula c. veneta* (0.13) *Navicula medisculus* (0.03) *Gyrosigma spenceri* (0.02) *Navicula p. rectangularis* (0.02) *Nitzschia capitellata* (0.02)
Cyanophyta	
Oscillatoria tenuis (0.27) *Phormidium tenue* (0.07) *Phormidium mucicola* (0.06) *Lyngbya ochracea* (0.03) *Trichodesmium lacustre* (0.03)	*Phormidium mucicola* (0.19) *Trichodesmium lacustre* (0.12) *Oscillatoria formosa* (0.07) *Oscillatoria tenuis* (0.05) *Phormidium tenue* (0.03)
1 April 1992 (high–low–water transition)	
SN+	SN–
Chlorophyta	
Cladophora glomerata (0.50) *Rhizoclonium crispum* (0.03) *Bulbochaete sp.* (0.02) *Chlorococcum infusionum* (0.01) *Palmellococcus miniatus* (0.01)	*Cladophora glomerata* (0.84)
Chrysophyta	
Cymbella sinuata (0.05) *Cocconeis pediculus* (0.04) *Cymbella graciles* (0.04) *Cocconeis placentula euglypta* (0.03) *Mastogloia smithii* (0.03) *Tabellaria fenestrata* (0.03)	*Gomphonema gracile* (0.01) *Gyrosigma spenceri* (0.01) *Nitzschia palea* (0.01)

Table 2 (continued)

Cymbella ventricosa (0.02) *Gomphonema gracile* (0.02) *Navicula c. veneta* (0.02) *Navicula r. radiosa* (0.01)	
Cyanophyta	
Oscillatoria tenuis (0.03) *Oscillatoria chalybea* (0.02) *Oscillatoria agardhii* (0.01) *Oscillatoria amphibia* (0.01) *Oscillatoria ornata* (0.01) *Phormidium tenue* (0.01)	*Oscillatoria tenuis* (0.04) *Phormidium tenue* (0.03) *Oscillatoria formosa* (0.02) *Oscillatoria ornata* (0.02) *Synechococcus aeruginosus* (0.01)
19 April 1992 (early low water)	
SN+	SN−
Chlorophyta	
Spirogyra sp. (0.08) *Rhizoclonium crispum* (0.03) *Cylindrocystis brebissonii* (0.01)	*Spirogyra spp.* (0.12) *Zygnema spp.* (0.06) *Rhizoclonium crispum* (0.04) *Pleurococcus vulgaris* (0.03)
Chrysophyta	
Navicula r. radiosa (0.06) *Gomphonema gracile* (0.04) *Cocconeis placentula* (0.03) *Gomphonema parvulum* (0.03) *Gyrosigma spenceri* (0.03) *Achnanthes brevipes* (0.02) *Cymbella ventricosa* (0.02) *Frustulia viridula* (0.02) *Navicula c. veneta* (0.02) *Navicula medisculus* (0.02)	*Navicula r. radiosa* (0.07) *Navicula c. veneta* (0.05) *Cocconeis pediculus* (0.04) *Frustulia r. rhomboides* (0.04) *Navicula medisculus* (0.04) *Gomphonema gracile* (0.03) *Gyrosigma spenceri* (0.03) *Cymbella ventricosa* (0.02) *Gomphonema parvulum* (0.02) *Nitzschia dissipata* (0.02)
Cyanophyta	
Oscillatoria ornata (0.20) *Oscillatoria formosa* (0.19) *Oscillatoria chalybea* (0.11) *Phormidium mucicola* (0.03) *Oscillatoria tenuis* (0.02)	*Oscillatoria chalybea* (0.15) *Oscillatoria tenuis* (0.09) *Lyngbya birgei* (0.04) *Oscillatoria formosa* (0.02) *Phormidium mucicola* (0.02)

Table 3. Algal dominants of the epilithon within the microhabitat of *Neotricula aperta* in the Mekong river at Ban–Xieng–Wang, Laos. Separate entries are made for those substrata bearing large numbers of *N. aperta* snails (SN+) and for those bearing few or no snails (SN–). The 5 most common chlorophycean, 10 most common chrysophycean and 5 most common cyanophycean taxa are reported (species diversity permitting) for samples collected between May 1991 and May 1992. Relative frequencies (as a proportion of the total cell count for the sample) are given for each algal dominant.

7 January 1992 (post spate recovery) SN+	SN–
Chlorophyta	
Pleurococcus vulgaris (0.06)	*Rhizoclonium hieroglyphicum* (0.66)
Palmellococcus miniatus (0.03)	*Pleurococcus vulgaris* (0.03)
Chlorococcum infusionum (0.02)	*Oocystis borgei* (0.01)
Cosmarium circulare (0.02)	
Gloeocystis gigas (0.01)	
Chrysophyta	
Fragilaria construens (0.15)	*Frustulia r. rhomboides* (0.07)
Navicula c. veneta (0.06)	*Fragilaria construens* (0.03)
Gomphonema olivaceum (0.03)	*Navicula c. veneta* (0.03)
Gyrosigma spenceri (0.03)	
Navicula oppugnata (0.03)	
Achnanthes brevipes (0.02)	
Frustulia r. rhomboides (0.02)	
Navicula medisculus (0.02)	
Navicula r. radiosa (0.02)	
Rhopalodia gibberula (0.02)	
Cyanophyta	
Oscillatoria tenuis (0.17)	*Oscillatoria tenuis* (0.10)
Oscillatoria formosa (0.13)	*Oscillatoria chalybea* (0.03)
Phormidium mucicola (0.06)	*Arthrospira sp.* (0.01)
Spirulina albida (0.05)	*Phormidium mucicola* (0.01)
Calothrix braunii (0.02)	

Table 3 (continued)

28 March 1992 (early low water) SN+	SN–
Chlorophyta	
Spirogyra spp. (0.44) *Oocystis borgei* (0.02) *Pleurococcus vulgaris* (0.02) *Chlorococcum infusionum* (0.01)	*Spirogyra spp.* (0.05) *Pleurococcus vulgaris* (0.02) *Chlorococcum infusionum* (0.01) *Rhizoclonium crispum* (0.01)
Chrysophyta	
Fragilaria construens (0.04) *Gomphonema parvulum* (0.02) *Navicula c. veneta* (0.02) *Rhoicosphaenia curvata* (0.02) *Cocconeis placentula* (0.01) *Cymbella lanceolata* (0.01) *Gyrosigma spenceri* (0.01)	*Cocconeis pediculus* (0.11) *Navicula c. veneta* (0.03) *Achananthes brevipes* (0.02) *Fragilaria construens* (0.02) *Navicula r. radiosa* (0.02) *Cymbella graciles* (0.01) *Cymbella tumida* (0.01)
Cyanophyta	
Oscillatoria ornata (0.17) *Oscillatoria chalybea* (0.07) *Oscillatoria agardhii* (0.03) *Oscillatoria amphibia* (0.02) *Oscillatoria tenuis* (0.02) *Phormidium mucicola* (0.02)	*Oscillatoria ornata* (0.28) *Oscillatoria chalybea* (0.06) *Oscillatoria agardhii* (0.05) *Phormidium mucicola* (0.03) *Oscillatoria formosa* (0.02) *Synechococ. aeruginosus* (0.02)

Table 4. Measurements of the greatest dimension (μm) for some dominant algal taxa comprising the epilithon sampled from *Neotricula aperta* microhabitats (SN+) and from relatively snail free substrata (SN–). The samples were collected throughout a 12 month period from the Mekong river at Ban–Khi–Lek, Thailand, and at Ban–Xieng–Wang, southern Laos. The data for the Achnanthaceae refer to *Cocconeis spp.* only (as no other taxa were prevalent). Data are mean ± S.D., n = 6–20, and reported to 3 significant figures.

	Achnanthaceae		Myxophyceae		Naviculaceae	
Date	SN+	SN–	SN+	SN–	SN+	SN–
BKL:						
02/05/91	19.8±3.01	15.1±1.50	55.3±59.7	40.7±22.0	29.4±13.0	-
18/05/91	20.7±2.98	27.0±0.06	38.5±82.0	30.7±21.5	38.6±0.49	26.9±8.79
18/02/92	-	-	65.8±54.0	48.7±30.5	26.7±5.94	25.9±5.58
1–19/4/92	31.1±9.53	43.1±3.81	89.3±71.3	-	25.9±7.33	32.6±24.4
BXW:						
07/01/92	30.6±0.74	28.0±1.13	74.9±67.9	39.4±41.2	27.7±19.3	23.8±1.42
28/03/92	21.1±2.05	32.6±8.83	82.1±52.1	48.3±47.2	24.7±10.4	36.2±22.1