FRESHWATER BIOLOGICAL ASSOCIATION

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DEAD ZONES, LIVE MARKERS

The biological environments of larger

U.K. rivers : Final report to DoE

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This report is submitted to the Department in accordance with contractual requirements and as evidence of the nature and extent of the investigations conducted on the Department's behalf (Contract PECD/7/7/200).

CONTENTS

CONTRACTUAL DETAILS

Title   : Biological environments of larger UK rivers

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Objectives:

    The conceptual basis of the present work was founded upon the contention
(i) that hitherto-accepted models of fluvial flow are inappropriate for the
estimation of dispersion rates of entrained solutes and particulate loads and
(ii) that the existence of viable, self-replicating phytoplankton in rivers is
paradoxical without the simultaneous and widespread existence in those rivers
of physical mechanisms for retaining significant volumes of water against the
general discharge. The single, aggregated dead-zone- (or ADZ-) model (Young &
Wallis, 1987) provided practical evidence that the ADZ-concept might furnish an
important basis for the investigation if (i) and (ii) above: as viable, growing
respondents of the physical environment of larger rivers, the dynamics of
natural phytoplankton populations ought to furnish useful markers of the
spatial- and short-term temporal-variability of the fluvial flow. The project
was conceived to provide insights into the mechanisms by which populations of

particles (in this instance, phytoplankton) behave in relation to fluvial flow and, thus, to better model the dispersive properties of rivers and the ecological principles governing the distribution of potamoplankton generally.

1. INTRODUCTION

1.1 BACKGROUND

On the night of 2 November 1986, a serious fire broke out on the premises of Sandoz Chemicals, Basel, Switzerland. During the course of fighting the fire, a quantity of concentrated pesticide entered the eluting hose-water and, thence, found its way into the drainage of the Rhine. The consequences on the aquatic life in the river, especially the fish populations were tragic enough, proving toxic for several hundreds of kilometers downstream. However, the aspect we would wish to emphasise here is that at the many draw-off points for drinking water, (inter alia, Frankfurt, the Ruhr and in the Netherlands) the estimated times of arrival, passage and eventual clearance of the contaminated water, calculated from the monitored rates of flow in the river, proved to be hopelessly wrong: rather than the anticipated 4-5 days to reach the North Sea, the 'tail' took some three weeks to fall back to acceptable safe levels for potable supplies.

This particular incident provides a rather harrowing and bizarre example of what is becoming recognized as a fundamental deficiency in our appreciation and understanding of channel flow. Time and again, it has been pointed out that the assumption of Fickian dispersion and downstream transport at one mean velocity consistently underestimates, sometimes by a large margin, the times taken to transport solutes and suspensoids downstream (Day & Wood, 1976; Chatwin & Allen, 1985; Water Authorities Association, 1986). What is especially remarkable is that the infinite variability in the velocity profiles in given locations in given rivers and at given times is generally recognized and accepted: clear intuitive evidence is provided by the distribution of different bed materials (from silts to coarse gravel and small boulders) which identify local differences if the competence of the flow (i.e. particle-load transport capacity, a close correlative of the exponent of current velocity); moreover, anyone who has gazed into a clear trout-stream will notice that floating particles pass the point of observation at, manifestly, quite different speeds and that migrating fish will 'lie', almost motionless, at various points along the water course, apparently in quite static water.

The question then resolves itself to "Is this behaviour general?" If so, can it be quantitatively expressed and adequately modelled? Neither are the answers purely esoteric: apart from the effects of instances of inadvertent pollution (see above), strategic questions are raised about load tolerances and consents to discharge to rivers, to which it is important to give the best

possible recommendations. Answers are also relevant to a further aspect of river quality, that is its capacity to support an active community of planktonic organisms, the pigments of which may colour the water in intense green or brown: it has been argued (Reynolds 1988) that such development would be untenable without the simultaneous and widespread existence of patches of sluggish or non-flowing water in which inocula were maintained to reinfect the flowing water.

Some important progress has been made towards the twin goals of a mathematical description of the processes resulting in flow restriction, local water retention and extended travel times through river channels and of some predictive relationship of these processes to readily quantifiable characteristics of the channel itself - its gradient, sectional shape (hydraulic radius), bed structure and discharge. In a sense, the Manning Equation recognizes the importance of these latter variables in relation to the mean velocity but a complete understanding of their influence will rely heavily on the satisfaction of the former objective. This has been the subject of considerable investigative efforts, most particularly those of Professor P.C. Young and his colleagues at the University of Lancaster (see summaries in Young & Wallis, 1987; Wallis, Young & Beven 1989). In essence, they have been able to demonstrate the almost universal existence of reach-retentive mechanisms in the selection of small- and medium rivers they have investigated in north-west England. Moreover, through the successful application of a dye-dispersion technique, they have developed a quantitative description of the aggregate effects of water retention on its elimination. This attributes the retention to ('dead-') zones of zero flow but which nevertheless exchange fluid with flowing water, dye-markers entering and leaving the dead zone at rates determined by the relative volumes of their masses and the rate of fluid exchange between them.

This aggregated dead-zone (or ADZ) model remains the best quantitative approximation to reach-retention. The next stages in its refinement are to identify the component zones, to estimate their dynamic behaviour and to extend the tenancy of the model to apply to larger rivers.

The latter, especially, requires the application of alternative techniques of measurement, principally for logistic reasons. One such alternative approach is that developed in the present work and which makes use of the presence of river plankton. If the supposition is correct that dead-zones retain actively-growing populations of pigmented algae, from which the population of the flow is continuously recruited, then these same zones should be distinguishable by their enhanced content of the relevant algae. Further,

novel, synoptic techniques (e.g. using _in vivo_ fluorescence of chlorophyll or its remote sensing) have become available which might be applied to detect localities of enhanced chlorophyll concentration and, at the same time, provide an index for fluid exchange, invoking the relative dynamics of self replication and removal of live, intact cells. Moreover, the application of the same techniques have the potential to rectify general deficiencies in our understanding of the ecology of planktonic populations. It is this rationale which has underpinned the study which is summarised in the present report.

1.2. SELECTION OF THE STUDY SITE : THE RIVER SEVERN

This study, intended as a necessary preliminary to further, more generalised work, has concentrated upon the upper- and middle reaches of one of the major UK rivers - the Severn. Several factors were prominent in this choice:

(a) It _is_ a large river by U.K. standards (see Fig. 1; length: 288 km; drainage-basin area: 11 655 km^2; mean discharge : 62.7 m^3 s^{-1}).

(b) It does support a distinctive and quantifiable phytoplankton (Swale 1969; Severn-Trent Water, personal communication to the authors.

(c) Much of its middle length flows across unconsolidated glacial drift. We can assume that, compared with many rivers in highland Britain, the form of the channel has been determined more by fluvial processes than by geological and geomorphological constraints. Moreover, the richness of these features, including a distinctive pool-riffle sequence, meanders, fanning and braiding with a commensurate variety of detailed flow structures such as backflows, cross channel currenting and plunging, offered opportunities to investigate a wide range of potential retentive mechanisms.

(d) Despite the undoubted influence of abstraction, effluent discharges and, most particularly, the presence of two major dams in the upper catchment (the Clywedog and Efyrnwy Reservoirs), which together qualify the Severn as a regulated river (Douglas, 1988), it is nevertheless a relatively 'flashy' river, its discharge being readily responsive both to episodes of heavy rainfall and run-off yield in the upper catchment and to the effects of summer drought periods.

In fact, we can point to a series of observations on the plankton of the river through a variety of contrasted reaches and under a full range of discharge conditions (see Fig. 2).

2. METHODS

The principal methods used in these studies may be conveniently separated among those directed towards the flow patterns in the river, those directed to the structure and abundance of phytoplankton and those directed towards the remote detection of both.

Water velocity was measured directly and simultaneously through a series of OH recording impellers variously arranged on a weighted, varied pole, ensuring measurements were taken horizontally and in the direction of flow. Readings were integrated and logged directly on a handheld 'Husky' microcomputer.

Variations in the quantity of river plankton at the same stations were analogised to measurements of in-vivo fluorescence of the chlorophyll photochemical systems. The principles of this method were established some time ago by Lorenzen (1966) but there has been an ongoing debate about the reliability and quantitative calibration of the measurements as an index of biomass (e.g. Harris, 1978, 1980). Even as a somewhat arbitrary assessment of the instantaneously unused photosynthetic capacity of channel intercepted light, it has been shown repeatedly to identify quickly and conveniently, significant discontinuities in phytoplankton distribution (e.g. Berman 1972, Heaney 1978). In the present work, rapid sequential spot estimations were made using a Chelsea Instruments 'Aquatracka II' (Chelsea Instruments : London) submersible remote fluorimeter. This approach, developed (inter alia) for work on oceanic-plankton patchiness, proved highly sensitive and well suited to river work: such is the precision of its spectral sensitivity that it picks up small variation in chlorophyll concentration despite an often overwhelming presence of inert suspended materials (silt, clay etc).

Apart from a few preliminary tests of what the 'Aquatracka' would actually determine, few independent tests of algal concentration (chlorophyll, cell counts) were conducted. The approach was to use the Aquatracka to 'home in' on fluvial patches identified by enhanced fluorescence and to sample and analyse these, in detail, following more traditional methods. In most cases, this meant separate water samples, fixed and labelled for archiving, and which were later analysed by microscopic methods (Lund, Kipling & LeCren 1958). These methods were also used in a 'background monitoring' of the plankton in the river and which eventually proved of value to general statements about downstream river growth. A total of 13 stations, one below Clywedog dam and

the rest on the Severn itself, between the Hafren Forest in the headwaters and
the Ironbridge Gorge, in the middle reaches (see Fig. 3 and Table 1), were
sampled on ten occasions through the year. Originally the intention had been
to establish the origin of the downstream populations but the data set provided
a broader overview of the distribution of fluvial processes, in space and time.
The same basic observation, of water depth (at a regular sampling point located
on a river crossing in each case), temperature, turbidity and pH were made at
each station.

Remote sensing suffered extensively from the vagaries of British weather
but it was eventually possible to complete two overflights of one study reach
(Leighton, between Station 11 and 12). A series of high resolution images on
the Daedalus 1268 system was obtained, anticipating spectral separation for
imagery analysis. With the help of Dr W. Slade's Group at Bangor, it was
eventually possible to analogize by colour gradients, distributions in 'Band 3'
(sensitive to chlorophyll) and 'Band 11' (sensitive to heat) to construct
images of these target determinands in the river. On both occasions, (May,
August 1988) a comprehensive series of point observations and samples for later
analysis were collected. Some of these have been processed subsequently where
the information seemed expedient but the samples remain in store if further
analyses are required. The information processed from these samples has been
used to validate, substantiate and calibrate (i.e. verify) the remote-sensed
angles.

3. RESULTS

3.1 GENERAL PROPERTIES OF THE PELAGIC ENVIRONMENT OF THE UPPER AND MIDDLE SEVERN

3.1.1 <u>Discharge and Transport</u>   The essential features of the pelagic environment of the Severn are dominated by the origin of its headwaters in the Cambrian Mountains, mostly of Silurian slates and mudstones, and by their rapid descent through glaciated channels to the drift deposits of the Marches and West Midlands. The descent from the sources in Plynlimon Fawr (max. altitude: 753 m) and of the Efyrnwy tributary in the Berwyn Mountains (max. altitude: 820 m) is in the region of 450 m in 20 km or more, before flat valley bottoms are encountered and where the gradient falls away to < 3 m km^{-1} and to less than 0.5 m km^{-1} after another 60 km or so. In consequence, the moist westerly airstream and the succession of eastward-tracking fronts that are intercepted by the Welsh uplands (typical annual rainfall: $>$ 1500 mm) where precipitation is often intense, generate frequent surges of channel flow in the Severn drainage (see Fig. 2). In the middle reaches, this behaviour is perceived as a susceptibility to flood, it is interesting to note the distribution of towns and river-crossing points in Shropshire has relied strongly on the presence of suitable geological constraints and the narrowing of the flood plain appropriately.

It is also important to realise that the Efyrnwy generates slightly over half the discharge in the Severn below their confluence at Melverley, Shropshire (just above Crew Green, Station 8). Thus the variability in daily mean discharges gauged at Montford generally follows the identical trend to those at Abermiwl, though usually (not always) with two to three times the discharge. It would be reasonable to deduce that much of the flow reaching, say, Ironbridge, Shropshire (just below Station 12) or Bewdley, Worcs., well-beyond the study area, is substantially influenced by rainfall events in central Wales. Certainly, there is excellent match between the corresponding peaks at the three gauging stations shown (Fig. 2), albeit with a mean lag of 1-1.5 days (equivalent to a surge velocity of 0.7 - 1.0 m s^{-1}). However, in winter, the Severn at Bewdley is substantially influenced by the additional runoff shed from the lowland areas via the Perry, Rea and Tern/Roden tributaries.

Equally, as run-off inputs subside, the flows in the upper Severn fall quickly back to an ambient (mainly through-flow-sustained) discharge level and, subject to the analogous winter-damping, the effect is carried through to the

middle and lower reaches. Thus, the basic hydraulic environment would appear to be one of some ambient flow condition subject to periodic disturbance by flood events (observed range at Montford Bridge 8 - 250 $m^3 s^{-1}$); in the middle reaches, this variability is accommodated chiefly by a rise in water level, wherein mean velocity increases scarcely over one order of magnitude 0.2 - 2.0 $m s^{-1}$, and which, ultimately, washes over the flood plain. In the upper reaches, the gradient does not permit significant rises in level or in reach storage, so the variability in discharge is met more by velocity fluctuations. These trends underlie the representation in Fig. 4 of spot-water depth measurements at the stations 1-12 covering the period of observations given in Table 1: the figure contrasts aspects of the relative stability of water level ("equilibrium" level) in the upper and middle reaches in relation to the gradient and distance downstream.

A second consequence of the abrupt transition from mountain stream to lowland river lies in the size distribution of the sedimentary material and transported particulates. In the upland reaches, the bed materials are generally coarse grained and the suspended loads of finer particles (silts, clays) are kept to a low level. Downstream, the banks and the bed of the river are cut through unconsolidated fine sedimentary infill, having been (mostly) deposited in the early kataglacial period. The more efficient flow regime, the faster average velocities and, most particularly, the greater water depth (Reynolds et al. 1989) all serve to maintain an environment dominated by particulates - in suspension and deposited on the bottom. Flood episodes both introduce new fine-particulate loads from the lowland catchment areas and resuspend material from the sediments. The result is that the river always tends to be more turbid in its downstream reaches and that turbidity is highest shortly after the onset of a severe flood event. These deductions apply well to the Severn (see Fig. 5): the water was usually found to be clear above Newtown (Stations 0-4) and never so below Crew Green (Stations 8-12), in the sense of being able to see to the bottom or very far into the water at all. At Welshpool (Station 7) this was possible only once (September 1987) but at Newtown (Station 6) impossible once. Thus, the transition in behaviour corresponds with the 'break of slope' of the river profile (Fig. 4).

3.1.2. Temperature

Water temperatures through the study period behaved much as would have been expected. At any given station, temperature varied with seasons, being

generally warmest in summer (maximum recorded: 19.5 Buildwas, 3 July 1987) and coolest in late winter (minimum recorded: 4.5 C; Mt Severn 23 February 1988; temperatures not taken in mid winter). On each occasion, some downstream warming was evident, being least in winter (from 6.5 C at Mt Severn to 8.5 C at Buildwas in March 1988) and greatest in sunny summer weather (July 1987: 11.7 C to 19.5 C over the same distance). In October 1987, a downstream fall in temperature was evident (from 10.5 C at Clywedog to 8.5 C at Buildwas).

3.1.3. Water chemistry

Apart from colorimetric readings of pH, which showed the expected downstream shift from values between 4.5 and 5.5. of waters emanating from the Plynlimon Fawr/Hafren Forest catchment to near-neutrality at Buildwas (though never exceeding pH 7: cf. Swale's (1969) data), chemical analyses did not figure in this present study. Although neither the Severn nor the Efyrnwy can be considered especially rich in dissolved nutrients, published information (e.g. Swale 1969; Severn Trent Water 1978 a.o.) indicates a sufficiency, at least in the middle reaches, of nitrogen and phosphorus to meet the requirements of moderate phytoplankton development (mean TON $>$ 1 mg 1^{-1} at stations below Llanidloes; SRP averaging up to 0.2 mg 1^{-1} at Atcham) and the assumption is made throughout that phytoplankton growth has not been limited by these nutrients. Soluble reactive silicon (SRSi), as 'silica' (SiO_2), is generally present in the middle reaches at concentrations of 5-6 mg 1^{-1} but is known to fall to indetectible levels following episodes of prolific diatom production (Swale 1969).

3.2. PHYTOPLANKTON STANDING CROPS IN THE UPPER AND MIDDLE SEVERN

3.2.1. Composition of the phytoplankton

The total biovolume of suspended algae recovered from the Severn (Fig. 7) were separated as far as possible into three broad categories, shown separately in Figs. 8-10:

(i) Species that are normally either epilithic, epiphytic or epipelic and detached into the flowing water. A large number of taxa were observed at least occasionally, mainly epilithic diatoms. As can be seen from Fig. 8, even the more common forms (species of Achnanthes, Cocconeis, Gomphonema, Meridion,

Pinnularia and Surirella) together contributed only a minor proportion of the suspended material.

Of course, the distinction between algae which obligately grow on surfaces and those which live a wholly planktonic existence is blurred by species which are not restricted to either: Synedra ulna and, especially, Navicula gracilis, are diatoms which seem capable of sustained growth whether attached or otherwise; since they showed regular downstream progressions consistent with planktonic growth they have been included in the 'eupotamoplankton' cagetory (iii, below). On the other hand, Melosira ambigua does not grow attached to surfaces but does normally inhabit the benthos of shallow eutrophic waters. Since its spasmodic appearance in the Severn, with respect to both time and space, is inconsistent with a truly planktonic life, it was retained in category (i). Melosira was the main component of the benthic complement at Atcham, Cressage and Buildwas in August 1987.

It is also pertinent to comment that, whereas we anticipated that a benthic component would be most in evidence during floods, i.e. when communities are actively destroyed, it was in fact during quiet weather and the height of the growth periods of these algae when they were encountered. Perhaps this represents the product of increasing instability as 'carpets' of these organisms build up on all available surfaces.

(ii) Species that are planktonic in ponds and lakes but do not persist downstream constitute the second category. There is evidence (Fig. 9) of an almost constant input of limnoplankton from Clywedog Reservoir, including species of Chrysophyte flagellates (Dinobryon, Chrysochromulina), Cryptophytes (Rhodomonas), 'oligotrophic' diatoms (Cyclotella comta, Tabellaria fenestrata) and, in summer, desmids like Pleurotaenium, Desmidium, Staurodesmus. Above Llanidloes, the Severn draining Plynlimon brings in a selection of other algae including such bog-pool desmids as Cylindrocystis and Roya. Members of this 'adventitious' category of species characteristically peter out and 'disappear' downstream.

(iii) Species that are planktonic and capable of strong positive in situ increase ('Eupotamoplankton'). Regardless of whether they are derived from limnoplankton or even from benthic communities or, in certain cases, not obviously from either, several species proved to be dominant components in the downstream plankton. Moreover, there were consistent trends towards downstream increases in their aggregate concentrations as well as in their seasonal abundance, (Fig. 10). At no time was there a significant potamoplankton in the

steeper headwater reaches above Caersws (Stn 4) and only episodically above
Abermiwl (Stn 6): these instances nevertheless coincide with downstream
abundances at Stns 7-12, which showed four major features:

    (a) a declining peak at the end of the first spring (1987)

    (b) a pronounced autumnal peak in September, 1987

    (c) a 'winter' minimum, October 1987 - March 1988

    (d) a renewed 'spring burst' in May 1988.

    These biomass peaks were mainly due to the growth of five species in
particular.

Stephanodiscus cf. tenuis Hust. is similar to the S. hantzschii of the River
Thames, from which it was distinguished with difficulty; S. tenuis was the name
given by Swale (1969) to the Severn Stephanodiscus. It varies in diameter
between 10 and 15 µm and between 5 and 8 µm in height. Its size overlaps with
the Cyclotella meneghiniana Kütz. that Swale (1969) described but which was not
distinguished here. The alga was never encountered above Llandinam and was
abundant only below Abermiwl (Fig. 11). Like the other species considered in
this section, the populations could be native to the river. Maximal recorded
populations were in the order of 6000 cells ml^{-1} (Buildwas, June 1987); some
1300 ml^{-1} constituted the May, 1988 peak. It was observed that though they
increased between Newtown and Welshpool, numbers fell away towards the end of
the summer at the downstream stations.

Navicula gracilis Ehrenb. (possibly plus N. viridula Kütz.) is a tapered
pennate diatom with certain planktonic preadaptations and, indeed, showed a
distribution in space and time (Fig. 12) similar to that of Stephanodiscus,
with a spring and late summer peak and a winter minimum (maxima: 1000 ml^{-1},
Welshpool, June 1987; 700 ml^{-1}, also at Welshpool, May 1988).

Chlorella sp. I (diameter $\sim$ 4 µm + pyrenoid) was a frequent component of the
plankton throughout the river during the study period (Fig. 13). It became its
most abundant during August 1987 (some 27 000 cells ml^{-1} at Montford Bridge),
apparently 'survived' the winter well at stations above Newtown (1000 cells
ml^{-1} there and downstream in February, 1988) but failed to dominate in the
middle reaches in 1988.

    Its place was substantially taken by a second Chlorella, a slightly larger
(diam. 4-5 µm) species lacking a pyrenoid ("Chlorella NOP"). Nevertheless,
this species appeared in the upper reaches in March 1988 (Mt Severn : 180 cells
ml^{-1}) though failed to increase beyond Llandinam until May (Buildwas:

4600 cells ml^{-1}). The most prolific downstream development came in July, when 100 000 cells ml^{-1} were recorded at Montford Bridge.

Scenedesmus quadricauda (Turp.) Bréb. was only one (but by far the most common) of several species of Scenedesmus observed in the Severn (S. acuminatus, S. bijuga were among others). Again, it was relatively more common downstream and in spring and summer, with a clear absence October-March. Maximal populations: Buildwas, July 1987: 2100 cells ml^{-1}; Atcham, July 1988; 5300 cells ml^{-1}).

3.2.2. Dynamics of the phytoplankton

From the preceding section two deductions may be made. The first is that the eumpotamoplanktonic species do generally increase downstream, subject to the effects of dilution or enrichment by tributaries; the second is that the extent of the downstream increment is strongly seasonal, reflecting the increased opportunities for growth in warmer water, under longer days and at reduced travel times. Reynolds (1988) indicated that enhanced turbidity, brought on by increased discharges, was the more likely correlate to interfere with growth. More recently, Reynolds et al. (1989) have been able to emphasise the importance of water depth to the maintenance of a plankton, especially to the heavier diatom species. The explanation of downstream change in specific populations is fairly simple in words but the quantitative algorithms involved are extremely complicated. Another approach is to attempt to reconstruct the growth of algae moving downstream according to criteria of water temperature, day length, etc and the time of travel. The latter is known only crudely and, besides, it is precisely the time of travel that we should like to investigate. So, taking this reasoning one stage further, if we can compare the reconstructed growth rate (r^*) with the actual increase in algal cells between two points L km apart, then we have an estimate of the time of travel (t). The mean velocity is then $U = L/t$

If r^* is the modelled rate of growth at point A and N_A, N_B are the populations at point A and point B, then:

$$r(t) = \ln N_B - \ln N_A$$

$$t = r/r^*$$

$$\underline{U} = \underline{L}/\underline{t}$$

The modelled aspects on growth rate comprise a simplified version of the model proposed by Reynolds (1989) and since validated on other classes of water (Freshwater Biological Association - unpublished). The modified model applied here assumes that $\underline{r}^*$ is a direct function of $\underline{r}'_{20}$, the light- and nutrient-saturated growth rate of an alga at 20C; for a given species,

$$\underline{r}'_{20} = 1.142(s/v)^{0.325}$$

(where $\underline{s}$ is the surface area and $\underline{v}$ the mean volume of its cells).

The growth rate at another temperature, θ, is predicted by:

$$\underline{r} = \beta[1000/(273+20)-1000/(273+\theta)].\underline{r}'_{20}$$

$$\text{where } \beta = 2388(\underline{s}/\underline{v})^{-2.505}$$

The growth rate modified by the length of the day to which it is exposed to light of intensity to sustain $> \frac{1}{2}\underline{r}'$. That may be $\underline{T}$, the length of the day in hours, or $\Sigma\underline{T}_p$, the daily sum of 'light windows' perceived in a turbid, mixed column.

$\Sigma\underline{T}_p$ is assumed to correspond to the product, $\underline{T}. \ \underline{z}_s/\underline{z}_m$, where $\underline{z}_s$ is the depth into the water that a white disc, 30 cm in diameter and attached to the sampling bottle, remains visible and $\underline{z}_m$ is the depth of the water at the midpoint of the sampling station (data in Fig. 5). Then,

$$\underline{r}^* = \frac{\underline{r}' \ \times \underline{T} \times \underline{z}_s}{24 \times \underline{z}_m}$$

One further precondition to the application of this model is that over the reach distance, $\underline{L}$, the river must be substantially free of significant tributaries, either bringing in large numbers of algae or, equally, providing large diluant volumes of algal-free water. Five such reaches were identified for this analysis, mainly on the latter premise (see Fig. 3).

A : (2) Llanidloes to (3) Llandinam   (11 km)

B : (4) Caersws to (5) Newtown   (15 km)

C : (6) Abermiwl to (7) Welshpool   (17 km)

D : (8) Crew Green to (9) Montford Bridge   (16.5 km)

E : (11) Cressage to (12) Buildwes   (9.5 km)

Some solutions of r^* are compared with the corresponding observations of downstream increase $r_{(t)}$ in Table 2, whence t and U are derived. At first sight, the derived velocities are rather widely scattered about any apparent average condition. In fact, there is clearly a general variability anticipated due to sample-to-sample differences in the discharge conditions under which they were taken, although Fig. 4 would suggest that the river behaviour would be comparable among dates of ambient, below-capacity flow. Omitting the high-flow cases (28 October 1987; 23 February 1988; 27 March) yields mean velocities of the order of 0.1 - 0.2 m s^{-1} in section A, 0.05 - 0.15 m s^{-1} in B and C, 0.05 - 0.2 m s^{-1} at D and 0.04-0.4 m s^{-1} at E. These derivations are even more remarkable because they assume that the algae increase downstream at the maximum hypothetical growth rate under the input conditions and no allowance is made for mortality, poor physiological performance or consumption by animals. If the net rate of increase is actually slower than the model suggests then more time is required to bring about a finite increase in the population; that is, the river must have flowed still more slowly on average to permit the observed downstream increment to have taken place!

Nevertheless, it is the fact that the inferred mean rates of flow are so low. While there is no unique velocity through any given channel section, the Manning Equation provides a useful estimate of mean hydraulic velocity, U:

$$U = 1.5 \ (A/P)(s/r_p)^{\frac{1}{2}}$$

where A is the cross-sectional area of the water filled channel, P is the wetted perimeter of the section, s is the gradient and r_p is the surface roughness (roundly, the effective height of projections from the bed). If we substitute into this equation appropriate values for A, P and s approximated from Table I and Fig. 4 and estimate the roughness factor, U can be solved very approximately for the sampling occasion to increase from the range 0.18 - 0.27 ms^{-1} above Llandinam to 0.7 - 1.4 m s^{-1} at Montford. The latter may well be exaggerated against the calculation of discharge divided by channel section for the corresponding occasion: 0.17 - 0.77 m s^{-1} at Montford Bridge;

corresponding data have also been calculated for Abermiwl: $0.04 - 0.25$ m s^{-1}.
At each point, a wide range of instantaneous velocities is to be expected but
the mean discharge through the cross section is, instantaneously, unique. The
main deduction is, then, that the algae are telling us _either_ that the water is
travelling less rapidly than our measurements would indicate, _or_ that some of
the water is detained upstream "in store" and, hence, liable to support the
products of that further growth. This is precisely the hypothesis we wished to
test.

3.3 Velocity structure and algal distribution

3.3.1. Investigations on the Montford Reach

A preliminary investigation of the Montford section revealed several
points with marked disparities of flow (see Fig. 16). At the low discharge
obtaining (1 June 1987: 9 m^3 s^{-1}) the riffle zones were not difficult to
recognize: the boat grounded several times in the shallow water! Poorly
flowing water is also easily observed close to the banks and downstream of
emergent _Phalaris_ patches: shedding vortices often marked a severe shear
boundary. Elsewhere, further into the main channel, there were evident at this
time, 'swarms' of _Daphnia_ (water fleas) which, apart from their own movements,
were not obviously drifting downstream. Spot measurements confirmed that the
velocity was negligible. On a subsequent exploration in September, 1987, no
Daphnia were in evidence but the same areas (marked on Fig. 16) were
identifiable with the 'Aquatracka' apparatus as evidence of enhanced algal
chlorophyll.

A 'permanent' transect ("MONTDP") was established to pass into one such
low flow zone and this was subject to a series of later studies. Fig. 17a
shows a carefully constructed velocity profile through the section: the
greatest velocity is away from shore and bottom and is slightly excentric to
the west (the outside bend). The mean velocity through the section (A = 63.6
m^2) was calculated to be 0.308 m s^{-1}; the discharge was 19.6 m^3 s^{-1}.
On the right of the figure, towards the right-hand (eastern, inside bank) there
is a substantial loss of water 'moving' at rather less than 10 cm s^{-1}.
Comparison with the distribution of i-v chlorophyll fluorescence (Fig. 17b)
shows a gradation which coincides with certain features of the velocity
profile. The 'main flow' bounded by the 0.4 m s^{-1} (40 cm s^{-1}) contour
encloses fluorescence readings (arbitrary relevant units) of $1.25 - 1.35$.

There is a suspicion of greater concentrations near the bottom but strikingly-so > 1.40 beyond the 0.3 m s^{-1} contour, and > 1.60 beyond the 0.1 m s^{-1} contour and in places reaching > 1.80. Thus, the difference in fluorescence from fast- to slow-flow is ~ 1.25; note, too, the fairly sharp gradient (1.35 to 1.50) associated with the 0.4 to 0.2 m s^{-1} velocity gradient.

Fig. 18 shows two further transects of flow structure determined during winter conditions (a: February 1988) and during high hydraulic discharge (b: November 1987). In the former, the mean velocity through the 58.7 - m^2 section has been calculated to be 0.478 m s^{-1}; in the latter, the areal section is 98.45 m^2, the mean velocity 0.815 m s^{-1} and the discharge 80.24 m^3 s^{-1}. In Fig. 19, it is demonstrated that even under these extremes, a recognisably enduring pattern of fluorescence distribution persists. The spacing of isopleths in Fig 19a does not obscure the impact of the deflection on the right bank which corresponds to the region where velocity is > 0.15 m s^{-1}: with respect to the main flow, the fluorescence is 1.15 times greater and the boundary zone between them coincides with the velocity gradient between 0.15 and 0.30 m s^{-1}. In the fluorescence profile of November, 1987, the verticality in the fluorescence contours is still evident, with fluorescence elevated by a factor of > 1.06 and up to 1.2 times, and with a similarly steep intermediate boundary zone. A second, weaker boundary exists further into the channel (about 10 m out from the right bank).

A series of samples, each collected just below the surface, was taken at selected intervals along the transect on 22 September 1987 and again on 4 May 1988. In both instances, the differences in fluorescence were qualitatively verified by the concentrations of live algal cells. On the earlier occasion (see Fig 20a), both the two most abundant species present (Chlorella I, Stephanodiscus tenuis) were significantly concentrated along the right bank (by nominal factors of 2.06 and 2.40 respectively) with respect to the main flow. On the later occasion, a short transect into the main flow was taken, samples being spaced at meter-intervals, but was repeated 4 h and 20 h later. In this case, all the transects produced similar results through time but important differences between species emphasise the dynamic nature of the mechanisms. With Chlorella and Stephanodiscus, the mean difference in concentration between the inshore and mainflow is about 1.35. In the case of Navicula, which was probably declining in abundance at the time (Fig. 12), the mean difference was 1.24. Scenedesmus, which was only beginning to be abundant in the river generally was counted only in the inshore zone.

The supposition of some fluid exchange taking place across the shear boundary of the inshore zone was tested separately by measuring the rates of depletion of particulates across the transect depicted in Fig. 20b. A well-shaken suspension of Lycopodium spores ($\sim 4 \times 10^7$ ml^{-1}) was poured carefully along the transect. Surface samples were taken immediately and at (initially short) intervals thereafter until 20 h later. The rates of change in concentration were calculated for each point (Fig 21). While the spores were very rapidly advected away from the points 2.5 and 3.5 m out from the bank, the concentrations declined exponentially at the inshore stations and, from the logarithmic plot, at similar rates -0.11 to -0.14 min^{-1} (i.e. -10% to -13% per minute). After 1-3 h the rate of decline altered to much gentler rate of removal (Fig 21b: -0.00159 to -0.00115 min^{-1}, or -6.6 to -9.1% per hour. This behaviour is interpreted as a period of dispersion (by diffusion into the adjacent water, together with some inevitable settlement) followed by one of progressive dilution by sinking loss and fluid exchange. This particular batch of spores had been used in a previous experiment and its properties had been established (Reynolds et al. 1989): given a water depth of 0.6 to 2.1 m and a sinking rate of 8.9×10^{-6} m s^{-1} could not account for a sinking loss rate greater than -1.5 to -5.2% hour at the outer and inner station respectively. If fluid exchange accounts for the balance, it would amount to some 7.6% h^{-1} of the 'storage volume' 1.5 m out and barely 1% h^{-1} 0.5 m away from the bank.

3.3.2. Modelling fluid exchange

How then does algal growth 'mark' non-flowing water? We propose here a simple logic to account for observed concentration differences across the MONTDP profile and in river flows generally.

Let us take a storage volume of undefined shape and bounds but with a volume of V m^3. It exchanges water across a shear boundary at the rate q m^3 s^{-1}. Then the theoretical time taken for the volume V to be replaced by successive increments of q m^3 will be $t' = V/q$ s

If the volume V is continuously and independently mixed (by convection or by internal circulation driven by shear stress), the 'old' water is replaced by 'new water', so the volume of old water 'decays' according to an exponential series; so,

$$V_t' = V_o \, e^{-1}$$

where V_o is the initial volume and e is the base of natural logarithms.

Now we wish to trace the elution through a population of particles, $\underline{N}_o$, uniformly distributed through volume $\underline{V}_o$ at time $\underline{t}_o$. Then,

$$\underline{N}_t' = \underline{N}_o \, e^{-1}$$

and at any intermediate point, t,

$$\underline{N}_t = \underline{N}_o \, e^{-\underline{t}/\underline{t}'}$$
$$= \underline{N}_o \, e^{-\underline{q}\underline{t}/\underline{V}} \tag{1}$$

This is a familiar statement of dilution of a particulate suspension by clean water. The exponent is equivalent to the value derived in 3.3.1. - 0.076 h^{-1} or -0.001. In one unit of time, $\underline{q}/\underline{V})$ is displaced by particle-free water, leaving $N_o(1-\underline{q}/\underline{V})$.

Our problem is that the incoming water also contains particles at a concentration $\underline{N}_f$.

Now, after one time step the population remaining is:

$$\underline{N}_t = (\underline{q}/\underline{V})\underline{N}_f + \underline{N}_o(1-\underline{q}/\underline{v}) \tag{2}$$

If N_f is constant and initially equal to $\underline{N}_o$, $\underline{N}_t$ would be constant. However, if we assume $\underline{N}_o$ to be increasing at a finite rate, $\underline{k}$ (where $k\underline{N}_o = \underline{N}_o e^{\underline{r}}$), equation (2) may be rewritten:

$$\underline{N}_t = (\underline{q}/\underline{V})\underline{N}_f + k\underline{N}_o(1-\underline{q}/\underline{V}) \tag{3}$$

Fig 22 contains a selection of solutions through time to illustrate the impact of different values of $\underline{q}\underline{t}/\underline{V}$ on storage-zone accumulation of algae growing at a rate, $\underline{k} = 1.01 \ h^{-1}$ (equivalent to $\underline{r} = 0.01 \ h^{-1}$ or 0.24 d^{-1}). The plots were asymptotic to a fraction the condition when the increment in growth is equal to the amount displaced by the exchange.

i.e. when $k\underline{N}_t(1-\underline{q}/\underline{V}) + \underline{N}_f(\underline{q}/\underline{V}) = \underline{N}_t$

whence $k\underline{N}_t(1-\underline{q}/\underline{V}) = \underline{N}_t - N_f(\underline{q}/\underline{V})$;

$$\underline{k}(1-\underline{q}/\underline{V}) = 1-\underline{N}_f/\underline{N}_t(\underline{q}/\underline{V})$$

whence $\underline{N}_t/\underline{N}_f = (\underline{q}/\underline{V})/[1-\underline{k}(1-\underline{q}/\underline{V})]$ (4)

Selected values of (q/v) and $\underline{k}$ have been interpolated in equation (4) to generate the composite plot of storage-volume algal biomass enhancement in terms of the rates of algal growth and of fluid exchange, shown in Fig. 23.

3.3.3. Investigations on the Leighton Reach

The Leighton-Buildwas study section is quite different from the Montford Section, most particularly in the outstanding diversity of fluvial structures it encompasses. Besides a well-developed pool and riffle sequence, the section encloses a renowned sweep of meanders which itself includes a complexity of structures with excentric and cross-channel flow, downwellings and backflows.

Just upstream there is a curious delta fan, perhaps of catastrophic formation, for the minor inflow cannot presently be described as being sediment rich.

The distribution of these structures is shown in the sketch map, Fig. 24. Despite the evident differences in velocity structure, neither sampling nor fluorescence tracing established significantly enhanced chlorophyll concentrations (although, at the time of writing, not all the algal collections had been fully analysed), save for a possibly significant transition in average concentration occurring between measurements upstream and downstream of the deep pool, (at C in Fig. 25), between the right- and left-banks across the line B and, most importantly, what proved to be the most exciting discovery of the whole study, in the eddy in the downstream lee of the delta fan at A, in which the water was near stagnant at low discharges.

Enhanced colour imagery of remotely-sensed properties of this reach of the Severn was carried out on film exposed during overflights of the area, by the Natural Environment Research Council's Scientific Services' Airborne Campaign, made on 7 May and 6 August 1988. On the earlier of these runs, the detail at A (reproduced here as Fig. 26) highlights the relatively extreme differences within and beyond this stagnating eddy structure. The colour image presented combines properties sensed in the spectral bands 3 and 11 and is therefore a compound of enhanced temperature (still, shallow water acquiring heat more rapidly in the May sunshine than the water flowing past) and enhanced chlorophyll concentration. What the image cannot distinguish, however, is whether the chlorophyll is in suspension (river plankton, sensu lato) or epilithic on the stones and gravel of the bed. A transect of close samples (A), collected on the same date, established that whatever the contribution of the bottom material, planktonic algae were most certainly concentrated in this eddy (Fig. 27a). Moreover, the variations along the transect generate a pattern which could be interpreted as consequential upon the eddy structure: the sketch map in Fig. 28 has contour lines drawn in to correspond with the colour gradients and these contours are approximately scaled according to values at their interesects on the transect (Fig. 27a). The maximum factor of concentration with respect to the main-flow (43.4:1) and even that of the 10-30 m section (>3:1) are larger than anticipated from the storage zones considered hitherto. This presumably means that the residence time is proportionately longer for the same algal growth rate, with the 'oldest'water being marked by the greatest chlorophyll-concentration enhancement.

The most astonishing fact was that this 'older water' should have been dominated not by Chlorellids (Fig. 27b) or diatoms (e.g. Fig. 27c) but by an alga not previously encountered in this study, Oscillatoria agardhii. Indeed,

this species is associated with well-mixed, shallow turbid lakes with a high
nutrient status, where their particular biological adaptations are manifestly
advantageous (e.g. Reynolds 1987), but, as a relatively slow-growing organism,
it is generally confined to non-flushing habitats. To have become dominant at
all, and to have built up such a large standing concentration would require
relative isolation for upwards of 25 days - most of the period, in fact, since
the previous occasion that the delta fan would have been inundated by flood
water. In comparison, it should be noted that neither Chlorella nor,
certainly, Stephanodiscus were abundant in this 'old' water: both represent the
early, exploitative stages of planktonic successions: nutrient depletion and
all losses to grazers and sedimentation (all requiring the passage of
significant periods of time to establish) are contributory factors to the
observed behaviour.

The growth rate of Oscillatoria ($r' = 0.86$ d^{-1}) modelled for the
appropriate conditions (mean water temperature in April : 10.5 C; daylength :
14 h) is calculated to be 0.161 d^{-1} (0.00671 h^{-1}; $K = 1.0067$). If the
chlorophyll gradient is stable, $N_t/N_p = 43.4$. Solving equation (4) on p.
21 in terms of fluid exchange rate, (q/V), suggests that the storage zone is at
least older than 6 d!

$$43.4 = (q/V)/1-(1.0067)(1-q/V)$$
$$= (q/V)/1.0067(q/V)-0.0067$$
$$(q/V) = 43.4(1.0067(q/V)-0.0067$$
$$= 43.6908(q/V)-2908$$
$$q/V = 0.0068 \text{ h}^{-1}$$

Clearly, then, this is an outstanding example of a hydrological dead zone
of sufficient magnitude and stability to maintain, in physical contiguity but
hydraulic isolation from the plankton suspended in the river, a microcosm of
quite different species composition and abundance.

4. GENERAL DISCUSSION

The work described in this report has shown that the presence of plankton at all and paradoxically prolific downstream abundance of algae in large rivers is a fully reproducible phenomenon and applies substantially to the River Severn. However, both the elimination of adventitious species and the establishment of a typical, native potamoplankton occur mainly in the section between Newtown and Welshpool; whether this is a function more of water depth or gradient cannot be stated with certainty but there is good evidence that both factors are important.

The study has also shown that there are substantial fragments of the river which are not flowing: the presence of dead zones was suspected in larger rivers (see Reynolds 1988) and has already been demonstrated in the Severn in an allied research programme (University of Lancaster, 1987), for which the ADZ model has been shown to be applicable. Under a wide range of discharge conditions, ADZ retention was occurring, with $\underline{V}e$, the aggregate non-flowing volume accounting for not less than 0.2 and, sometimes, as much as 0.4, of given reach volume (University of Lancaster 1987; Dr K. Beven, personal communication). This study has identified and defined several non-flowing areas which have been found to survive a full range of hydraulic-discharge conditions. The original hypothesis, that such zones were not only essential reservoirs of planktonic algal inocula but that the algae are found more abundantly therein, has also been supported. We have shown that the algal concentration is sensitive to the rate of fluid exchange and have used the fact to relate the concentration factor to a factor of the rates of growth and fluid exchange. "Dead zones" (or storage zones), undoubtedly provide $\underline{a}$ mechanism by which river populations can be recruited and enhanced.

Coincidence of phenomena with demonstrated mechanisms does not constitute an explanation. The final consideration here is "can the ADZ hypothesis explain the apparently exaggerated downstream increase of algal populations?"

According to the development of Young & Wallis (1987), the dead-zone model visualises a volume of water, $\underline{V}$, not flowing but continuously mixed itself and exchanging fluid across its interface (shear boundary) with the steady flow $\underline{Q}$ outside. The addition and removal of a conservative solute, of concentration $\underline{N}_o$, is expressed by a simple dynamic mass balance equation:

$$d(\underline{NV})/d\underline{t} = \underline{Q}\,\underline{N}_o - \underline{Q}\,\underline{N}_t$$

If both Q and V are assumed to be constants, the equation for the change in solute concentration can be written

$$dN/dt = (-Q/V) N_t + (Q/V) N_o \tag{5}$$

The aggregate dead-zone model applies to the sum of the effect of such zones through a given reach. For the whole reach, in which the aggregate dead-zone volume is (V_e), an analogous solution to (5) applies:

$$dN/dt = (-Q/V_e)N_t + (Q/V_e)N_o \tag{6}$$

The advective effect is accommodated by a time-delay factor (τ) corresponding to the ADZ retention time, given by V_e/Q.

The empirical equivalent of (6) is

$$dN/dt = (-Q/V_e \, N_t + (Q/V_e) \, N_o \, (t-\tau) \tag{7}$$

Integrating,

$$N_t = Q/V_e \cdot e^{(-Q/V_e)(t-\tau)} \tag{8}$$

Solutions added at a given point in time disappear asymptotically to zero. If instead of a solute, algal particles are fed into the flow, at concentration N_f, the dead zones are recharged. A steady state is attained when $N_f = N_o = N_t$ and $dN/dt = 0$. If there is now a positive increase in N_o in the dead zones, then the main flow becomes enriched. Equation (7) is rewritten accordingly:

$$dN/dt = (Q/Ve) \, N_t + (Q/V_e)N_o \, (t-\tau)$$

V_e occupies a fraction of the reach volume V_r. Let us suppose that the MONTDP reach is typical of the section from Crew Green to Montford Bridge, where the summer algal increase is in the order of 1.062-fold km^{-1} (r_t in Table 2 : > 0.06 km^{-1}). Taking the mean velocity of the flow to be 0.3 m s^{-1} (Figs 17, 18) the average travel time of water will be 0.93 h km^{-1}. Given the modelled specific rate of algal increase for such periods (0.3 d^{-1}) the expected downstream increase would be only 1.013-fold h^{-1}, i.e. 1.0116-fold per km travelled. The value of τ is supposed to be equivalent to (ln 1.062)/(ln 1.0116), or roughly 5-fold: the mean velocity of the algal travel is therefore 0.06 m s^{-1}.

We shall hypothesise that dead-zone storage alone accounts for this delay. Let us also assume that, at a downstream sampling point, the water sampled is made up in exactly the proportion, Ve:(Vr-Ve). Then we can say that for a downstream increment equivalent to 1.0116-fold in plug flow, the growth in V_e supplies a 'supplement' sufficient to raise the mean by 1.062. If V_e/V_r is the fraction of the total volume so affected, then:

$$1.062N = 1.0116 \left(\frac{Vr-Ve}{Vr}\right) N + x \left(\frac{Ve}{Vr}\right) N$$

where x is the equivalent to the equilibrium 'concentration' factor, N_t/N_f, for the aggregate dead-zone volume.

The relation is plotted in Fig. 29: to obtain the observed downstream increase in phytoplankton between Crew Green and Montford requires an ADZ of between 0.2 and 0.4 the instantaneous channel volume of the section supporting a chlorophyll level, enhanced by a factor of 1.14 - 1.26 with respect to that in the adjacent 'open' flow and which, in turn, requires the combination of an algal growth rate of 1.01 h^{-1} and a fluid exchange rate of < 5% of ADZ per h.

The conclusions to be drawn from this study are that:

1. Dead-zone formation is as much a character of larger rivers as it is of smaller ones.

2. Dead-zones can survive a wide variety of discharge conditions although their boundaries must be flexible and the rates of fluid exchange are presumably variable according to the shear stress applied.

3. Different algal dynamics apply to the dead-zone plankton: dead zones provide a reservoir of cells that inoculate the fluvial flow and other growth 'nodes' further downstream.

4. A mechanism is demonstrated by which the dynamics of a series of dead-zones accounts for the otherwise untenable downstream increase in suspended algal populations. Conversely, dead zones are essential to the maintenance of plankton in rivers.

5. That being so, algae do indeed constitute a useful sensor of fluvial processes.

Finally, there can be little doubt that these conclusions apply also to other rivers. However, before a general model relating dead-zone dynamics (as revealed by algae) to properties of the river (order, gradient, dimensions, etc) and its flow (discharge, velocity) can be derived, some further investigations need to be conducted on the fluid-exchange reactions of some individual dead zones to altered flows. The outcome must be viewed as being relevant not only to the quality of river water, as determined by its algal populations, but also to its capacity to displace itself, its solute - and suspensoid-loads to locations downstream.

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6. REFERENCES

Berman, T. (1972). Profiles of Chlorophyll concentrations by in vivo fluorescence: some limnological implications. Limnology and Oceanography, 17: 616-618.

Chatwin, P.D. & Allen, C.M. (1985). Mathematical models of dispersion in rivers and estuaries. Annual Review of Fluid Mechanics, 17: 119-149.

Day, T.J. & Wood, I.R. (1976). Similarity of the mean motion of fluid particles dispersing in a natural channel. Water Resources Research, 12: 655-666.

Douglas, J.R. (1988). Regulating the River Severn. Regulated Rivers, 2: 309-321.

Harris, G.P. (1978). Photosynthesis, productivity and growth: the physiological ecology of phytoplankton. Ergebnisse der Limnologie, 10: 1-171.

Harris, G.P. (1980). Spatial and temporal scales in phytoplankton ecology: mechanisms, methods, models and management. Canadian Journal of Fisheries and aquatic Sciences, 37: 877-900.

Heaney, S.I. (1978). Some observations on the use of the in vivo fluorescence technique to determine chlorophyll a in natural populations and cultures of freshwater phytoplankton. Freshwater Biology, 8: 115-126.

Lorenzen, C.J. (1966). A method for the continuous measurement of in vivo chlorophyll concentration. Deep-sea Research, 13: 223-227.

Lund, J.W.G., Kipling, C. & LeCren, E.D. (1958). The inverted microscope method of estimating algal numbers and the statistical basis of estimations by counting. Hydrobiologia, 11: 143-170.

Reynolds, C.S. (1987). The response of phytoplankton communities to changing lake environments. Schweizerische Zeitschrift für Hydrologie, 49, 220-236.

Reynolds, C.S. (1988). Potamoplankton: paradigms, paradoxes and prognoses. In Algae and the aquatic environment (ed by F.E. Round), pp. 285-311. Biopress, Bristol.

Reynolds, C.S. (1989). Physical determinants of phytoplankton succession. In Plankton Ecology (ed by U. Sommer). Science Publishers, Madison (in press).

Reynolds, C.S., White, M.L., Clarke, R.T. & Marker, A.F. (1989). Suspension and settlement of particles in flowing water: comparison of the effects of varying water depths and velocity in circulating channels. Submitted to Freshwater Biology.

Severn-Trent Water Authority (1978). Water Quality 1976/77. STWA, Birmingham.

Swale, E.M.F. (1969). Phytoplankton in two English rivers. Journal of Ecology, 57: 1-23.

University of Lancaster (1987). Tracer experiments on the River Severn in the Shrewsbury Area. Unpublished report, Institute of Environmental and Biological Sciences, University of Lancaster, Lancaster.

Wallis, S.G., Young, P.C. & Beven, K. (1989). Experimental investigation of the aggregated dead zone model for longitudinal solute transport in stream channels. Proceedings of the Institution of Civil Engineers (in press).

Water Authorities Association (1986). Water pollution from farm waste. W.A.A., London.

Young, P.C. & Wallis,S.G. (1987). The aggregated dead zone model for dispersion in rivers. Proceedings of the Conference on Water Quality Modelling in the inland natural Environment, pp. 421-433. BHRA, Cranfield.

TABLE 1

Station Code	Station Name	NGR	km from source	altitude, m O.D.
0	Clywedog Br	SN 918864		221
1	Mount Severn	SN 943839	15.5	168
2	Llanidloes	SN 955846	18.0	159
3	Llandinam	SO 025886	29.0	131
4	Caersws	SO 032917	34.5	122
5	Newtown	SO 107919	49.5	107
6	Abermiwl	SO 163952	58.0	88
7	Welshpool	SJ 236069	75.0	64
8	Crew Green	SJ 330157	103.0	58
9	Montford Bridge	SJ 432153	119.5	55
10	Atcham Bridge	SJ 541093	153.5	46
11	Cressage	SJ 593046	166.0	42
12	Buildwas	SJ 645045	175.5	38

Channel Width (m)	Approx Mean Gradient (m km^{-1})	Approx Riffle Frequency km^{-1}	Notes
12	15	30-65	Below Dam. W.A. staff gauge
14	50	20-25	
55*	3.0	15-18	* very braided
25	2.3	3-5	
30	1.2	2.5-3.3	
35	2.4	5-7	First Ranunculus
35	2.4	2.5-5	
40	0.4	2.5-5	
45	0.26	2.0-3.5	
35	0.26	1.5-3.0	
70	0.27	2-3	
60	0.27	2	
45	0.27	1.5	

TABLE 2 Algal-growth calculated velocities

A: Llanidloes - Llandinam

Date	Alga	Observed increase $\underline{r}(t)(km)^{-1}$	Modelled growth $\underline{r}^* (d^{-1})$	$\underline{U} = \underline{r}^*/\underline{r}_{(t)}$ (km d^{-1})	(m s^{-1})
3 Jul 87	Chlorella I	0.0457	0.889	19.45	0.225
2 Sep 87	Chlorella I	0.0920	0.565	6.14	0.071
23 Feb 88	Chlorella I	0.0197	0.233	11.83	0.136
27 Mar 88	Chlorella NOP	0.0790	0.291	3.68	0.043
3 May 88	Chlorella NOP	0.1900	0.424	2.23	0.026
7 June 88	Chlorella NOP	0.1004	0.545	5.43	0.063

B: Caersws - Newtown

Date	Alga	Observed increase $\underline{r}(t)(km)^{-1}$	Modelled growth $\underline{r}^* (d^{-1})$	$\underline{U} = \underline{r}^*/\underline{r}_{(t)}$ (km d^{-1})	(m s^{-1})
3 Jul 87	Chlorella I	0.0062	0.854	137.74	1.59
4 Aug 87	Chlorella I	0.0987	0.691	7.00	0.081
2 Sep 87	Chlorella I	0.0558	0.692	12.40	0.143)
"	Stephanodiscus	0.1526	0.489	3.20	0.037)
28 Oct 87	Chlorella I	0.0085	0.203	23.88	0.276
23 Feb 88	Chlorella I	.0306	0.223	7.29	0.084
27 Mar 88	Chlorella NOP	-0.0193	0.125		
3 May 88	Chlorella NOP	.0426	0.480	11.27	0.130)
"	Stephanodiscus	.0263	0.296	11.25	0.130)
7 Jul 88	Chlorella NOP	.0447	0.193	4.32	0.050

C: Abermiwl - Welshpool

Date	Alga	Observed increase $\underline{r}(t)(km)^{-1}$	Modelled growth $\underline{r}^* (d^{-1})$	$\underline{U} = \underline{r}^*/\underline{r}_{(t)}$ (km d^{-1})	(m s^{-1})
3 Jul 87	Chlorella I	0.0665	0.889	13.37	0.155
4 Aug 87	Chlorella I	0.0335	0.749	22.36	0.259
2 Sep 88	Chlorella I	0.0369	0.692	18.75	0.217
"	Stephanodiscus	0.0670	0.489	7.29	0.084
28 Oct 88	Chlorella I	0.0019	0.036	18.95	0.219
23 Feb 88	Chlorella I	0.0145	0.181	12.48	0.144
27 Mar 88	Chlorella NOP	-0.0546	0.055	-	-
3 May 88	Chlorella NOP	0.0305	0.384	12.59	0.146)
"	Stephanodiscus	0.0184	0.237	12.88	0.149)
7 Jul 88	Chlorella NOP	0.0289	0.402	13.9	0.161)
"	Scenedesmus quad	0.0343	0.324	9.45	0.109)
4 Aug 88	Chlorella NOP	0.0408	0.663	16.25	0.188

D: Crew Green - Montford Bridge

Date	Alga	Observed increase $\underline{r}_{(t)}$ (km)$^{-1}$	Modelled growth $\underline{r}^*$ (d^{-1})	$\underline{U} = \underline{r}^*/\underline{r}_{(t)}$ (km d^{-1})	(m s^{-1})	
3 Jul 87	Chlorella I	0.0852	0.531	6.23	0.072	)
"	Stephanodiscus	0.1791	0.393	2.19	0.025	)
4 Aug 87	Chlorella I	0.0749	0.379	5.06	0.058	
2 Sep 87	Chlorella I	0.0199	0.454	22.82	0.264	)
"	Stephanodiscus	0.0174	0.324	18.62	0.216	)
23 Feb 88	Chlorella I	-0.0180	0.079	-	-	
3 May 88	Chlorella NOP	0.0175	0.200	11.43	0.132	)
"	Stephanodiscus	0.0183	0.125	6.83	0.079	)
7 Jul 88	Chlorella NOP	0.0158	0.156	9.87	0.114	)
"	Scenedesmus quad	0.0615	0.128	2.08	0.024	)

E: Cressage - Buildwas

Date	Alga	Observed increase $\underline{r}_{(t)}$ (km)$^{-1}$	Modelled growth $\underline{r}^*$ (d^{-1})	$\underline{U} = \underline{r}^*/\underline{r}_{(t)}$ (km d^{-1})	(m s^{-1})	
3 Jul 87	Chlorella I	0.0780	0.297	3.81	0.044	)
"	Stephanodiscus	0.1391	0.224	1.61	0.018	)
4 Aug 87	Stephanodiscus	0.0568	0.410	7.21	0.084	
2 Sep 87	Chlorella I	0.0129	0.531	41.17	0.476	
23 Feb 88	Chlorella I	-0.0129	0.043	-	-	
3 May 88	Chlorella NOP	0.0244	0.233	9.55	0.110	)
"	Stephanodiscus	0.0410	0.149	3.63	0.042	)
7 Jul 88	Chlorella NOP	0.0109	0.273	25.0	0.289	)
"	Scenedesmus	0.0056	0.227	40.54	0.469	)
4 Aug 88	Chlorella NOP	0.0334	0.308	9.22	0.106	

Figure 1. The Severn Basin
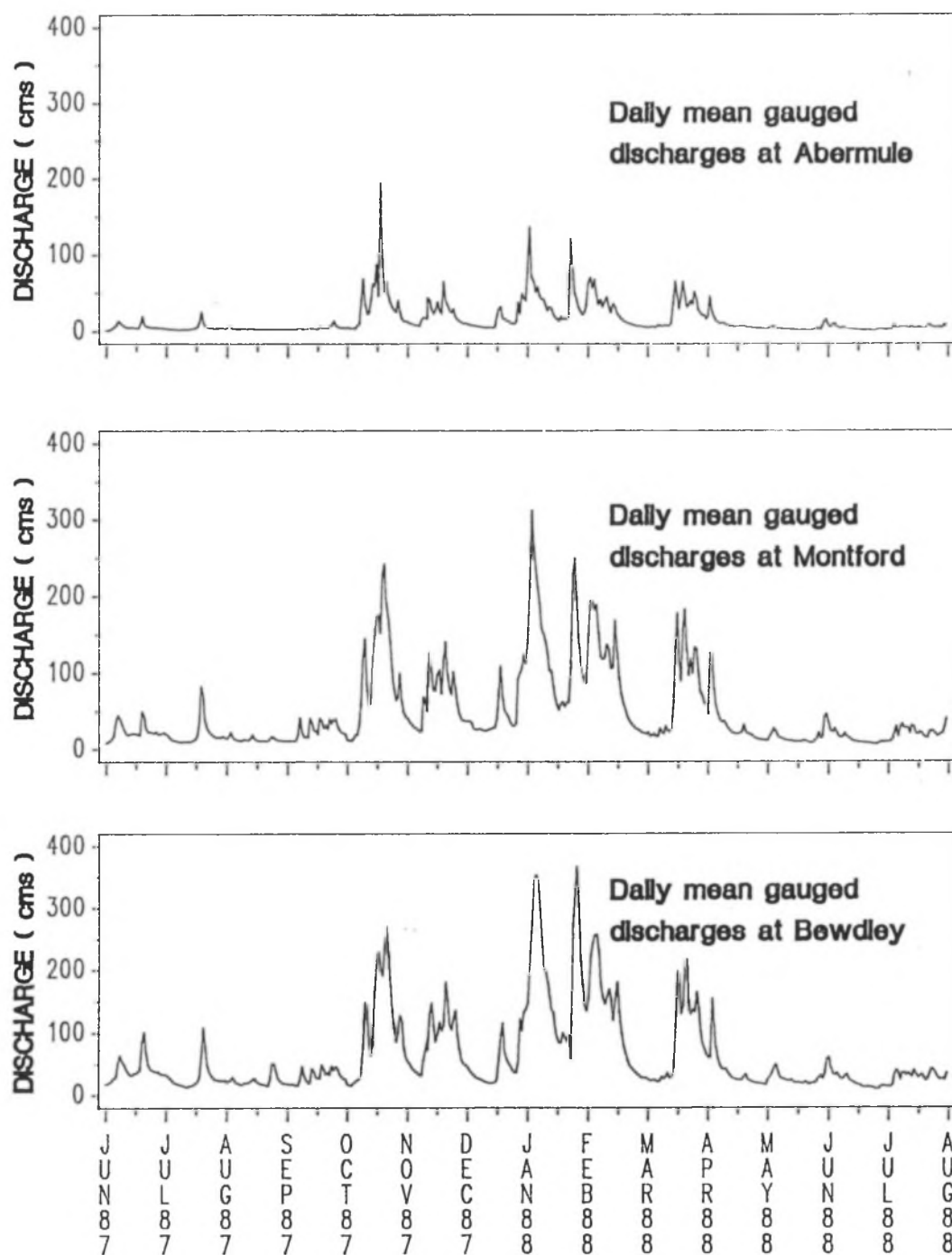
Figure 2.   Discharges in the Severn between June 1987 and July 1988 inclusive

(Data of Severn Trent Water and archived at Institute of Hydrology).
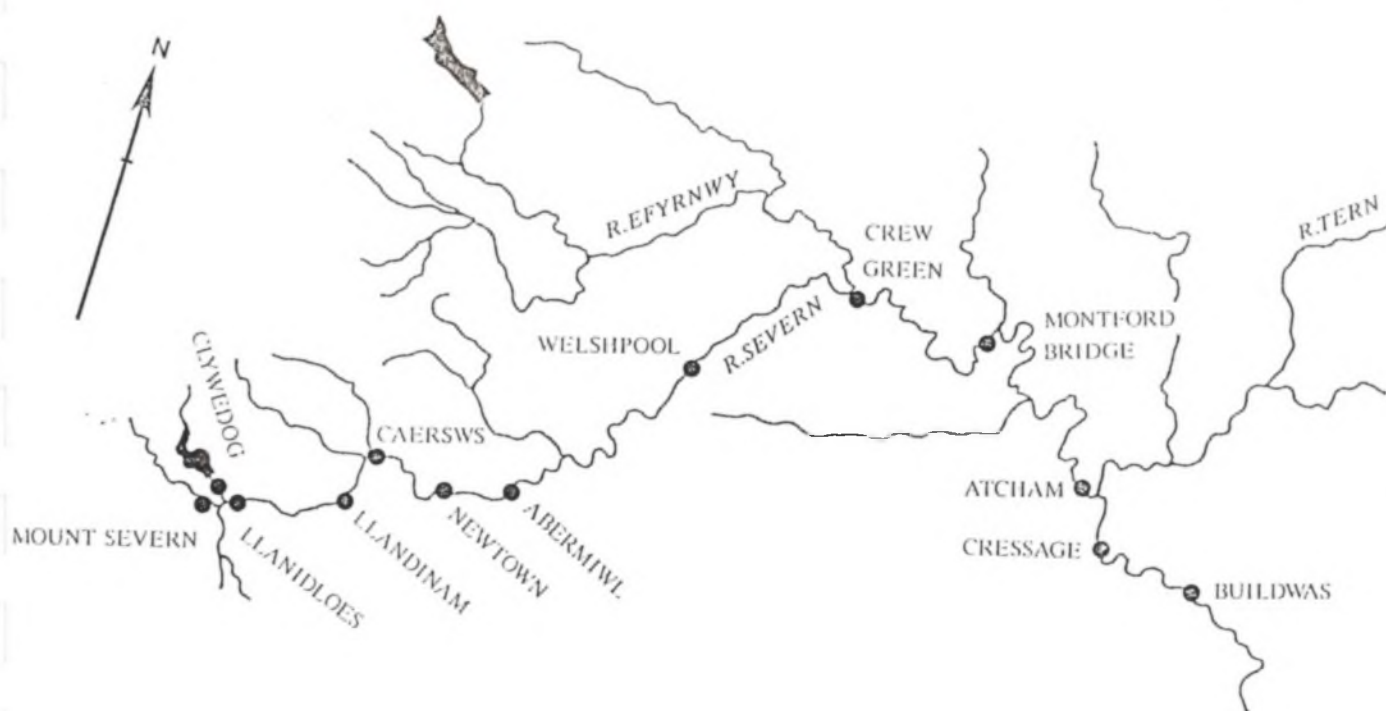
Figure 3. River Severn: detail of study area showing the 13 stations for routine observations.
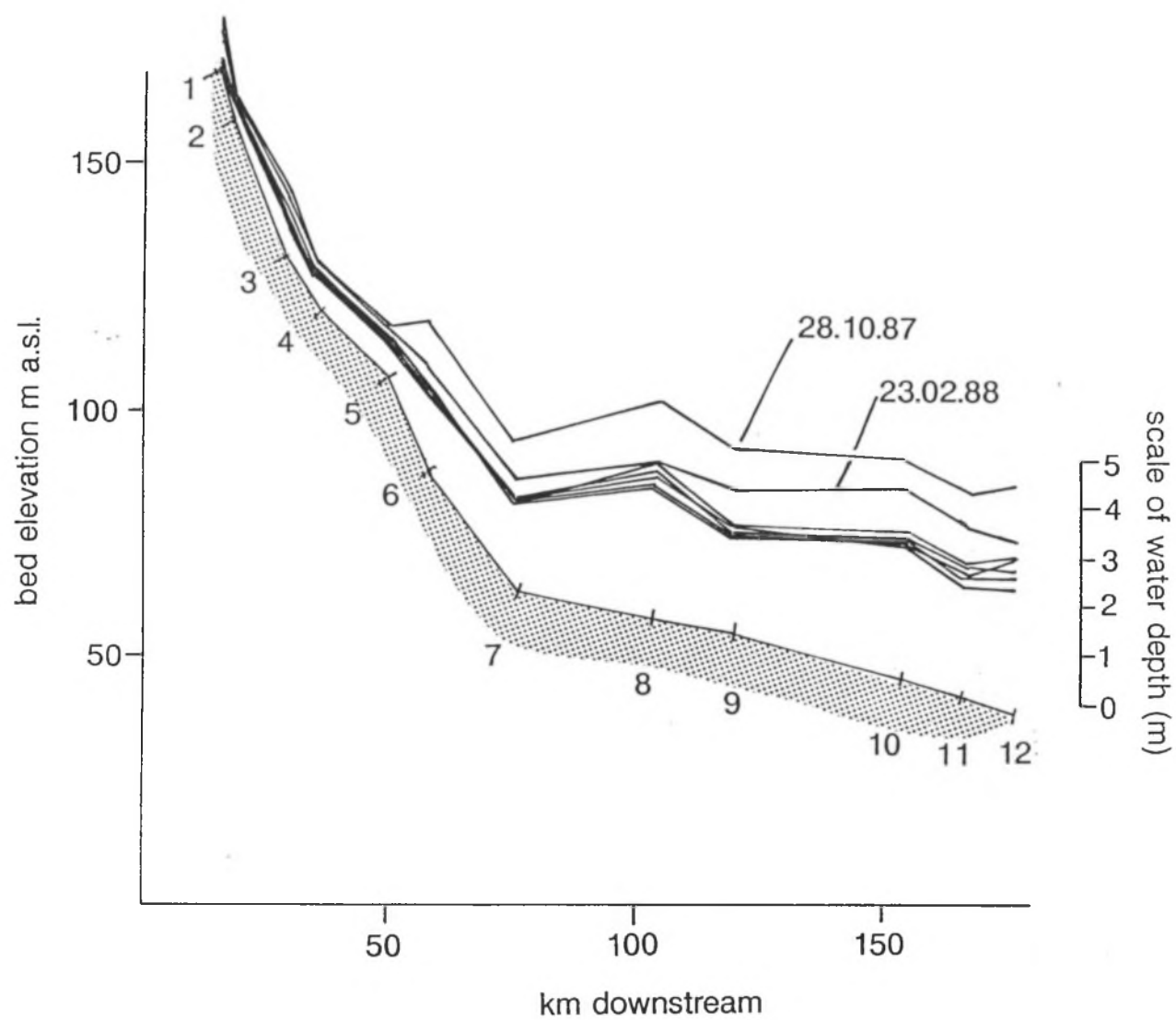
Figure 4. Long profile of Severn, covering the study area to show gradient and typical water depths. Two flood-events are included.
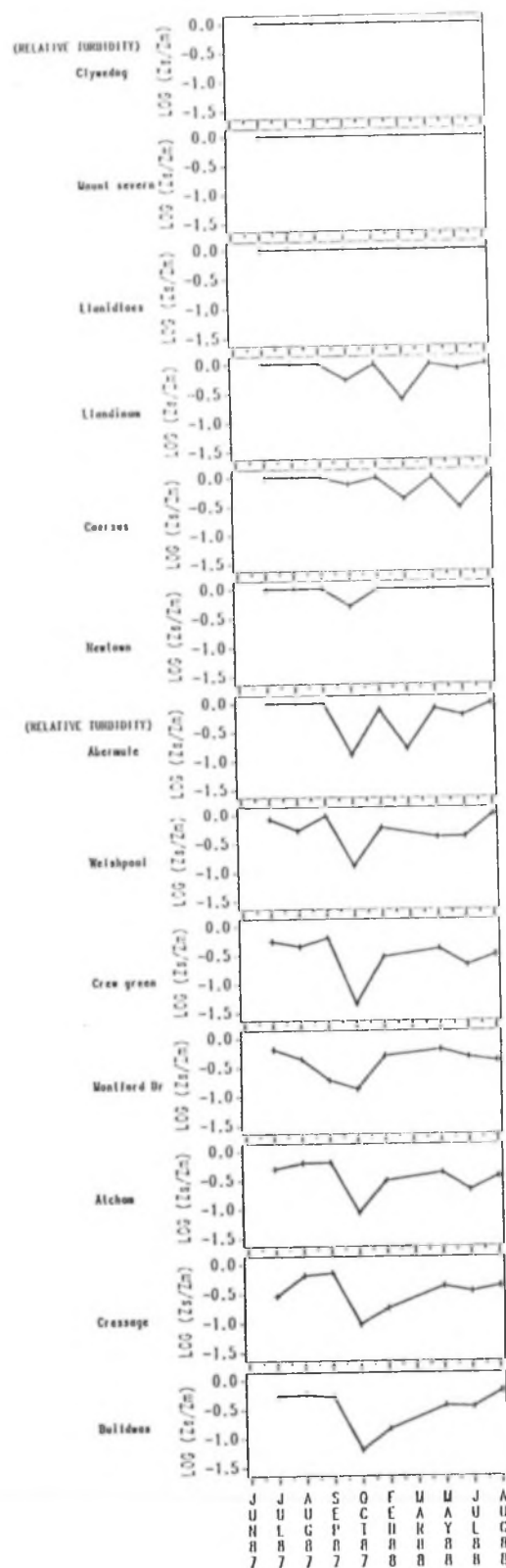
Figure 5. Relative turbidity in the Severn as a function of time and downstream location. The turbidity is shown as a ratio of transparency depth to full water depth, and plotted on a log scale. Thus, at Clywedog the water is always clear to the bed;at Buildwas it never is and is, indeed, often very cloudy.
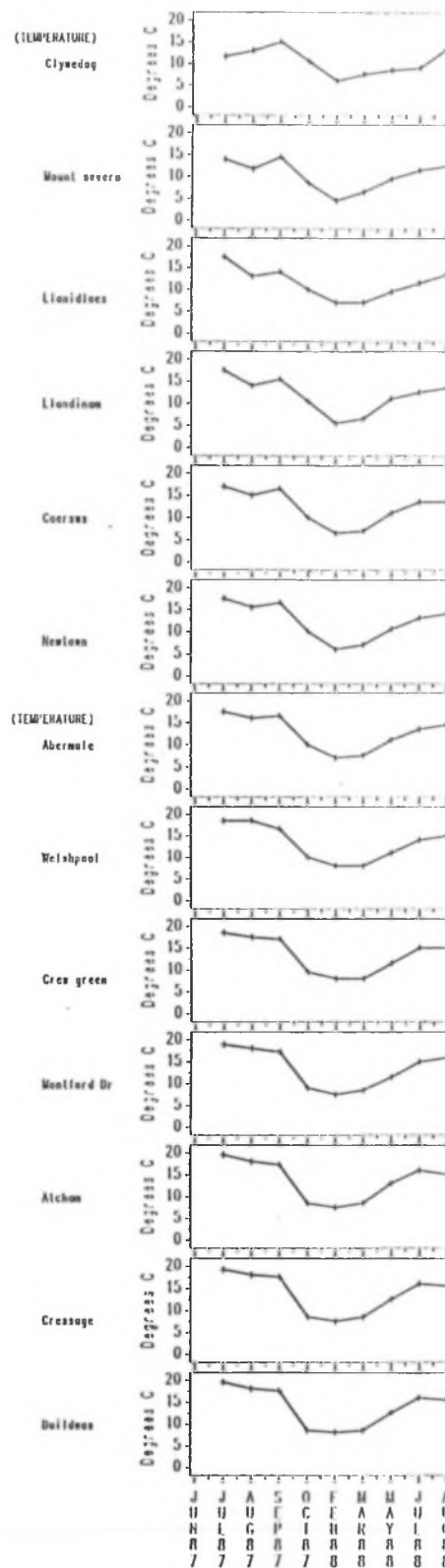
Figure 6. Variations in water temperature, in time and as a function of downstream distance.

Figure 7. Algal biovolume suspended in the Severn as a function of time and downstream distance.
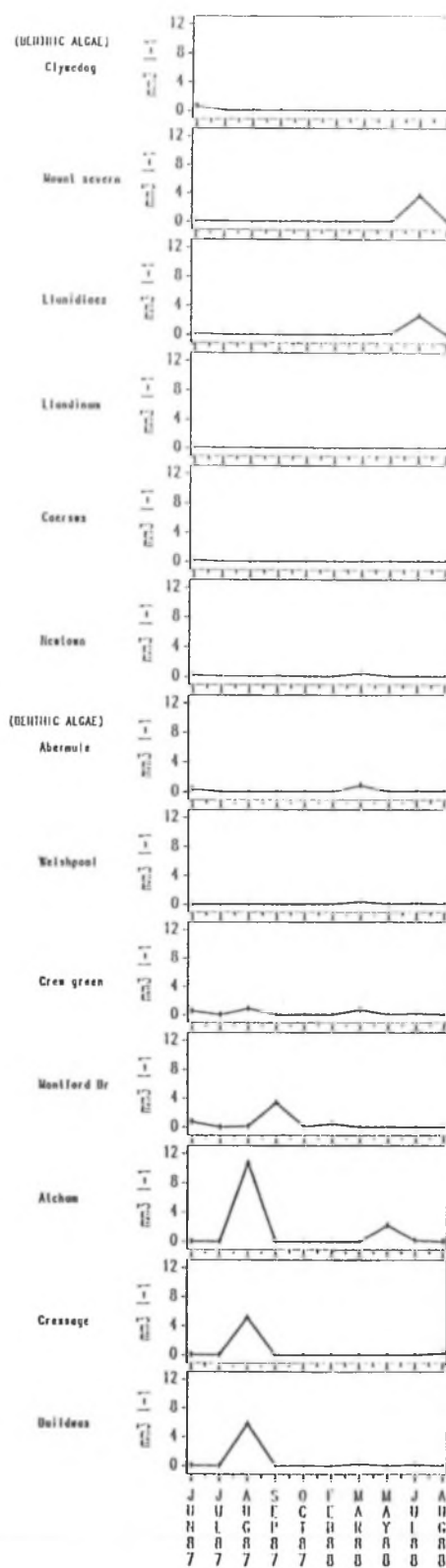
Figure 8. Algal biovolume of species judged to epiphytes and epiliths and not part of plankton.
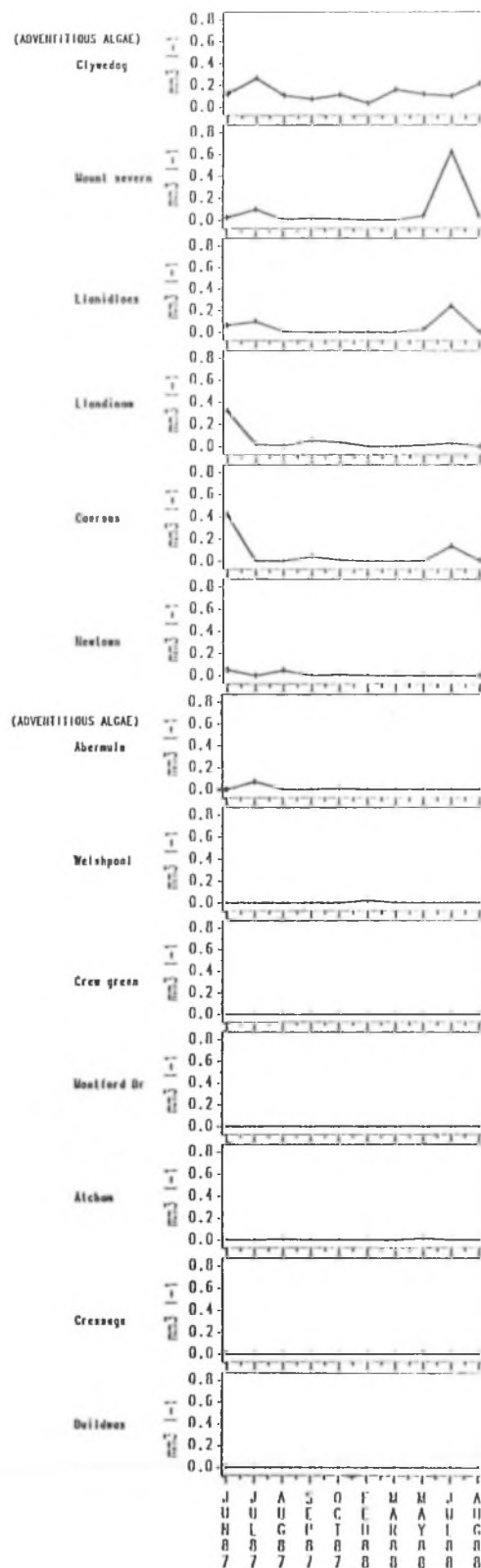
Figure 9. Algal biovolume of planktonic algae but whose growth is not maintained downstream and hence not considered part of the true potamoplankton.
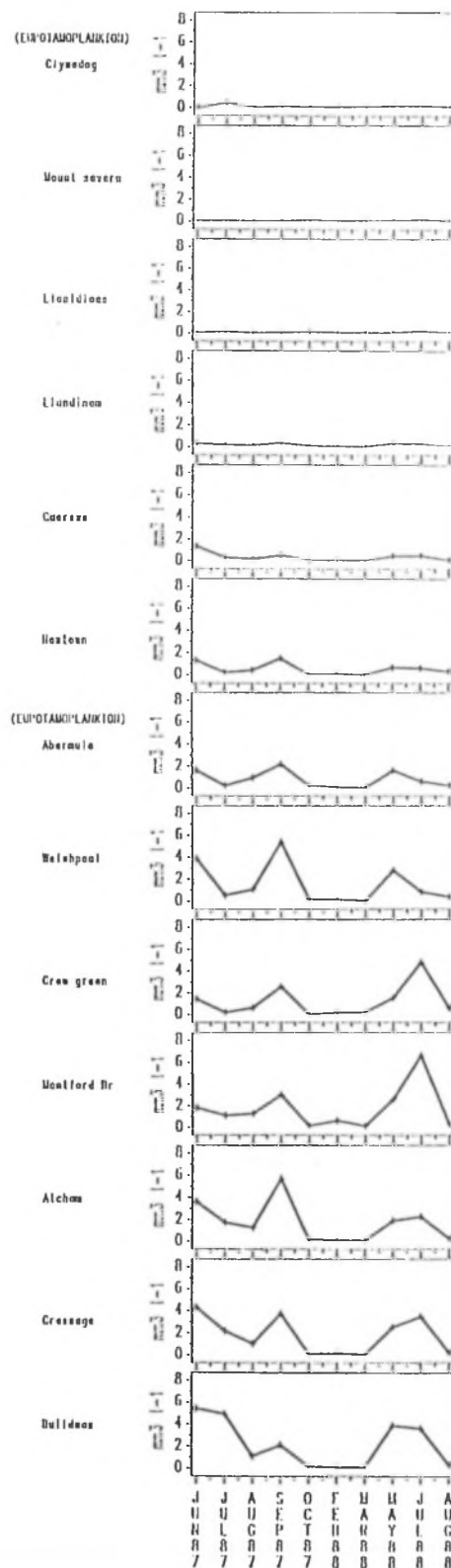
Figure 10. Algal biovolume of species consistently planktonic and capable of downstream growth on occasions - the true river plankton, or eupotamoplankton.
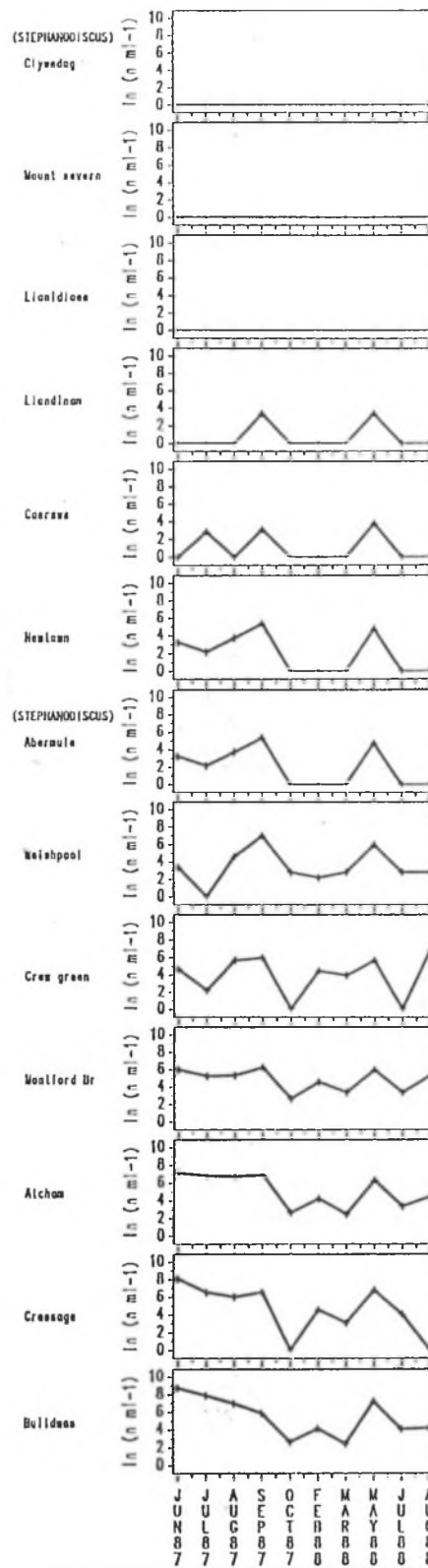
Figure 11. Distribution of _Stephanodiscus cf. tenuis_ in the Severn.
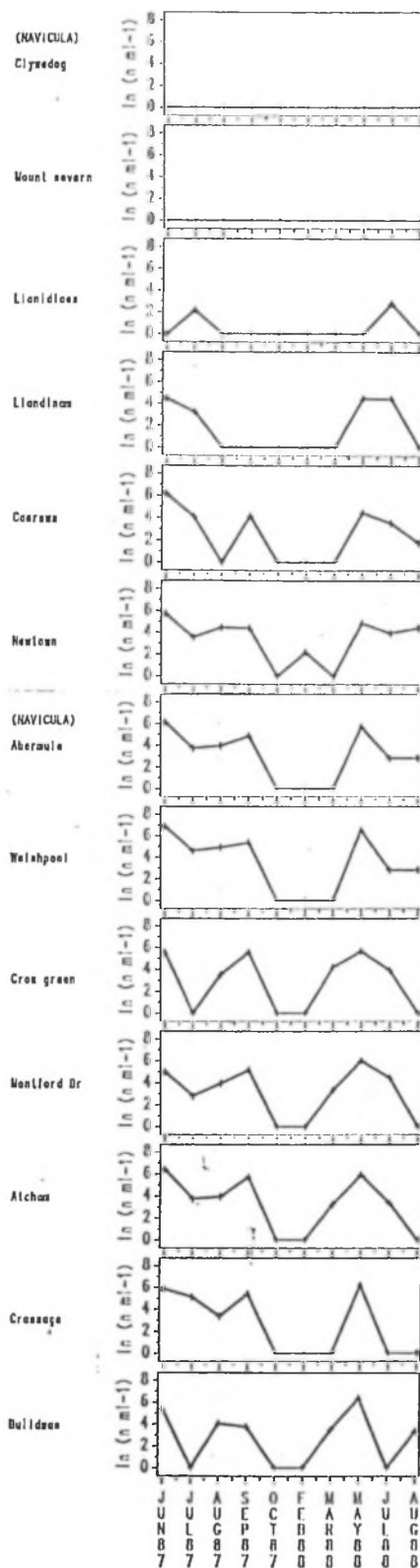
Figure 12. Distribution of *Navicula gracilis* (+ *N. viridula*) in the Severn.
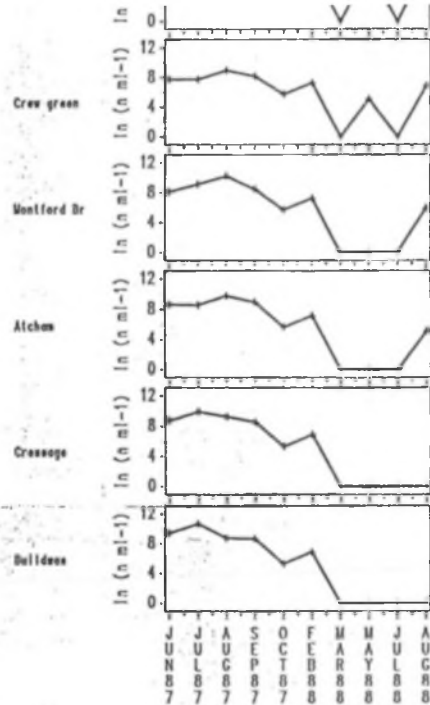
Figure 13. Distribution of <u>Chlorella</u> (SpI) in the Severn.
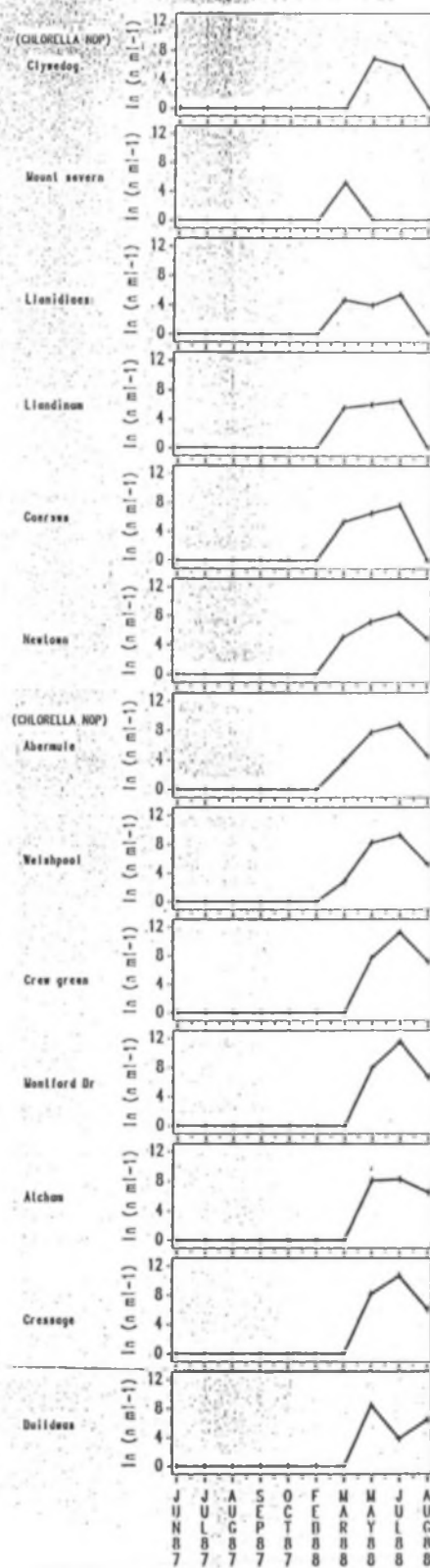
Figure 14. Distribution of <u>Chlorella</u> ("NOP") in the Severn.
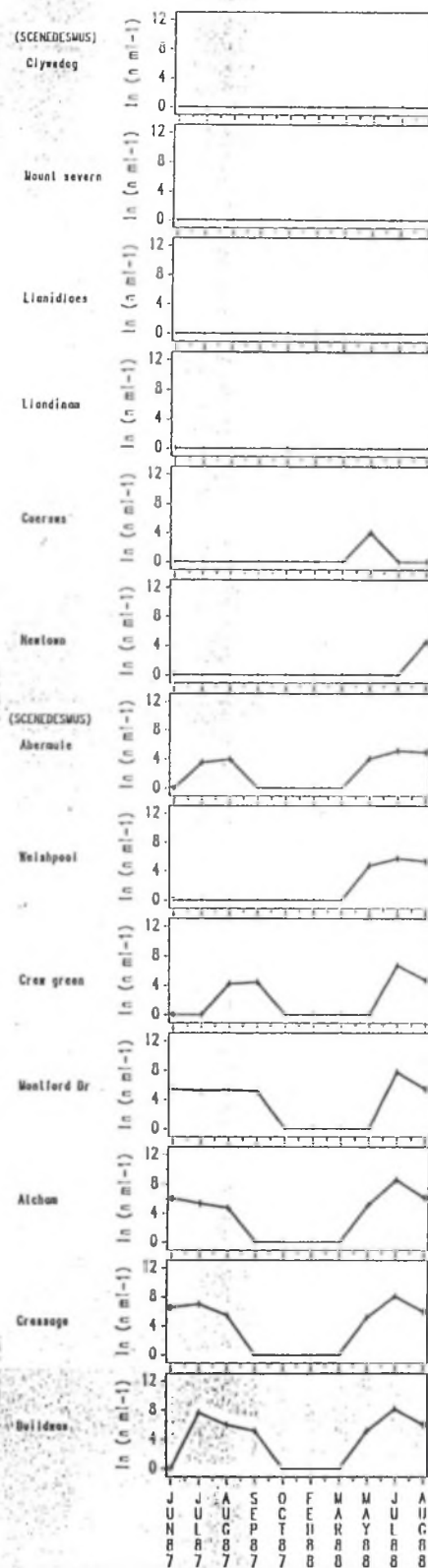
Figure 15. Distribution of _Scenedesmus quadricauda_ in the Severn.
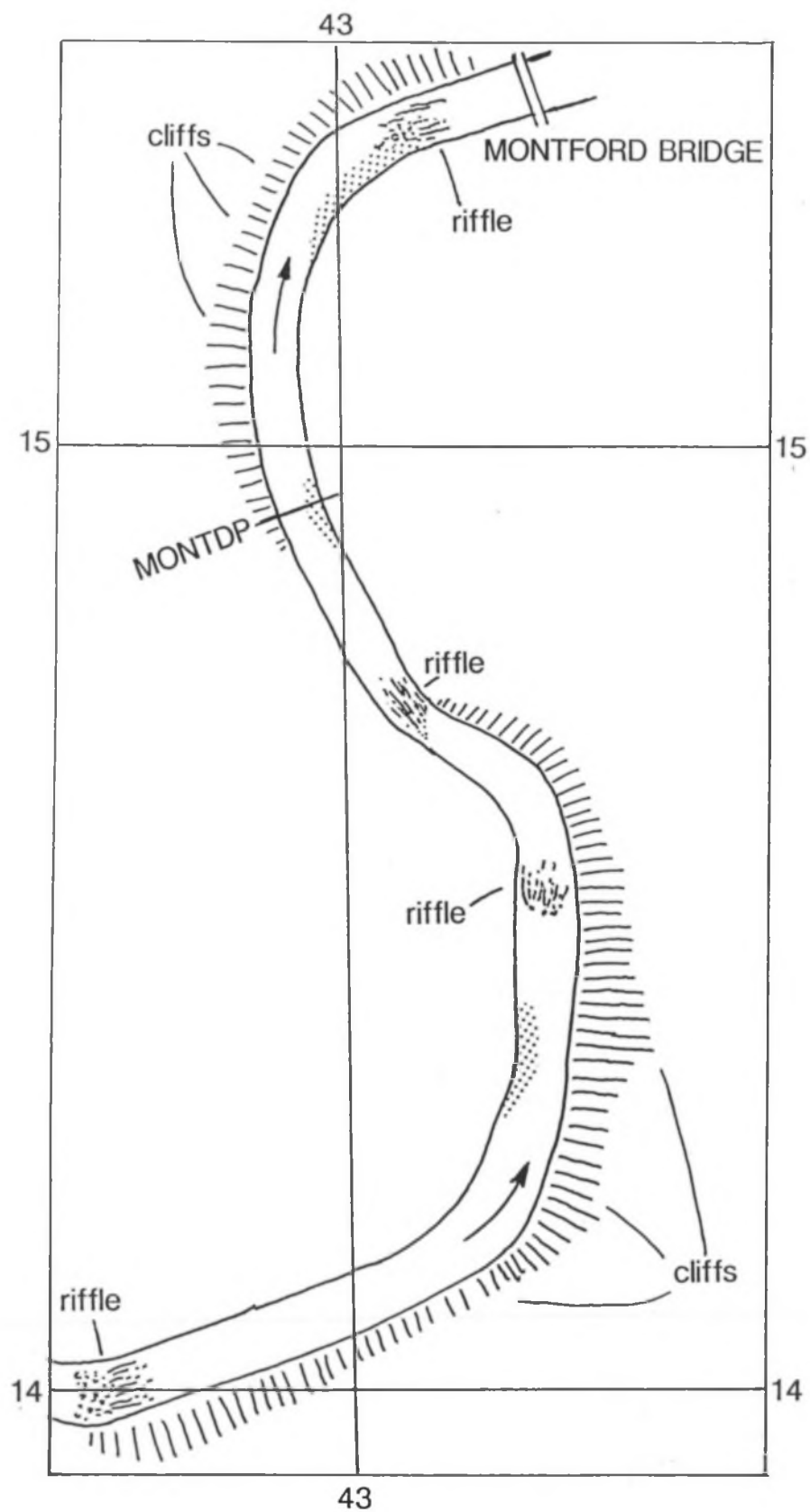
Figure 16. The Montford study reach, showing the distribution of riffles and pool areas of low flow and with evidence of local algal concentration (stipple).
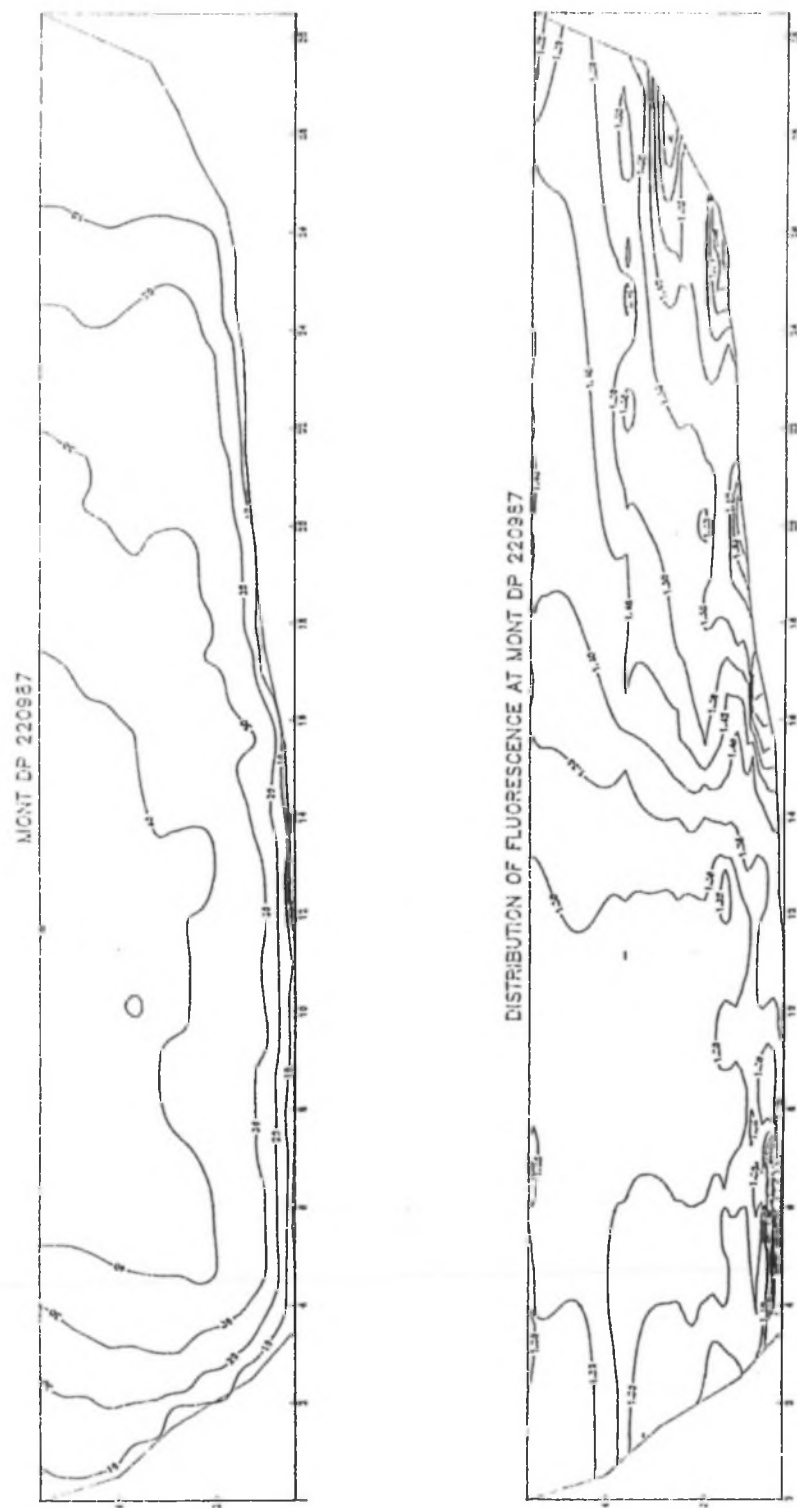
Figure 17. (above) Velocity profile through the MONTDP section on 22 September 1987; (below) distribution of chlorophyll fluorescence.
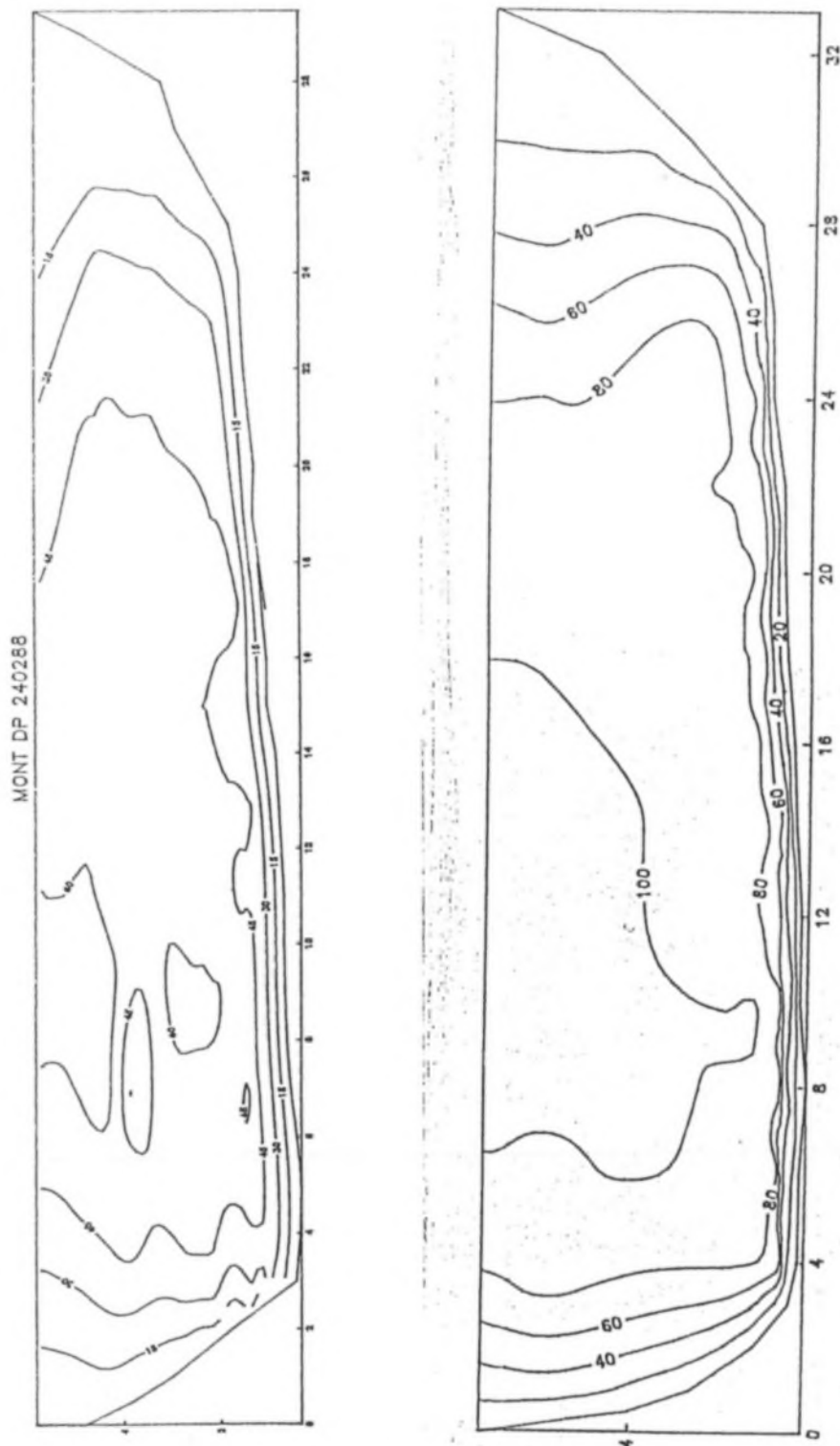
Figure 18. Sections through MONTDP flow (above) during winter and (below) a high discharge event (9 March 1989).
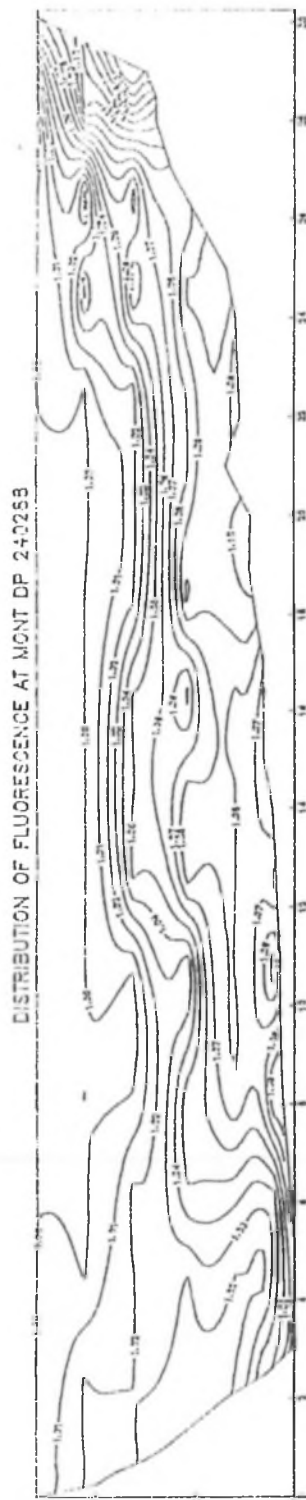
Figure 19. Distribution of fluorescence in the MONTDP section under
(above) moderately high and (below) flood discharges.
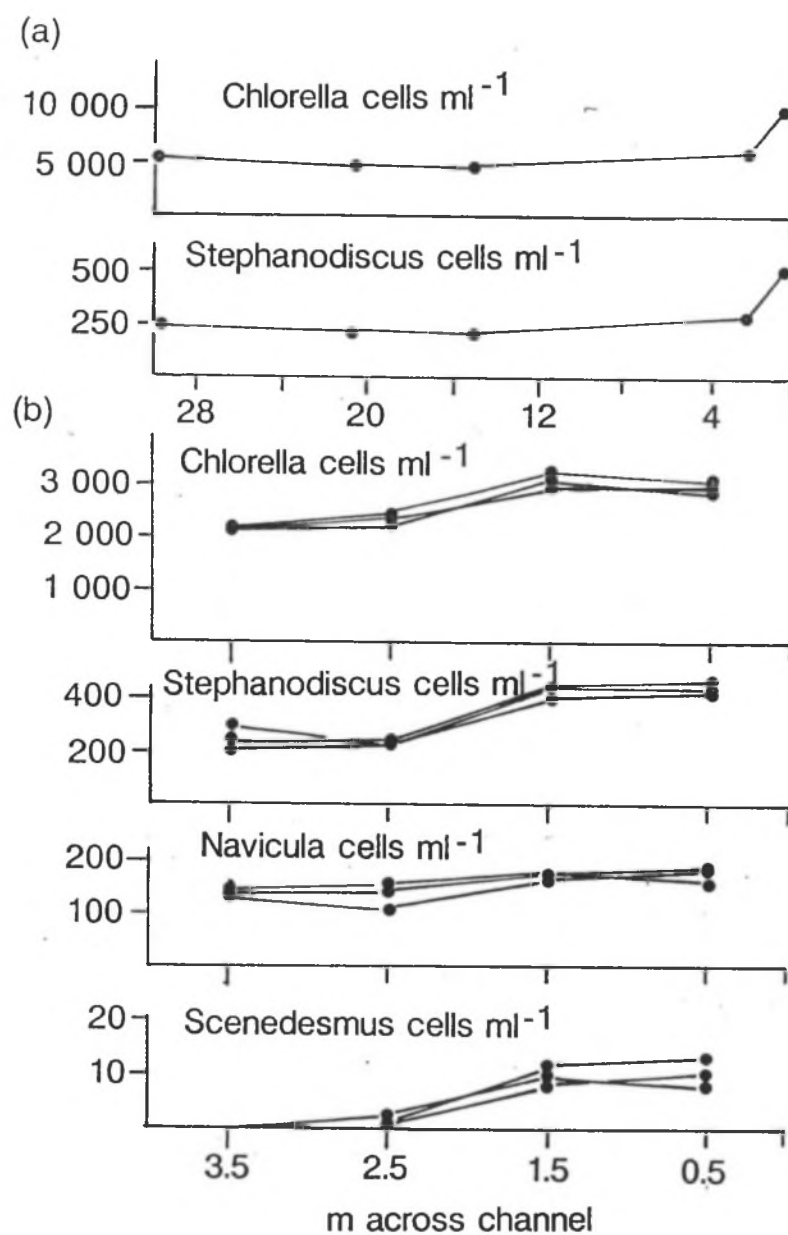
Figure 20. (a) Distribution of Chlorella I and Stephanodiscus across a MONTDP
profile on 22 September 1987. (b) Of selected algae across a short
profile from the east bank at MONTDP; three sets of counts were
undertaken on samples collected over a period of about 20 h.
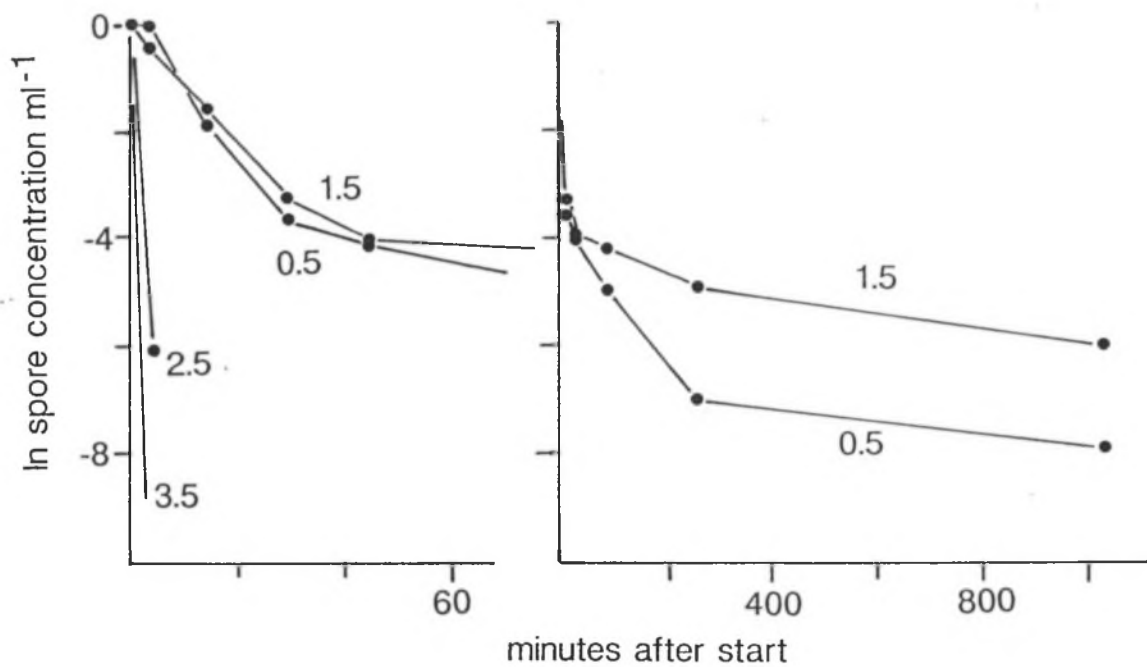
Figure 21. Elimination of Lycopodium spores introduced into the water across

the MONTDP transect from 0 to 3.5 m out from the bank. 2.5 and 3.5 m

out is well into flow and population is removed within minutes;

after an initial dispersion phase, the inshore population is eluted

quite slowly.
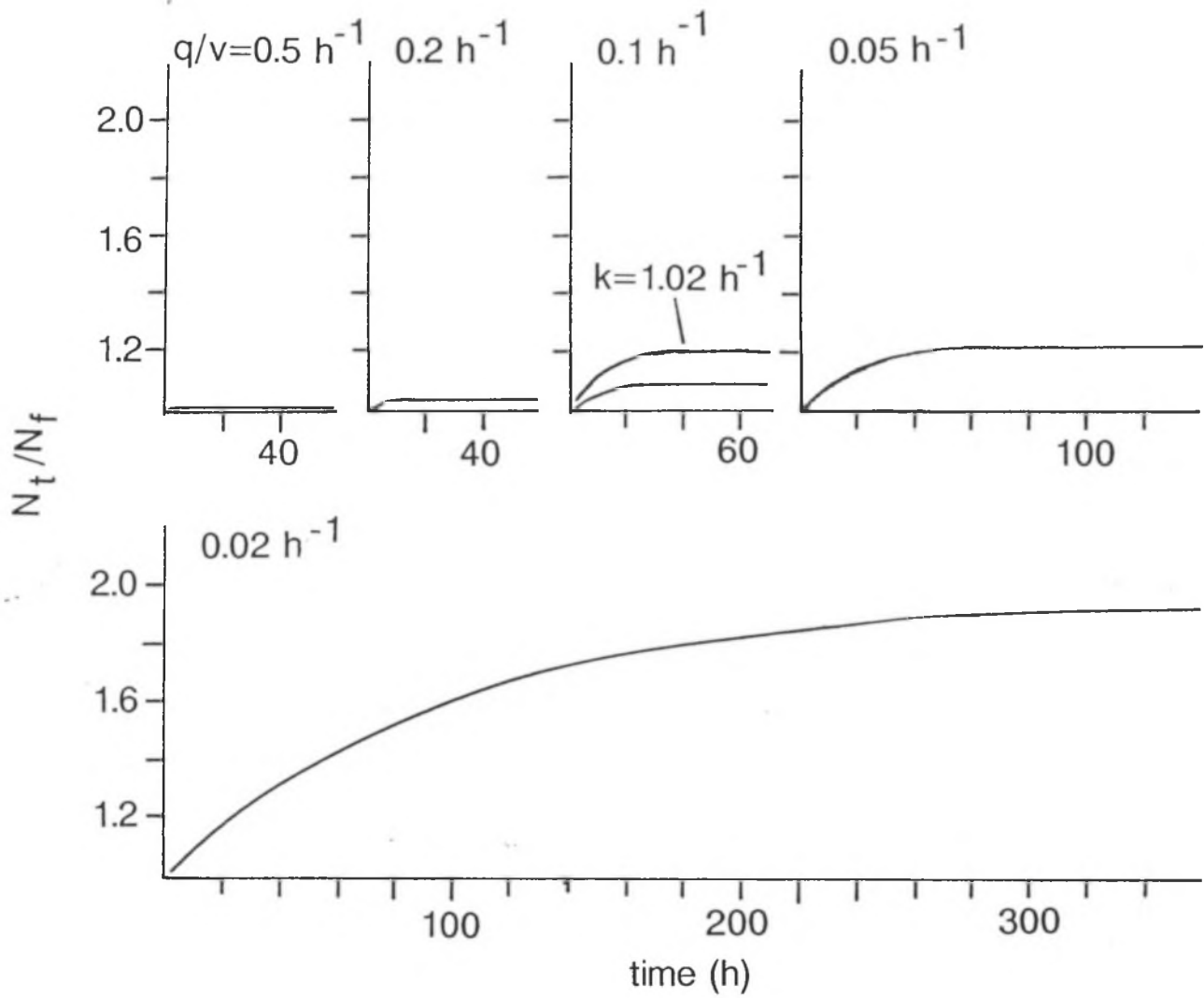
Figure 22. Modeled development of enhanced algal concentrations in dead zones exchanging at the rate (q/v) given and assuming the algal increase rate, k, to be 1.01 h⁻¹ (one case where k = 1.02 h⁻¹).
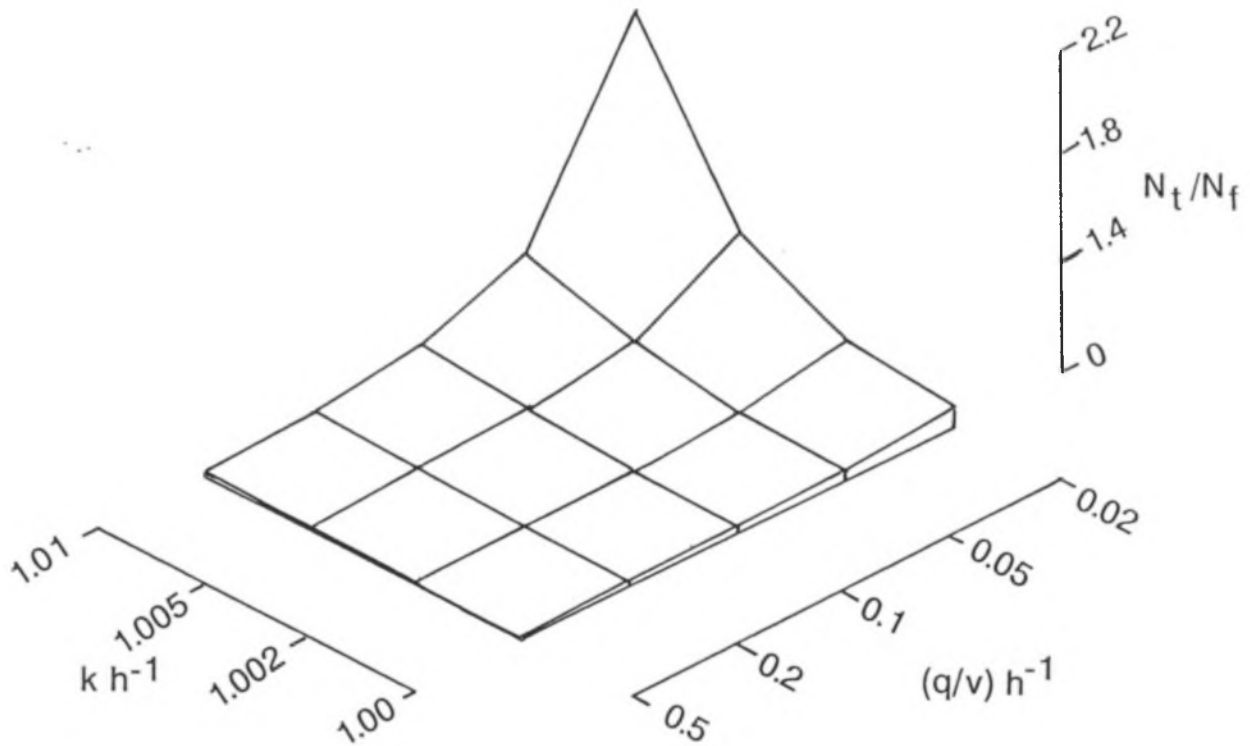
Figure 23. Enhanced algal concentration as a function of growth rate, $\underline{k}$, and fluid exchange rate ($\underline{q}/\underline{v}$) at steady-state equilibrium.
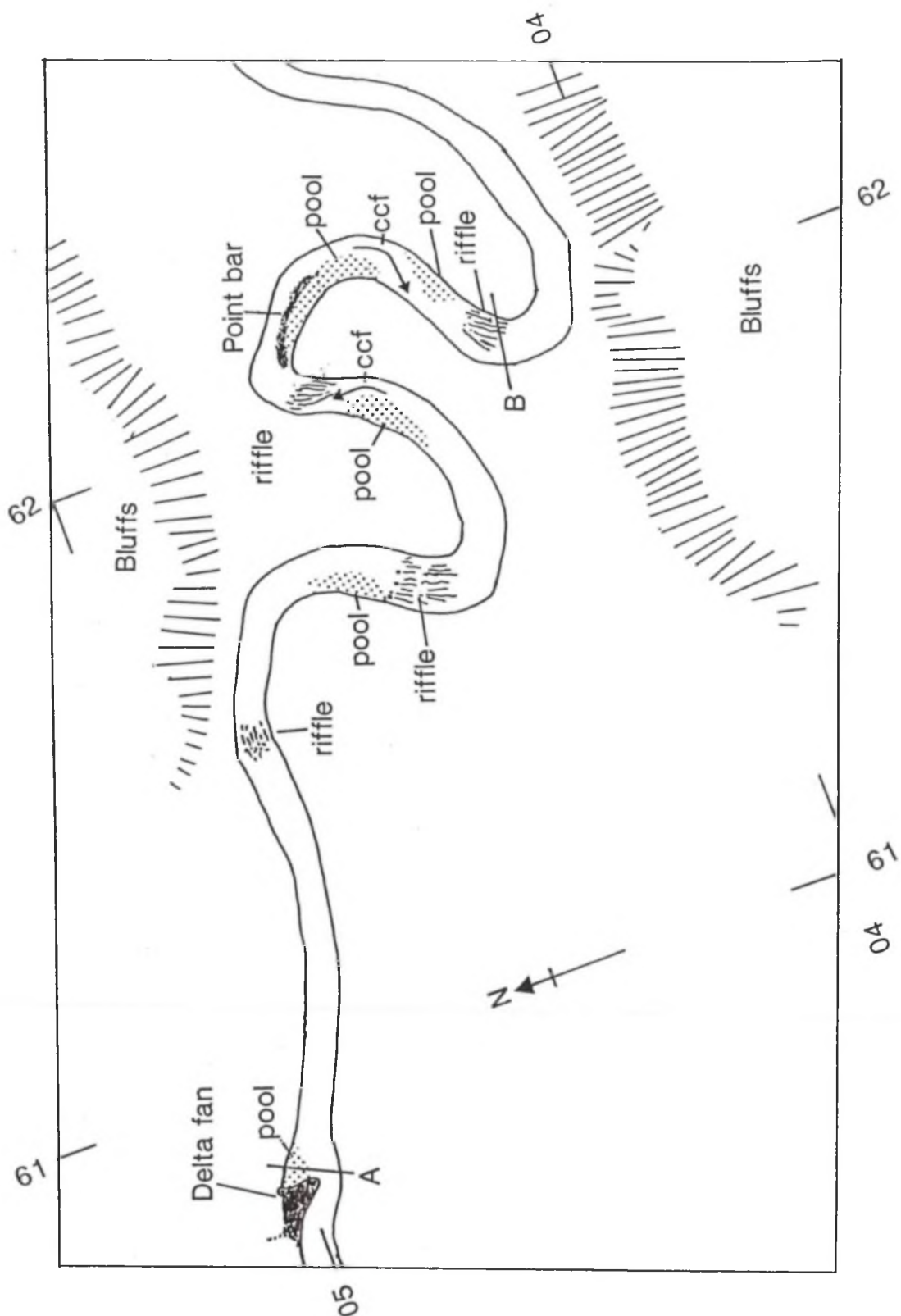
Figure 24. The Leighton study reach, showing the variety of fluvial structures
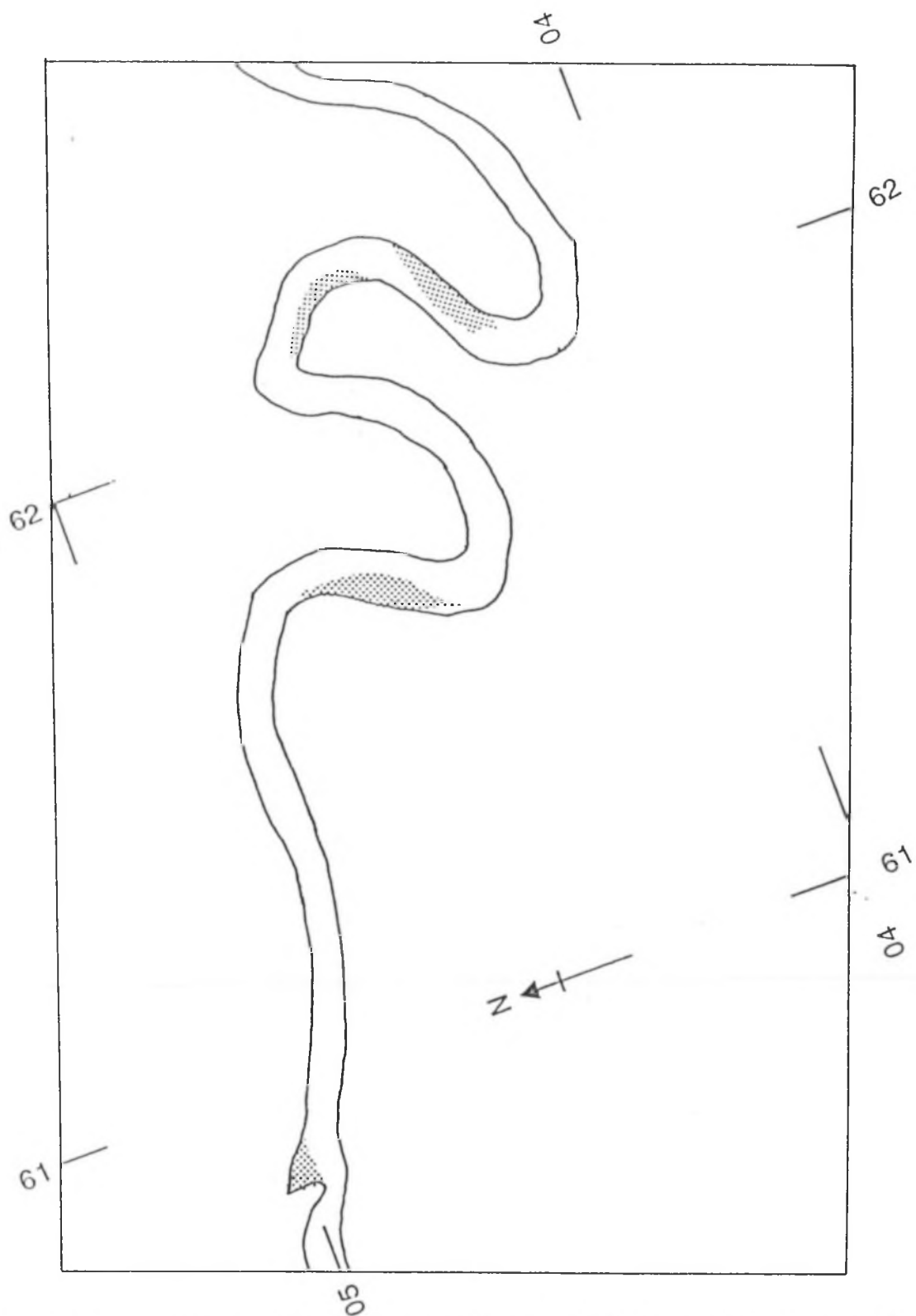present: points of cross channel flow are identified "ccf".

Figure 25. Sketch to show areas of enhanced algal concentrations, sensed remotely
(but not all verified on the ground at present) or apparent from
casual observation.