Phytoplankton dynamics of the feeder rivers of the Humber estuary

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PHYTOPLANKTON DYNAMICS OF THE FEEDER RIVERS OF THE HUMBER ESTUARY.

by

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This thesis results entirely from my own work and has not previously been offered in candidature for any other degree or diploma.

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ABSTRACT

The effect of environmental conditions upon the growth, production and development of river phytoplankton was investigated for the feeder rivers to the Humber Estuary. The study was part of the Land Ocean Interaction Study LOIS) and focused upon the Rivers Trent and Yorkshire Ouse.

The influence of physical, chemical and biological factors upon phytoplankton development were measured through routine fieldwork and laboratory analyses. During fieldwork measurements were collected which complemented measurements collected by LOIS colleagues. Data collected in this study included phytoplankton species composition, density and biomass and is situ rates of growth and production. In situ rates of loss through grazing and respiration were also measured. Laboratory investigations concentrated upon the effects of light and temperature upon dominant phytoplankton species and were developed to complement fieldwork.

The project focused around four main aims. These were basically to assess the size and composition of phytoplankton maxima in the Trent and Ouse, measure in situ rates of growth and production, estimate losses from grazing and to develop models, using the data collected to assess the effect of environmental conditions upon phytoplankton development and autochthonous carbon in the Humber Estuary.

The results showed that phytoplankton dynamics in the Trent and Ouse were controlled primarily by discharge, light and temperature. During spring, when conditions were favourable for growth, rapid phytoplankton growth and maximum rates of production were observed. However, spring floods often interrupted the large phytoplankton populations which developed. Other factors such as grazing and sedimentation were also considered as potentially important in the loss of phytoplankton. The turbid nature of the rivers resulted in a fine balance between photosynthetic gain and respirational loss. This temporal change in environmental conditions resulted in a temporal waxing and waning of the phytoplankton. This in turn had an impact upon the seasonality of the flux of autochthonous carbon to the Humber Estuary. Laboratory investigations and development of a photosynthetic model confirmed the importance of light and temperature upon phytoplankton development in these rivers.

In terms of phytoplankton growth and production and the flux of autochthonous carbon, the Trent and Ouse were found to be typical of many other European rivers. The study highlighted the importance of the Trent as a source of autochthonous carbon to the Humber Estuary.

LIST OF ABBREVIATIONS

ANOVA	analysis of variance
F	variance ratio
n	number of measurements
ns	not significant
P	probability
r	correlation coefficient
α	initial slope of curve (μmol O_2 (mg chl *a*)-1 mol photon^{-1}m^{-2})
β	photoinhibition factor (μmol O_2 (mg chl *a*)-1 mol photon $^{-1}$m^{-2})
I_k	Onset of light saturation (μmol m^{-2} s^{-1})
I_b	Onset of photoinhibition (weighted photoinhibition factor, μmol m^{-2} s^{-1})
I_m	Onset of maximal photosynthesis (μmol m^{-2} s^{-1})
PIZT	photosynthesis, irradiance, depth, time model
P_m	light saturated gross photosynthetic rate (μmol O_2 (mg chl *a*)$^{-1}$ h^{-1})
P_s	potential net rate of light saturated photosynthesis (μmol O_2 (mg chl *a*)$^{-1}$ h^{-1})
δ	solar declination
2_a,	zenith angle
E_t	downwelling irradiance
I	irradiance
PAR	photosynthetically active radiation
Q_s	total daily PAR
R	respiration rate (μmol O_2 (mg chl *a*)$^{-1}$ h^{-1})
K_s	vertical attenuation coefficient (m^{-1})
s	second
min	minute
h	hour
d	day
wk	week
yr	year

l	litre
ml	millilitre
pg	picogramme
µg	microgramme
mg	milligramme
g	gramme
t	tonne
nm	nanometre
µm	micrometre
mm	millimetre
cm	centimetre
m	metre
km	kilometre
µmol	micromole
M	molar
N	normal
v/v	volume/volume
w/w	weight/weight
chl *a*	chlorophyll *a* concentration
TEM	transmission electron microscope
Q	discharge
°C	degrees celcius
z	depth
POC	particulate organic carbon
atm	atmospheres

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1. INTRODUCTION

1.1 Preamble

The transport of particulate and dissolved nitrogen, phosphorus and carbon compounds by rivers can result in considerable amounts of material being carried to estuaries and the sea (Meybeck *et al.*, 1988). Of all investigations into riverine transit, the flux of carbon has received increasing attention over recent years. This may be because it plays such an important role in the carbon cycle (Meybeck, 1993; Sedjo, 1993) and has wider implications for riverine and coastal food webs and heterotrophic metabolism in estuaries and coastal waters. Once transported to coastal waters, burial of carbon within sea sediments may be an important global sink for carbon (Ittekkot & Laane, 1991).

Phytoplankton has been shown to comprise a considerable contribution to riverine Particulate Organic Carbon (POC), particularly in larger rivers during spring and summer months (& van Zanten, 1988; Tipping *et al.*, 1997) and can be a major source of POC to estuaries (Soetaert & Herman, 1995). In larger rivers, this phytoplanktonic source may be more important than the contribution by benthic algae or macrophytes. This living carbon is often of autochthonous origin, having increased *in situ* during its journey downstream (Reynolds & Glaister, 1993). In contrast, transported dissolved organic carbon predominantly derives from allochthonous sources (Tipping *et al.*, 1997).

The growth and development of phytoplankton is controlled by various environmental factors which are discussed later in this study. The environmental influences upon growth and development of phytoplankton populations also affect the flux of autochthonously produced carbon transported by rivers to estuaries and coastal waters. To understand the factors responsible for governing the production and flux of autochthonous carbon, the factors which influence phytoplankton growth and production must be understood.

1.2 Historical Literature

Although authors such as Vannote *et al.*, (1980) have described larger rivers as heterotrophic systems, devoid of substantial numbers of phytoplankton, larger rivers do often develop large populations of phytoplankton (Kowalczewski & Lack, 1971; Descy *et al.*, 1988; Köhler, 1994a). Phytoplankton are an integral component of these larger rivers, particularly those of third order and above (Reynolds & Descy, 1996) and one of the most important components of lowland rivers (Williams, 1972; Whitehead & Hornberger, 1984; Köhler *et al.*, 1993). They are often major primary producers of energy and autochthonous organic carbon assimilated by higher trophic levels (Forsberg *et al.*, 1993). They play a role in the biogeochemical cycling of elements such as nitrogen, phosphorus and silicon (Nienhuis, 1993; Meybeck *et al.*, 1988; Admiraal & van Zanten,

1988), contribute to the oxygen status of rivers and are an important part of riparian food chains (Nusch, 1987).

Although studies upon river phytoplankton (potamoplankton) have been underway for a century (e.g. Schroeder, 1898; Fritsch, 1902) the subject has received less attention than phytoplankton of lakes and oceans (Descy *et al.* 1987, Reynolds & Glaister, 1993). Because of net sampling methods, early studies concentrated mainly upon the composition of larger phytoplankton. However, Reynolds and Descy (1996) explain that the theories put forward by these early studies and the classic studies by Butcher (1924) and Welch (1952) have been left scarcely validated or challenged until quite recently.

Recent studies have attempted to relate the periodicity and species composition of the phytoplankton with environmental and human (i.e. agricultural and urban - Stevenson & White, 1995) variables. This research has been carried out upon rivers worldwide. The River Blue Nile, Africa, was the site of a classic study of the effect of environmental factors, particularly hydrological regime, upon phytoplankton development by Talling and Rzóska (1967). The Murray-Darling river system (Walker, 1979), and River Moruya (Potter *et al.*, 1975) have been the site of Australian research which includes the effects of temperature, discharge and herbivory. River phytoplankton studies conducted in the USA include those for the Rivers Hudson (Cole *et al.*, 1991) and Mississippi (Baker & Baker, 1979). Studies into phytoplankton of the Hudson concentrated upon the effects of unfavourable and ever changing light regime upon phytoplankton production while the Mississippi investigations also consider temperature and discharge.

European studies into the effect of environmental conditions upon phytoplankton growth and development, particularly in the larger rivers, are numerous. Over fifty years of research has been conducted on the Danube, Hungary, and recent studies have added to this research, particularly in recent years (Kiss, 1994; Kiss *et al.*, 1994; Schmidt, 1994). The River Meuse, Belgium, has been the site of extensive work upon phytoplankton growth and production for over a decade (Descy *et al.*, 1987; Descy & Gosselain, 1994; Gosselain *et al.*, 1994). The larger French river systems, particularly the Seine (Billen *et al.*, 1994; Garnier *et al.*, 1995) and Sambre (Prygiel & Leitao, 1994) have been the focus of phytoplankton research with respect to modelling of phytoplankton dynamics. The River Spree, Germany, has received much recent attention in the form of excellent, descriptive papers by Köhler (1993, 1994a, 1994b, 1995). Longtitudinal development and production are also considered in these studies. Like the Danube and Meuse, the Rhine has been the site of intensive phytoplankton research. Development of phytoplankton, particularly with respect to irradiance and light penetration through the water column was the subject of the study by Friedrich and Viehweg (1984). Other studies on the Rhine include the relationship between

phytoplankton development and physiochemical parameters (De Ruyter van Steveninck *et al.*, 1990; Admiraal *et al.*, 1992) and biological activity (Admiraal & van Zanten, 1988).

British studies include research upon both the small, fast flowing rivers and the larger, slower flowing rivers. Holmes and Whitton (1981) studied the development of phytoplankton populations with a change in hydrology for four fast flowing rivers; the Tyne, Wear, Tees and Swale, in North East England. Other small river investigations consider phytoplankton development and water chemistry for the Bure (Moss *et al.*, 1984), hydrology for the Derwent (Jones & Barrington, 1985) light, water chemistry and hydrology for the Lee (Swale, 1964) and light and hydrology for the Wye (Jones, 1982).

Studies upon larger, slower flowing rivers of the United Kingdom have remarked upon the large concentrations of phytoplankton which develop. The classic paper by Lack (1971) related phytoplankton development in the Thames to physiochemical and biological variables. The Thames is perhaps the most intensively studied British river with respect to phytoplankton with the research of Kowalczewski and Lack (1971) setting a precedent for this type of research. Accounts for the River Severn by Reynolds and Glaister (1993) concentrated primarily upon river discharge and retentivity as a control of phytoplankton growth while Swale (1969) includes discharge and other environmental factors in her paper. Research into the slow flowing River Avon (Moore, 1976) includes data upon attached algae and their role in the recruitment of phytoplankton with respect to water velocity..

Overall, phytoplankton studies on the Trent and Yorkshire Ouse systems are limited. The phytoplankton flora for the Trent was described by Fritsch (1905) based on net samples while McCollin (1995) described the phytoplankton populations in two arms of the Trent near Newark based on whole water samples. A description of the seasonal pattern of phytoplankton biomass has been carried out for the Trent and Ouse (Marker *et al.*, 1993; Pinder *et al.*, 1997), using chlorophyll *a* as a surrogate for biomass. Apart from Skidmore *et al.* (1998), the study of phytoplankton dynamics of the Derwent (Jones & Barrington, 1985) is the only known study concerning phytoplankton of a tributary to the Trent. However, Holmes and Whitton (1981) gave a floral account of the phytoplankton of the Swale, the upper part of the Swale-Ouse and an overview of the biology of the Humber rivers has been compiled (Whitton & Lucas, 1997).

Phytoplankton below the tidal limits of the Ouse (Uncles *et al.*, 1998) have also investigated with respect to the development of phytoplankton with respect to water chemistry and light.

A large number of papers describing the effect of environmental and human impacts exist. Most of these explain the growth of phytoplankton in rivers as a function of water chemistry, physics and biology. What is not clear is where phytoplankton actually originate.

1.3 Sources of phytoplankton

There is no clear distinction between true phytoplankton species and those which are benthic and washed into the water column. Reynolds and Descy (1996) regard algae which can grow in the water column as phytoplankton with benthic derived species being described as tychoplanktonic and those phytoplankton which pass through a benthic survival phase as meroplanktonic.

Phytoplankton, or at least algae in suspension, may originate from epilithic, epiphytic or epipelic sources. Algae from the benthos or from macrophyte stems, for example, may become detatched and proliferate when in the water column. This is common in smaller, faster flowing rivers (Blum, 1954; Kowe *et al.*, 1998) and in larger rivers during flood events (Lack, 1971; Marker & Gunn, 1977). Indeed, the river bed and shallows have been implicated as sources of phytoplankton for the Rivers Hull (Butcher, 1940) and Danube (Stoyneva, 1994). Phytoplankton in rivers may not necessarily originate from an autochthonous source. The phytoplankton may originate from reservoirs (Nusch, 1982), flushed lakes (Friedrich & Viehweg, 1984; Reynolds & Glaister, 1993) and side arms (Kiss & Genkal, 1993). Reynolds and Glaister (1993) found three categories of suspended algae in the River Severn. These were (1) species which had become detached, (2) planktonic species from ponds and lakes which did not persist downstream and (3) planktonic species which increased downstream. The third category covered those species which were autochthonous. They were apparently neither washed from the benthos nor introduced from lakes or other impoundments. Where these autochthonous phytoplankton species first originate is unclear and a believable theory has yet to arise from the literature. However, Reynolds and Descy (1996) suggest that they may arise from either benthic or limnetic sources. Phytoplankton found at downstream reaches of larger rivers may be autochthonous, originating from the upstream reaches as these species can successfully grow and proliferate in the water column of a river during their transport downstream.

Although loss of populations to the sea is an inevitable fate of lotic phytoplankton (Reynolds, 1988), substantial populations can develop, particularly in long, slow-flowing rivers before being lost from the system. Recent studies have devoted their attentions towards the growth of phytoplankton during downstream transport. The growth of large populations in many rivers invokes a paradox. Many rivers appear too short to allow the development of the large phytoplankton populations observed within the limits of plausible phytoplankton growth. This was coined as 'the paradox of the potamoplankton' (Reynolds, 1988).

Downstream increase in phytoplankton biomass is a common feature of many larger rivers including the Lee, UK (Swale, 1964), Spree, Germany (Köhler, 1994a), Bure, UK (Moss *et al.* 1984), Meuse, Belgium (Descy and Gosselain, 1994) and the Trent, UK (Skidmore *et al.*, 1998). The study of four rivers in N-E England (Holmes and Whitton, 1984) showed a downstream increase in phytoplankton abundance in all but the Wear.

The downstream increase in biomass is probably largely a result of *in situ* growth although Reynolds and Descy (1996) comment that it is difficult to determine to what extent the same phytoplankton population with the same growth rate is being sampled if successive downstream samples are obtained. Nevertheless, studies made by following a parcel of water downstream have demonstrated that *in situ* growth can occur (Friedrich & Viehweg, 1984; De Ruyter van Steveninck *et al.*, 1990).

The downstream growth of phytoplankton is feasible given the *in situ* growth rates calculated from previous research. Growth rates of 0.53 d^{-1}, 0.57 d^{-1} and 0.7 d^{-1} were calculated for the Severn (Reynolds and Glaister, 1993), Trent (Skidmore *et al.*, 1998) and Rhine (Reynolds & Descy, 1996 for the Rhine using data of De Ruyter van Steveninck *et al.*, 1992), respectively. Growth rates reported for other rivers are somewhat lower, ranging between 0.23 d^{-1} for the Lot (Capblancq & Décamps, 1978) and 0.28 d^{-1} for the Meuse (Gosselain *et al.*, 1994).

It has been suggested that a series of 'dead zones' are needed along some rivers to allow large phytoplankton populations to grow over relatively short river lengths (Reynolds & Glaister, 1993; Reynolds, 1994). These dead zones act as storage cells, where phytoplankton concentration and rates of growth (Reynolds & Glaister, 1993) are greater than in the main river channel. Given the reported maximum, estimated, *in situ* rates of growth of 0.7 d^{-1} and rates in culture of up to 1.18 d^{-1} for centric diatoms (Reynolds, 1984). Skidmore *et al.* (1998) suggest that the calculated growth rates in rivers such as the Trent are achievable without needing to invoke the existence of 'dead zones'. Even so, downstream increase in phytoplankton biomass usually occurs during spring and summer when discharge and velocity are low and so a river must be retentive enough to enable a high phytoplankton biomass to develop.

1.4 Chemistry

Nutrients play a major role in the growth and production of attached micro and macro algae, especially in small, upland rivers (Carr & Goulder, 1990; Christmas *et al.*, 1997). However, water chemistry is thought to play only a small part in the regulation of potamoplankton in larger rivers (Descy & Gosselain, 1994; Reynolds & Descy, 1996) because concentrations exceed the suggested limiting concentrations of 5-10 x 10^{-6} mol N l^{-1}, 3-6 x 10^{-8} mol P l^{-1} (Reynolds & Descy, 1996). However, in temperate estuaries evidence of P and N limitation of primary productivity has been documented (Doering *et al*, 1995) as has the increase in column productivity with increased nutrient loading (D'Avanzo *et al.*, 1996). Silica concentration may also limit growth of centric diatoms and so affect species composition. The prevention of the further growth of centric diatoms as a result of silica limitation has been documented (Swale, 1969; Köhler, 1994a) though is not always the case (Swale, 1964; Jones & Barrington, 1985). Although water chemistry apparently has little role in the control of potamoplankton development, anthropogenic, industrial, chemical

pollution has been shown to be responsible for low growth rates (Tubbing *et al.*, 1995) and a decrease in phytoplankton biomass (Descy, 1995) in the Meuse.

1.5 Discharge

The effect of river discharge and velocity has been mentioned previously with respect to overall river retentivity. Descy (1993) notes that flood events are the major causes of disturbance of biomass and composition of phytoplankton in rivers. An increase in discharge can remove large phytoplankton populations from river systems and flush them out to the estuary and to the sea. Jones and Barrington (1985) found a negative relationship between numbers of phytoplankton cells and discharge at downstream sites but a positive relationship for upstream sites as a result of resuspension of benthos. Spring and summer floods often result in a temporary decrease in phytoplankton populations although high biomass may return if favourable conditions are resumed (Swale, 1964).

As well as dilution and hydraulic wash out of phytoplankton populations, an increase in discharge can result in an increase in turbidity. The action of increased turbidity reducing the amount of light penetrating through the water column as a result of an increase in discharge is a common occurrence in many rivers (e.g. Swale, 1969; Kiss & Szabó, 1975).

1.6 Light

The amount of light penetrating through the water column depends upon factors above the water surface such as the time of day, year, atmospheric conditions (Kirk, 1994) and attenuation under the surface. Non-algal suspended solids (Kirk, 1980) and dissolved substances such as tannins (Herrera-Silveira & Ramírez-Ramírez, 1996), humic and fulvic acids (Kirk, 1976; 1980) and minerals (Threlkeld & Søballe, 1988) all compete with phytoplankton for light in rivers (Kirk, 1994). Turbulence in rivers results in an algal cell being exposed to constant changes in amounts of light (Dokulil, 1994; Smayda, 1980). The light climate of these turbulent, turbid environments determines species composition. For example, Reynolds (1994) reports that a high level of turbulence and turbidity will favour only spherical and round algal cells, such as centric diatoms.

The exposure of phytoplankton to an ever changing regime of high and then low light has been found to either increase or decrease phytoplankton growth and productivity or have no effect at all (Dokulil, 1994). An increase in phytoplankton production in shallow rivers has been observed as a reduction in photoinhibition and the mitigation of turbidity induced light limitation (Mallin & Paerl, 1992). Indeed, Brunet *et al.*, (1996) found that constant high light caused damage to the centric diatom *Skeletonema costatum* in laboratory studies. The problem in laboratory studies has been how to best reproduce the fluctuating light climate to which phytoplankton cells are exposed (Descy & Gosselain, 1994). Many studies estimate productivity by assuming a non-turbulent

system or static phytoplankton cells. Attempts to recreate the fluctuating light climate (e.g. Mallin & Paerl, 1992) may not reproduce the turbulent path of a cell nor the light climate to which it is exposed (Descy & Gosselain, 1994). However, an *in situ* approach, using a containing apparatus (Köhler & Bosse, 1998) has attempted to recreate the turbulence and light climate experienced by river phytoplankton.

A further problem facing phytoplankton in deeper rivers is one of how to survive under the low water transparency and high mixing depth regime (Cole *et al.*, 1991, 1992). Indeed, the mixing to euphotic depth ratio is often one of the most important factors influencing productivity (Grobbelaar, 1989, 1990; Kirk, 1994). Talling and Rzóska (1966) report that, in order for net photosynthesis to occur, the mixing to euphotic depth ratio must not exceed 5. Kirk (1994) explains that the critical depth, the depth below which net photosynthesis is not possible, is a major factor influencing net column productivity.

If the mixing to euphotic depth ratio is exceeded, or the cells are mixed below the critical depth, then phytoplankton biomass is lost as a result of increased respirational losses in proportion to photosynthetic gain as cells are exposed to a length of time without light. Phytoplankton may compensate in some way for this by pre-adaptation to their time in darkness (Köhler, 1993) or may be acclimated to low light in the downstream reaches of a river (Cole *et al.*, 1991).

Another aspect of light, important to the development of phytoplankton is daylength. Swale (1969) explains that the increase in daylength may be the most important factor influencing the increase in the spring centric diatom bloom.

Overall, the literature reflects the view that the success of phytoplankton in rivers depends on the mixing and euphotic depth and the length of time the cells are able to stay in the dark before net loss occurs.

1.7 Temperature

By influencing enzymatic reactions, temperature affects the rate of phytoplankton growth, production and respiration. The effect of temperature upon these processes has been well documented both in the laboratory and in the field. Laboratory studies have shown that the rates of growth and production of phytoplankton generally increase regularly with increasing temperature (Chisholm & Costello, 1980; Ojala, 1993) until an optimum temperature is reached, after which rates decrease. In the field, high rates of growth and production, coupled with high phytoplankton biomass, have been observed during the spring and summer months when temperatures increase (Baker & Baker, 1979; Descy & Gosselain, 1994). Centric diatoms are often dominant during the spring, when river temperatures are between 10 and 15 °C as they are reported to be low temperature adapted species (Kiss, 1994), with optimal rates of growth and production (Descy, 1987) at lower temperatures than Chlorophyta. It has been suggested that

temperature controls species succession in phytoplankton populations (Baker & Baker, 1979). However, increasing temperature can lead to an overall loss of algal carbon, particularly in turbid rivers as the respirational loss in a turbid environment is exacerbated (Dokulil, 1994; Cole *et al.*, 1991). An increase in temperature during spring and summer may increase the rate of loss of phytoplankton from other loss processes and is discussed later (Section 8.34).

Low winter temperature normally results in no or very low rates of phytoplankton growth and production. However, Kiss (1993) observed a bloom of the centric diatom *Stephanodiscus hantzchii* in the River Danube during winter. This suggests that temperature may not be the primary cause of low phytoplankton biomass in winter.

Low temperature in winter results in low rates of growth and production and so biomass is usually low. Increasing temperature, as well as increasing light availability, during spring result in an increase in the rates of growth and production, so biomass increases. Maximum temperatures during summer may cause maximal rates of both growth and production but the increase in loss such as respiration and grazing often leads to a general decline in riverine phytoplankton biomass.

1.8 Sedimentation

Although the loss of phytoplankton by sedimentation has been studied extensively in lakes (Rust, 1982), the additional forces at work in a river (Ryder & Pesendorfer, 1989) make the loss of phytoplankton to sedimentation difficult to quantify. Swale (1964) explains that in rivers, turbulence will result in reduced loss of phytoplankton by sedimentation and will increase re-suspension of sedimented cells. Limited studies in the field have shown that sedimentation may be important in rivers (Moore, 1976, De Ruyter van Steveninck *et al.*, 1990). Laboratory studies have shown that sedimentation increases as channel depth decreases (Reynolds *et al.*, 1990). This will have implications for summer populations as river discharge (and so river depth) is usually at a minimum during this time of the year. Diatoms are likely to be especially sensitive to sedimentation loss given their high specific gravity. Some species of phytoplankton reduce the loss to sedimentation by reduction of form (Reynolds, 1984).

The importance of sedimentation as a loss process in rivers has still to be adequately quantified. However, it may be that other loss processes are far more important.

1.9 Grazing

Much research into the behaviour of zooplankton (Starkweather, 1980; Pourriot, 1977) and their interaction with phytoplankton (Bainbridge, 1953; Lair & Ali, 1990) has been conducted, particularly for lakes. However, grazing in rivers has still to be quantified adequately and the importance properly assessed (Gosselain *et al.*, 1994). However, laboratory investigations and the

increasing number of *in situ* studies are suggesting that grazing could be a major loss process, especially during spring and summer.

Many studies of riverine grazers have identified rotifers, particularly *Keratella* spp. and *Brachionus* spp. as the most important grazers of phytoplankton in rivers (Garnier *et al.*, 1995; Viroux, 1997). However, copepods and cladocerans are sometimes important during summer (Bothár & Kiss, 1990). Ciliates may be important, especially during summer, as they often represent a large proportion of the zooplankton biomass, as seen for the Danube (Bereczky & Nosek, 1994). Unfortunately, traditional methods of zooplankton sampling, such as sampling with a 75-μm mesh net (Bothár, 1987), probably miss many of the ciliates and smaller rotifers which may be important in the grazing of phytoplankton.

As with phytoplankton, zooplankton is lost from the river system by the unidirectional flow towards the sea. To develop large populations and exert significant grazing pressure upon phytoplankton populations, smaller, faster-growing species are usually more important in river systems than larger, slow growing species (Hynes, 1970; Admiraal *et al.*, 1994). Indeed, where grazing by zooplankton has been found to be important, it has been most marked through the spring and summer months when discharge has been low and temperature high (Gosselain *et al.*, 1998), conditions which are optimum for both phytoplankton and zooplankton development (Admiraal *et al.*, 1994). A number of authors have reported an increase in grazing rate with increasing temperature (Bogdan & Gilbert, 1982; Joaquimjusto *et al.*, 1995). Therefore, during the spring and summer months, zooplankton grazing may contribute a major loss of phytoplankton from the system.

Grazing by zooplankton may be selective and so influence the species composition of phytoplankton. For example, investigating the grazing of green algae by the rotifer *Brachionus*, Schlüter *et al.* (1987) found that there was a switch from a *Scenedesmus* dominated plankton to a *Microactinium* dominated plankton as *Brachionus* could not injest *Microactinium.* In a different study, the rotifer *Polyarthra* was reported to feed at twice the rate on flagellated cells than on cells without flagella and that *Keratella* and *Bosmina* found *Chlorella* unpalatable (Gilbert & Bogdan, 1981).

Perhaps protozoa are the most underestimated and least understood grazers. This may be because problems lie in the sampling methods employed in such studies (as mentioned earlier) or that researchers insist that animals so small could never attain biomass high enough to impart serious loss on the phytoplankton population. Nevertheless, studies have attempted to analyse the importance of this component as a major grazing force. The importance of protozoa may be higher in rivers than in lakes as a result of greater turbulence. Experimental work suggests that the grazing rate of some non-swimming and weak swimming protozoa increases sigmoidally with increased turbulence by increasing the number of encounters with phytoplankton prey (Shimeta *et al.*, 1995). The importance of protozoa in the field has also been noted. Phagotrophic

microplankton were thought to be responsible for the downstream loss of plankton in the Rhine (Admiraal *et al.*, 1994).

A popular view, adopted by recent studies, is the role of benthic grazers in the loss of phytoplankton. The most important taxa in the literature are *Dreissena polymorpha*, *Unio* spp. and *Anodonta* spp. (Köhler, 1995; Roditi *et al.*, 1996; Caraco *et al.*, 1997). Experimental work has shown that *D. polymorpha* can influence phytoplankton biomass and species composition (Bastviken *et al.*, 1998).

Other forms of grazing, reported as being important include that by simuliid larvae (River Wye, Uk; Jones, 1984) and larval lampreys (Moruya River, Australia; Potter *et al.*, 1975). Fungal, bacterial and viral attack may also be important in the biological loss of phytoplankton, especially during summer. Parasitization of centric diatoms by the chytrid fungus, *Rhizophidium* sp. has also been reported (Swale, 1964; Garnier *et al.*, 1995).

Grazing by benthic filter-feeders, protozoa, parasitism and viral attack are all potentially very important sources of loss of phytoplankton during the summer months. They are among the least understood and least researched category of grazers. Further studies are required to try and understand the dynamics of this potentially important source of algal loss.

The literature suggests that discharge is the most important factor in the control of riverine phytoplankton. Increased discharge leads to a rapid removal of populations from the system. Other important impacts upon remaining populations result from an increase in turbulence, lower river retentivity and, perhaps more importantly, decreased light. The combination of high discharge, low light and high temperature can lead to adverse conditions and loss of phytoplankton through respiration.

Water chemistry is thought to play a very minor role in potamoplankton ecology except perhaps during late spring when SiO_3-Si concentrations may become limiting to growth.

Although inconclusive, sedimentation and grazing are though to be important. The literature suggests that grazing, particularly the benthic aspect, is potentially very important in loss of phytoplankton. It is important that more time is devoted to quantify the impact of sedimentation and grazing upon phytoplankton populations in larger rivers.

1.10 Modelling

The environmental factors described above will all interact to influence the development of river phytoplankton which will in turn affect the flux of algal carbon. Workers have attempted to model the effects of environmental factors upon phytoplankton development in rivers. The RIVERSTRAHLER model (Billen *et al.*, 1994; Garnier *et al.*, 1995) was developed to determine the importance of different environmental factors upon phytoplankton biomass and species

composition for the Seine River system. Soetaert and Herman (1995) developed an ecosystem model describing the carbon flux in the Westerschelde estuary, Netherlands. Other workers have attempted to investigate the importance of environmental variables upon phytoplankton development using a multivariate approach (del Giorgio *et al.*, 1991; Stevenson & White, 1995) and the influence of seasonality and the trophic status of waters on phytoplankton (Seip & Reynolds, 1995).

One branch of modelling has concentrated upon phytoplankton photosynthesis and production in rivers. Over 20 models have been formulated to describe the photosynthetic response of phytoplankton to irradiance (P vs I response, Baumert, 1996). Of those produced, earlier models (e.g. Baly, 1935; Talling, 1957; Chalker, 1980) did not include the possibility of photoinhibition while more recent models make provision for this (e.g. Platt *et al.*, 1980; Eilers & Peeters, 1988). While these models have measured the response of static phytoplankton, dynamic models also exist which take into account mixing of phytoplankton populations in turbulent systems (Pahl-Wostl & Imboden, 1991). Excellent reviews of the photosynthetic response of phytoplankton to irradiance are available (Henly, 1993; Baumert, 1996)

Using the P vs I response, water depth, water transparency and a measure of surface irradiance, models have been developed to estimate column production. A static approach has been used to estimate the production of phytoplankton in waters over a range of depths (Fee, 1973, Descy, 1987; Walsby, 1997). However, models have also been developed that estimate phytoplankton production in systems with differing mixing depths (Grobbelaar, 1990).

1.11 Aims

The project was designed to complement the overall objectives of the Land Ocean Interaction Study (LOIS) project, funded by the Natural Environment Research Council (NERC). The aims of LOIS are:

1) To estimate the contemporary fluxes of momentum and materials into and out of the coastal zone.
2) To characterise key physical and biogeochemical processes that govern coastal morphodynamics and the functioning of coastal ecosystems.
3) To describe the evolution of coastal systems from Holocene to Recent in response to changes in climatic conditions.
4) To develop coupled land-ocean models to simulate the transport, transformation and fate of materials in the coastal zone for the next 50-100 years.

A full description of the LOIS project can be found elsewhere (Wilkinson *et al.*, 1997; Leeks & Jarvie, 1998).

At the heart of the LOIS project is the Rivers, Atmosphere, Coasts and Estuaries Study (RACS) the aim of which was to study land-sea interactions in the coastal zone and the major fluxes by way of rivers, estuaries and the atmosphere. This RACS component comprised three integrated components: RACS (R-Rivers), RACS (C-Coasts) and RACS (A-Atmosphere). The current project was targeted under RACS (R), the objectives of which are:

1) To determine contemporary land-sea fluxes of water, sediment, biological matter, major dissolved constituents, nutrients and selected contaminants.
2) To identify and characterise key processes governing the fluxes.
3) To develop models capable of predicting changes in fluxes under future environmental changes.

The overall objective of this particular project was to identify, quantify and model the important environmental factors responsible for controlling phytoplankton growth, production and loss in the feeder rivers to the Humber Estuary. The project had four main aims:

1) To quantify the seasonal changes in the size and composition of the phytoplankton with particular reference to the Yorkshire Ouse.
2) To estimate the *in situ* growth and production rates of dominant phytoplankton species at different times of the year in contrasting environments during both the waxing and waning of naturally occurring growth cycles.
3) To quantify the major loss processes, involving grazing and sedimentation.
4) To develop models to predict the effect of changes in environmental conditions on the development of phytoplankton in large river systems and the output of autochthonous carbon to the Humber Estuary.

In view of the importance of the Trent in the transport of phytoplankton carbon to the Humber Estuary the focus of the project moved to concentrate upon the Trent system.

2 GEOGRAPHICAL BACKGROUND AND SITE DESCRIPTION

2.1 River Trent

The River Trent is the second largest UK river in terms of mean annual discharge and catchment area and the fifth largest in terms of length (Lester, 1975). Draining the Midlands, the Trent rises at 290 m above ordnance datum (AOD), (Law *et al.*, 1997) at Biddulph Moor, 11 km north of Stoke on Trent (Lester, 1975) then flows 274 km through England from Staffordshire to Humberside (Fig. 2.1).

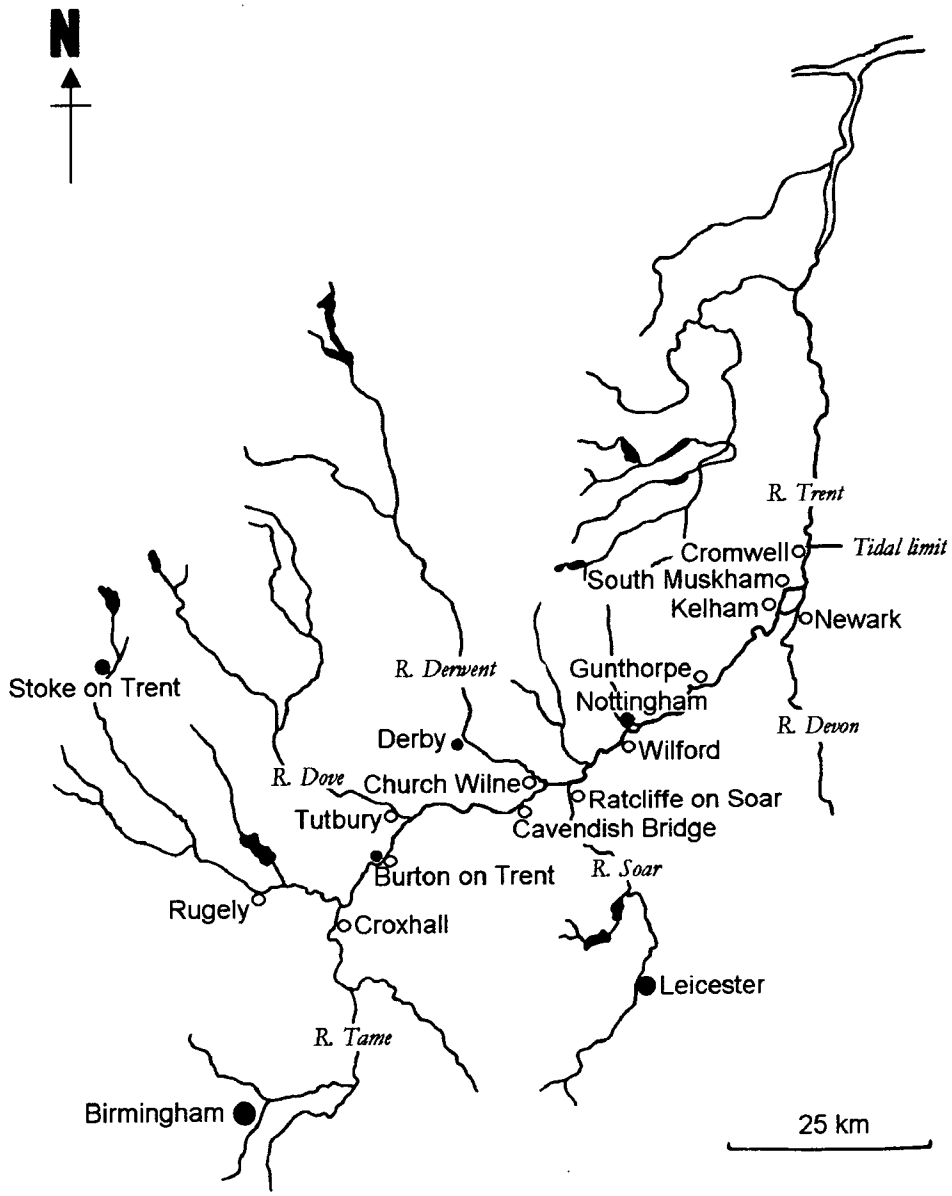

Figure 2.1 The Trent and its tributaries.

The Trent begins to flow in a south Easterly direction and drops 180 m over the first 32 km. Over the remaining 242 km it drops only 90 m.

The Trent catchment comprises mainly Triassic Bunter Sandstones, Keuper Marls with Jurassic Limestone to the South-East and Carboniferous Rocks to the North of the catchment (Jarvie *et al.*, 1997). The Trent catchment has an area of 8238 km^2 and a population of around six million living mainly in the larger urban areas of Birmingham, Leicester, Nottingham, Derby and Stoke on Trent (Marsh & Sanderson, 1997). Because of use by industry, urban areas and agriculture the Trent is more affected by towns and industry than the northern rivers such as the Swale, Ure and Nidd which also drain into the estuary (Robson & Neal, 1997; Jarvie *et al.*, 1997; House *et al.*, 1997).

Water quality in the river is high (class 1b) until it reaches Stoke where effluent from industry, sewage and agriculture diminish water quality to class 2 (NRA, 1995). Further pollution by Fowlea Brooke at Hanley then causes a further drop to class 3 until Stone. The input of the River Sow improves the water quality and this, together with self purification, improves water quality until the power station at Rugeley (NRA, 1995). The River Tame joins the Trent near Croxall (Fig. 2.1). The Tame has been greatly improved by sedimentation pools at Lea Marston (NRA, 1995). From this point the Trent flows in a north easterly direction. The Trent and Mersey canal joins the Trent close to where the Rivers Dove and Derwent meet the Trent at Repton and Shardlow respectively (Fig 2.1), improving water quality. The Rivers Soar and Erewash join the Trent at Sawley and the Trent then flows through Nottingham and towards Newark (Fig. 2.1). Before Newark, the river divides into a main channel that flows through Kelham and South Muskham and a navigational channel which flows through Newark, where the Devon joins (Fig. 2.1). The two channels meet again at Crankly Point. The Trent becomes tidal below Cromwell Lock, 8 km downstream of Newark and subsequently meets the Ouse to form the River Humber at Trent Falls (Lester, 1975), having contributed around one-quarter of the total discharge to the Humber Estuary (Law *et al.*, 1997).

2.11 Trent system sampling sites

2.111 Rugely

Rugely (SK049189) is 58.2 km from the source of the Trent. This site was only sampled once; on 9 May 1996. Samples were taken from a bridge. No light attenuation measurements were made.

2.112 Burton upon Trent

Burton upon Trent (SK254221) is 93.3 km from the source. This site was only sampled once; on 9 May 1996. Samples were taken from a bridge near the centre of town. No light attenuation measurements were made.

2.113 Cavendish Bridge

Cavendish Bridge (SK448299) is 124.5 km from the source of the Trent, before the confluence with the Derwent. Sampling was conducted from a road bridge. Light attenuation coefficient was measured from the river bank, 20 m upstream of the bridge (Fig. 2.2). This site was sampled throughout the sampling period.

Figure 2.2 Trent at Cavendish Bridge. Photo shows view from the bridge. Light attenuation was measured at A.

2.114 Wilford

Wilford (SK569381) is 144.6 km from the source of the Trent, near the centre of Nottingham. Water samples were obtained from a footbridge. Light attenuation was measured from the river bank (Fig. 2.3). This site was sampled between April and October 1995.

Figure 2.3 Trent at Wilford. Photo shows downstream view from the bridge. Light attenuation was measured at 'A'.

2.115 Gunthorpe

Gunthorpe (SK681437) is 161.2 km from the source of the Trent. Water samples were obtained from the bridge, or, during bridge repair, from a jetty owned by the local water skiing club (Fig. 2.4). The jetty was also used to measure the light attenuation coefficient. This site was sampled throughout the sampling period (April 1995 – August 1997).

Figure 2.4 Trent at Gunthorpe. Photo shows view from jetty where light attenuation was measured. The bridge where samples were obtained, upstream of the jetty, is shown in the background.

2.116 Kelham

Kelham (SK796567) is 183 km from the source. Kelham is on the natural arm of the Trent as the river divided before reaching Newark (Fig. 2.1). Water samples were obtained from a road bridge (Fig. 2.5). Access did not permit measurement of the light attenuation coefficient. This site was sampled between April and October 1995.

Figure 2.5 Trent at Kelham. Downstream view of river from bridge.

2.117 South Muskham

South Muskham (SK778553) is 184.8 km from the source. Like Kelham, this site also is situated on the natural arm of the Trent. Water samples were obtained from a bridge (Fig. 2.6) although no light measurements were taken because of restricted access. This site was sampled between April and October 1995.

Figure 2.6 Trent at South Muskham. Downstream view of river from bridge.

2.118 Newark

Newark (Sk796541) is 184.1 km from the source of the river, on the navigational arm of the Trent. The site was downstream of the confluence with the Devon.. Water samples were obtained from a road bridge (Fig. 2.7) between April and October 1995.

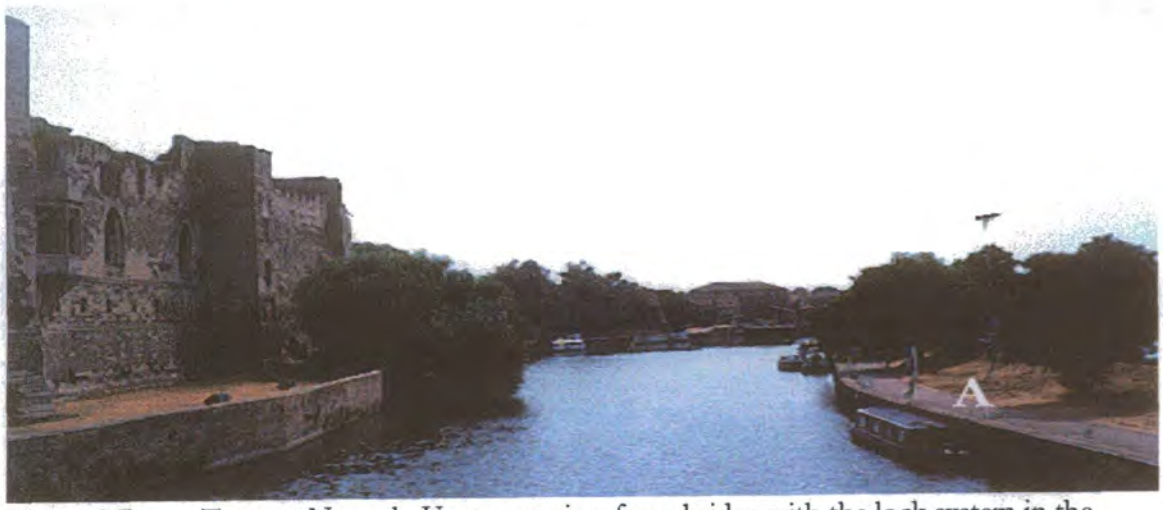

Figure 2.7 Trent at Newark. Upstream view from bridge with the lock system in the background. Light attenuation was measured at 'A'.

2.119 Cromwell

Cromwell (SK807612) is the tidal limit of the Trent and is 192.1 km from the source. Water samples were taken from the end of the lock wall (Fig. 2.8). Cromwell was sampled throughout the sampling period and was the only Trent site to be sampled as part of the LOIS Core sampling programme. The average depth through the sampling period was 3.5m.

Figure 2.8 Trent at Cromwell. View of river looking upstream. Light attenuation was measured at 'A'.

2.1110 River Derwent at Church Wilne

The Derwent passes through Matlock and Derby. The sample site at Church Wilne (SK452314) is situated near a water treatment works and 1.9 km upstream of the confluence with the Trent. Water samples were obtained from a footbridge (Fig 2.9). Light attenuation was not measured because access was restricted. This site was sampled from April to October 1995.

Figure 2.9 Derwent at Church Wilne. Downstream view from the bridge.

2.1111 River Soar at Ratcliffe on Soar

The River Soar flows through Leicester and Loughborough. The sample site (SK491289) was 2.1 km upstream of the confluence with the Trent, just upstream of the Ratcliffe on Soar power plant. Water samples were made from a road bridge (Fig 2.10). Poor access, coupled with low river depth prevented light attenuation measurement. This site was sampled from April to October 1995 and again from March to June 1997.

Figure 2.10 Soar at Ratcliffe on Soar. Upstream view of the river.

2.1112 River Devon at Newark

The Devon was sampled 0.1 km before the confluence with the Trent. The site (Sk787532) was near the centre of Newark and water samples were obtained from a small road bridge (Fig. 2.11). Only two light attenuation measurements were made as the land access was owned by a local boating club and was closed a lot of the time. This site was sampled from April to October 1995.

Figure 2.11 Devon at Newark. Upstream view showing the build up of *Lemna minor*.

2.1113 River Tame at Croxhall

The Tame was sampled once, on 9 May 1996 at Croxhall (SK188139). The Tame flows through Birmingham and Tamworth and meets the Trent 1.1 km downstream of the sampling site. Samples were obtained from a bridge.

2.1114 River Dove at Marston

The Dove was sampled at Marston (SK235288), 5.7 km from the confluence with the Trent. The Dove is a clean river, the only major urban areas it flows through being Ashbourne and Uttoxeter. The site was sampled only once on 9 May 1996. Samples were taken from a small bridge.

2.2 Yorkshire Ouse

The Ouse, the UK's ninth longest river and thirteenth largest river in terms of mean annual discharge is fed by three main tributaries; the Rivers Swale, Ure and Nidd (Fig. 2.12). The Pennine region of the Swale-Ouse system is predominately Carboniferous Limestone and Millstone Grit while the Vale of York comprises mainly Jurassic limestone and clays (Jarvie *et al.*, 1997). The Swale-Ouse system differs from the Trent as it drains a predominantly rural, low populated

catchment. . The area has no major historical industrialisation and farming has been restricted to mainly rough grazing, sheep and cattle rearing.

With a catchment area of 3521 km^2, the Ouse starts life as the Swale, rising at 500 m AOD in the Yorkshire Dales National Park, Northern Pennines. Arkle Beck joins at Grinton and the Swale flows south-eastwards through Richmond and Catterick. In the upper Swale, river retentivity is low as a result of the steep, narrow Swaledale valley. The Swale-Ouse system is subjected to intense flooding during the winter months, with large areas of rural and urban land being inundated with water. The Swale remains in a natural state until Brompton on Swale (NRA, 1994), after which, engineering work has straightened sections of the channel. Inputs from Cod Beck and the River Wiske lower water quality as do effluents from Richmond and Catterick (NRA, 1994). The Swale joins the River Ure two km east of Boroughbridge after flowing some 109 km.

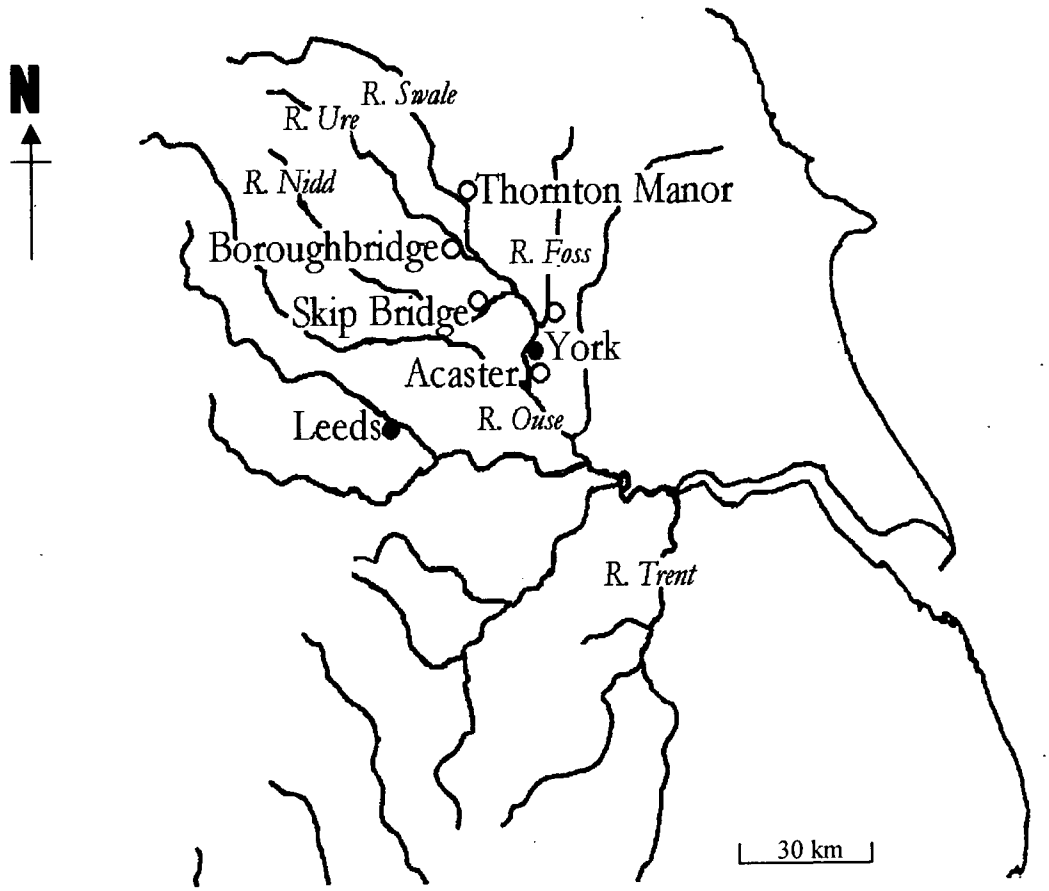

Figure 2.12 The Ouse and its tributaries

The Ure also rises in the Pennines at 640 m AOD. The Ure flows in a south-easterly direction and flows through Ripon and Boroughbridge (Fig. 2.12). Main tributaries are the Rivers Bain, Cover, Burn, Skell and Tutt. Like the River Swale, the Ure is also prone to flooding. Because of this, flood alleviation schemes have been implemented in and around Boroughbridge. The Ure becomes the Ouse at the confluence with Ouse Gill Beck, near Linton on Ouse (Fig. 2.12), 25m AOD, after travelling 111 km.

The Nidd the joins the Ure downstream of the Swale-Ure confluence (Fig. 2.12). The Nidd rises on peat bog, 595 m AOD. Three reservoirs; Angram, Scar House and Gouthwaite, partially regulate flow at the top of the river. From here, the river flows in a south-easterly direction over Millstone Grit, through the town of Knaresborough. The Nidd flows 97 km before joining the Ouse. The Ouse then flows in a southerly direction, through York, towards the Humber (Fig. 2.12). The tidal limit is at Naburn Weir. Other tributaries to the non-tidal Ouse include the Rivers Foss and Kyle. The tidal Ouse flows through Selby and Goole before meeting the Trent at Trent Falls. Tributaries joining this tidal reach include the Wharfe, Aire, Calder and Derwent. The total length of the Swale-Ouse is 192 km.

2.21 Ouse system sampling sites

2.211 River Swale at Thornton Manor

Thornton Manor (SE433715) is 11.8 km upstream of the confluence with the Ure. Samples were taken from a bridge (Fig. 2.13) and light attenuation measurements were made from the river bank. During late summer, however, light attenuation was not measured as macrophyte growth, steep banks and low river depth restricted access. This site was sampled as part of the LOIS Core sampling regime.

Figure 2.13 Swale at Thornton Manor. Picture shows the Swale during a winter flood. Light attenuation was measured from the near bank.

2.212 River Ure at Boroughbridge

Boroughbridge (SE395671) is 4.3 km upstream of the confluence with the Swale. Samples were taken from a road bridge. If river depth was so low that the benthos would be disturbed by sampling from the bridge, a sample was taken by wading part way into the river. Light attenuation was measured by the weir (Fig. 2.14), 100 m upstream of the bridge as water was deep enough to allow accurate readings. This site was sampled as part of the LOIS Core sampling regime.

Figure 2.14 Ure at Boroughbridge. Upstream view from the bridge showing the weir. Light attenuation was measured at A.

2.213 River Nidd at Skip Bridge

The site on the Nidd at Skip Bridge (SE482561) is 7.2 km upstream of the confluence with the Ouse. Samples were obtained from a bridge supporting the road layby (Fig. 2.15). Light attenuation measurements were made from the river bank, 20 meters upstream of the bridge when river depth and macrophyte growth allowed. This site was sampled as part of the LOIS Core sampling regime.

Figure 2.15 Nidd at Skip Bridge. Looking downstream towards the bridge. Light attenuation readings were taken from the near bank.

2.214 River Ouse at Clifton

Between April and October 1995, the Ouse was sampled at Clifton (SE587528), 9.2 km upstream of the tidal limit at Acaster Malbis. Samples were taken from a road bridge. Light attenuation measurements were not made as the river bank was canalised and very steep. This site was sampled as part of the LOIS Core sampling regime.

2.215 River Foss at York

The Foss (Fig. 2.16) was sampled between April and October 1995 at York (SE608525). The site is 1.5 km from the confluence with the Ouse. Water samples were taken from a bridge 20 m downstream.

Figure 2.16 Foss at York. View downstream, notice slow flow and shading by trees. The bridge where samples were taken can be seen to the centre right of the picture.

2.216 River Ouse at Naburn/Acaster Malbis

From April to June 1995 the tidal limit of the Ouse was sampled at Naburn Weir (SE594445), 142.4 km from the source. Samples were taken from a wall at the end of a lock island in the middle of the river channel. Because of problems with light attenuation measurements, from July 1995, samples and light attenuation measurements were obtained from a jetty at Acaster Malbis (Fig 2.17), across the channel from Naburn Weir and 50 m upstream. This site was sampled throughout the sampling regime and was sampled as part of the LOIS Core sampling regime. The average depth throughout the sampling period was 5.5m.

Figure 2.17 Ouse at Acaster taken from sampling jetty. View looking upstream.

3 MATERIALS AND METHODS

3.1 Water collection and storage

Water samples were taken from a bridge, lock wall or jetty (Sections 2.11 & 2.21). Samples were taken by lowering a weighted 1-l sampling bottle into the top 30 cm of the water column, avoiding incorporating the surface scum. Between 2 l and 3 l of water were placed into a plastic container and mixed well. From this container, samples for chlorophyll *a* determination, phytoplankton species composition and abundance were taken. Samples for chlorophyll *a* determination were placed in 1-l polycarbonate sample jars and placed in a cool-box in the dark. Samples for the determination of species composition were fixed immediately with 1% v/v Lugol's iodine. Samples for primary productivity estimations were placed in 25-l carbuoys and kept out of direct sunlight.

All sampling containers were scrubbed with tap water, rinsed with distilled water and then rinsed with river water before sampling.

Between April and September 1995, fortnightly samples were collected from seven sites on the Trent: Cavendish Bridge, Wilford, Gunthorpe, Kelham, South Muskham, Newark and Cromwell; plus three tributaries: the Derwent at Church Wilne, Soar at Ratcliffe on Soar and Devon at Newark (Fig. 2.1). From October 1995 to June 1997, sampling was continued at three sites, Cavendish Bridge, Gunthorpe and Cromwell, but with different frequencies: weekly between April and June, fortnightly in March, July and August and monthly during the remaining months.

A similar routine was followed for sampling the Swale-Ouse system. Between April and September 1995, fortnightly samples were collected from six sites: the Swale at Thornton Manor, Ure at Boroughbridge, Nidd at Skip Bridge, Ouse at Clifton and Acaster Malbis and the Foss at York (Fig. 2.12). From October 1995 to June 1997, sampling was continued at four sites, the Swale at Thornton Mannor, Ure at Boroughbridge, Nidd at Skip Bridge and the Ouse at Acaster, but with different frequencies: weekly between April and June, fortnightly in March, July and August and monthly during the remaining months.

In May 1996, when the concentration of phytoplankton chlorophyll *a* was high, samples were also collected further upstream at five sites on the River Trent; Rugely, Burton upon Trent, Cavendish Bridge, Gunthorpe and Cromwell, and five tributaries, the Tame at Croxhall, Dove at Marston, Derwent at Church Wilne, Soar at Ratcliffe on Soar and Devon at Newark (Fig 2.1).

3.2 Light attenuation measurement

The attenuation of photosynthetically available radiation (PAR, 400-700 nm) was determined using a pair of PAR sensors, using the method of Westlake *et al*. (1986). Initially, between April 1995 and July 1996, two SKYE PAR (Sk 280) sensors were used. These sensors were connected to a

SKYE datalogger, to which a Microscribe microcomputer interface was also connected. However, between August 1996 and August 1997, two Macam SD101QCos 2π PAR sensors connected to a Macam Q102 radiomenter were employed. With both systems, one light sensor was placed above the water surface and out of the shade, to act as a reference to record any difference in the incident light while the other sensor was attached to a metal frame attached to a wooden pole graduated at 0.1 m intervals (Fig. 3.1).

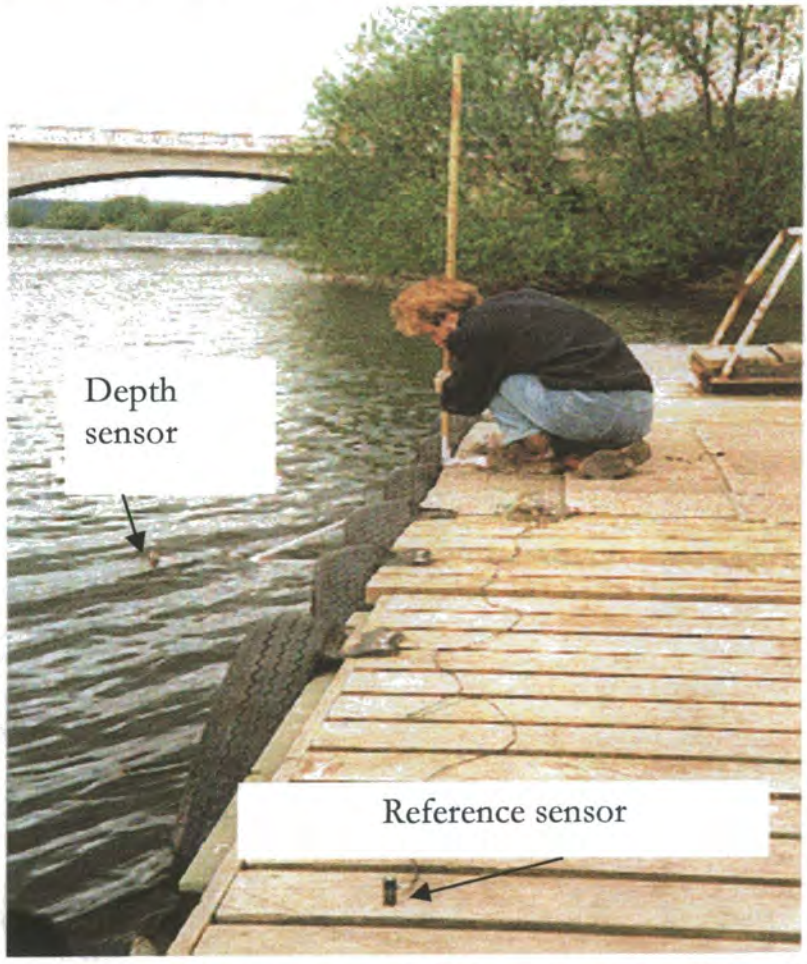

Figure 3.1 Measurement of the light attenuation coefficient (K_d).

The frame was lowered to 0.1, 0.3, 0.5, 0.7 and 0.9 m and the reference and depth irradiance reading recorded. This procedure was repeated until at least three sets of readings were obtained. The attenuation of downwelling light (K_d) was calculated from a linear regression of the natural log of corrected irradiance versus depth using the following equation:

$$K_d\ (m^{-1}) = [\ln(I_e/I_z)]/z \qquad \textbf{(Eq. 3.1)}$$

Where I_e = irradiance at the surface ($\mu mol\ m^{-2}\ s^{-1}$)

I_z = irradiance at depth z ($\mu mol\ m^{-2}\ s^{-1}$)

Z = depth (m) (Kirk, 1994).

Variation of the attenuation coefficient between replicate readings ranged from 0.29 to 44% and averaged 6%.

3.3 Spectroradiometric measurements

To measure the spectral quality of underwater light, two Macam SR 913 F sensors attached to a Macam SR 9910-PC spectroradiometer were used and controlled using a portable computer. One sensor was placed above the surface and out of the shade to measure changes in incident light. The other sensor was lowered through 0.25 m depth intervals until the river bed was reached. The measurement of light between 300 and 700 nm was recorded at 5nm intervals and stored on the portable computer. A profile of depth versus light at the recorded wavelengths was constructed from these data on three occasions: 11 February, 29 April and 5 June 1997, for the Trent at Cromwell and the Ouse at Acaster.

3.4 Species composition and phytoplankton density

3.41 Field material

The method of Lund *et al.* (1958) was used to quantify phytoplankton density and species abundance. A sedimentation chamber was one quarter filled with distilled water and two drops of Lugol's iodine added. A sample was shaken and a subsample pipetted into the sedimentation chamber. The sample was allowed to settle for at least 24 h to allow very small cells and Cyanophyta to sediment. Cell counts were made using a Leitz Diavert inverted microscope. The bottom of the chamber was scanned under x 250 magnification to make sure the cells were not aggregated locally. The cells were then counted under x 500 magnification using random staggered transects, counting at least 30 fields of view (Jones & Barrington, 1985). At least 400 cells were counted, giving a counting accuracy of ± 10% with 95% confidence intervals (Lund *et al.*, 1958; Kiss & Padisák, 1988). Counts were converted to cell density using the following equation:

$$\text{Number of cells } (ml^{-1}) = (T.M)/(F.V) \qquad \text{(Eq. 3.2)}$$

Where:

T = total number of cells counted

M = multiplication factor

F = fields of view

V = volume of sample (ml)

M was calculated by using the following equation:

$$M = (A/E).V \quad \text{(Eq. 3.3)}$$

Where:

A = area of chamber (mm^2)

E = area of eyepiece (mm^2)

V = volume of chamber (ml)

Cells were identified to species level where possible and at least to genus level using the flora of Bourrelly (1966, 1968, 1970), Belcher and Swale (1978, 1979), and Tikkanen (1986). Other than diatoms, groups (colonies, coenobia and filaments) were treated as single units. Algal species were coded according to the algal coded list of Whitton *et al.* (1998) which uses an 8-digit code to record each species of algae and provides a standard set of names and identifying codes. The new list is an expanded and improved version of the earlier algal coded list (Whitton *et al.*, 1978).

Although centric diatom species were not regularly quantified, preliminary investigations were undertaken to distinguish the dominant species during the spring blooms of 1995, 1996 and 1997. Centric diatoms were identified to species level using transmission electron microscopy (TEM). Cells were prepared by burning off all organic matter with concentrated hydrogen peroxide (Kiss & Padisák, 1988) or a combination of dilute HCL, concentrated H_2SO_4, saturated oxalic acid and potassium permanganate (Hastle & Fryxell, 1970). After the organic matter was removed (indicated by frustules turning white), traces of chemical were removed by subsequent rinsing with distilled water, centrifuging for 10 min at 2500 rpm and the supernatent discarded. All samples were rinsed at least six times. The rinsed sample was then suspended in a couple of ml of distilled water, shaken and a drop placed on a TEM grid and allowed to dry. When dry, the cells on the grid were examined using a JEOL 100 CX TEMSCAN combined transmission and scanning electron microscope. At least 50 cells were counted (Kiss, 1986; Genkal & Korneva, 1992) and identified to species level using the flora of Kramer and Lange-Bertalot (1991) with reference to Lowe (1975), Håkansson (1986) and Speller (1990). The proportionate count was used to identify the dominant species during spring blooms and as the procedure was not performed regularly the data have not been presented.

3.42 Growth experiments

After mixing the sample, a sub-sample was taken for enumeration and fixed with 1 % v/v Lugol's iodine. The sample was shaken and a sub-sample taken with a pipette and placed in a Lund cell (Lund, 1959) which had been gravimetrically calibrated to calculate the volume of each field of

view. The sample was counted using a Wild Heerbrugg light microscope under x 250 magnification. At least 200 cells were counted under at least 36 random, staggered fields of view. Counts were converted to cell density using equations 3.2 and 3.3 described previously.

3.5 Chlorophyll *a* estimation

3.51 Routine estimation

Chlorophyll *a* concentration was determined using overnight extraction with cold methanol (Marker, 1994). Methanol was selected following a comparison with ethanol which showed no statistical difference between extraction with methanol or ethanol (A. F. H. Marker, pers. comm.). A measured volume of sample, usually 1 l, was filtered through a pre-weighed GF/C glass-fibre filter using a slight vacuum (not below three atm) to avoid cell damage. Test showed that chlorophyll concentrations measured using GF/C filters were not significantly different compared to those measured using GF/F filters (author's unpublished data). After filtration, air was allowed to run through the filter paper for 30 s. The filter paper was then allowed to dry slightly in a dark cupboard for about ten minutes until the residual water on the filter weighed approximately 5% of the weight of the filter. This action was taken to prevent excessive dilution of the solvent during extraction. The paper was then folded three times, placed in a snap cap vial, and 10 ml of 100% methanol was added to completely cover the filter paper and the top placed on the vial. The vial was left for between 18 and 30 h at 4 ^{0}C in the dark. Water was then added to dilute the solvent to 90 %. The sample was well mixed and the filter paper removed, squeezing as much of the solvent back into the vial as possible. The solvent was centrifuged in a covered tube for 10 min at 3000 rpm. The clear extract was measured in a Shimadzu UV-150-02 double beam spectrophotometer at 665 nm with a reading at 750 nm to correct for turbidity. A blank of 90 % v/v methanol/water was used in the reference beam of the spectrophotometer. Either 1-, 4- or 5-cm cuvettes were used, depending upon the absorbance of the extract so that absorbance at 665 nm was within the range 0.05 to 0.70 to ensure precise measurements (Marker, 1994).

To correct for phaeopigments, the following further steps were carried out. 0.1 ml of 0.3 M HCl (or proportionately more or less depending upon volume of extract in cuvette) was added to 10 ml extract. The extract was then mixed with a glass rod and left for between 5 and 30 minutes, (usually 5 minutes). The acid was then neutralised with the same amount of organic base, comprising 3 ml 2-phenythylamine, made up to 100 ml with 100 % methanol. This was mixed and the extract read at 665 nm and 750 nm. To calculate the corrected, undegraded chlorophyll *a* concentration the following equation was used:

Chlorophyll *a* concentration ($\mu g\ l^{-1}$) =

$$\frac{13\ (2.667.(A_n - A_m)).v}{d.V} \qquad \text{(Eq. 3.4)}$$

Where:

A_n = pre-acidified 665 reading - pre-acidified 750 reading

A_m = post - acidified 665 reading - post-acidified 750 reading

v = volume of extract (ml)

d = cell pathlength (cm)

V = volume of sample filtered (l)

13 = absorption coefficient of chlorophyll *a* in methanol

2.667 = correction coefficient for absorption of acidified chlorophyll *a*

Triplicate samples were taken at Cromwell and Acaster from 30 July 1996.

On six occasions, samples were taken across the river channel to assess the latitudinal variation in chlorophyll *a* concentration. For the Swale at Thornton Manor (28 June 1995), Ure at Boroughbridge (17 July 1995), Ouse at Clifton (1 August 1995; Fig. 2.12) and Trent at Gunthorpe (14 August 1995), Kelham (12 September 1995) and Cavendish Bridge (5 June 1996; Fig 2.1), triplicate samples were taken from three positions across the river; the right bank, the middle and the left bank. Samples were taken two minutes apart so that temporal variation could also be assessed. Cross-channel variability was not investigated for the Ouse at Acaster or the Trent at Cromwell as neither a bridge nor boat was available.

3.52 Daily estimation

Between 14 March and 1 July 1997, daily chlorophyll *a* measurements were taken from the Trent at Cromwell in order to increase the temporal sampling resolution and assess the day to day variation not monitored during weekly sampling. Samples were taken by lowering a weighted plastic container of known volume into the top 30 cm of the water column, avoiding the surface scum (Section 3.1). This sample was filtered through a 55-mm GF/C filter using field filtering apparatus. The filter was then placed in a numbered well of a plastic container and placed in the freezer. Samples were left for a maximum of three weeks before collection. Upon collection, they were placed in the cool and dark during transport. Upon return to the laboratory the filters were

analysed for chlorophyll *a* and phaeopigments using the method of Marker (1994), described in Section 3.51.

3.53 Fluorometric estimation

To assess the daily cycle of change in chlorophyll *a* concentration, a Chelsea Instruments Aquatracka field fluorometer (Fig. 3.2) was placed *in situ* in the Trent at Cromwell between 15 April and 18 June 1997. The fluorometer was programmed to take readings every 15 minutes. On each occasion the fluorometer was programmed to switch on but not take readings for the first 20 s as preliminary tests had shown that the lamp needed around 20 s to warm up before stable readings were obtained. After the initial 20 s, the fluorometer would record readings every second for approximately 15 s. The fluorometer output, in mV, was recorded and stored using a Datataker 500 series 2 data-logger and Mitsubishi 1 MB Melcard memory card. The memory card was renewed between one and four times a month. Data from the memory card was downloaded using a Datataker MCI-01 Memory Card Reader and converted to a Microsoft Excel file.

Figure 3.2 Field fluorometer used for *in situ* measurement of chlorophyll *a*.

To keep the fluorometer in working order and obtain reliable readings, during each sampling visit, between every one and four weeks, the fluorometer perspex screens were cleaned with a sponge and distilled water to remove debris and then calibrated. For calibration, the fluorometer was placed in a bucket containing a series of concentrations of river water. The bucket and fluorometer were covered with black, plastic sheeting to cut out interference from daylight. Either tap water or net concentrated water was added to the sample in the bucket to vary the chlorophyll *a* concentration. Approximately 60 readings (one every second) were taken for each sample and between four and ten different chlorophyll *a* concentrations used per calibration. After readings were taken, a sub-sample was taken and placed in a plastic sampling vessel and stored in the cold and dark. This was used to determine the chlorophyll *a* concentration using the method of Marker (1994; Section 3.51).

In an attempt to understand the influence of irradiance upon phytoplankton fluorescence, experimental work focused upon the fluorometric response of a species of centric diatom; *Cyclotella meneghiniana* and natural Trent river water when incubated at different light levels. For the first experiment, *C. meneghiniana*, obtained from cultures of isolates from the Trent (Section 3.72) was incubated in 1-l glass bottles in a water bath (Section 3.61) at 14.5°C and at five different light levels; 19, 80, 109, 411 and 1377 μmol m^{-2} s^{-1}, for three hours. The irradiance inside each bottle was measured using a 4π sensor described in Section 3.61. Each bottle was mixed at least once every hour. After three hours, the contents of each of the 1-l glass bottles were poured into a plastic container and the fluorometric reading was measured as described for the calibration of the fluorometer above. After each reading, the perspex window of the fluorometer was rinsed with distilled water. A sample was taken from each bottle to measure the chlorophyll *a* concentration according to the method of Marker (1994; Section 3.51).

For the second experiment, river water, collected from the Trent at Cromwell was incubated in the water bath described above at 16°C at 9, 30, 65, 196 and 643 μmol m^{-2} s^{-1} for either one, three or five hours. The irradiance inside each bottle was measured using a 4π sensor (Section 3.61). Each bottle was mixed at least once every hour. After incubation, the fluorometric reading of the contents of each bottle was measured and a sample was taken from each bottle to measure the chlorophyll *a* concentration as described above.

3.6 Estimation of production

3.61 Estimation of the P Vs I response curve

A constant temperature water bath (Steeman-Nielsen & Jensen, 1957) was used for photosynthesis vs irradiance (P vs I) incubations. The water bath (148x38x21cm) was made from dark, opaque perspex with a clear perspex window at one end. Water temperature was controlled using a Churchill water cooler/heater system which circulated water around the tank and maintained temperature within ± 0.2°C (author's unpublished data). Two OMBIS 150 W metal halide lamps were placed outside at one end of the tank, providing a light source. Kodak neutral density filters were used to reduce irradiance within the tank. Between April and October 1996, the incubation irradiance was measured using a Macam SD101QCos 2π-probe and Macam Q102 radiometer, multiplying the recorded value by 1.25 to correct for submersion (Macam pers. comm.). Later investigation, using a Biospherical Instruments QSP-200 4π-probe and QSP 170A meter, showed that use of the 2π-sensor resulted in underestimation of irradiance received by some bottles. This was a result of reflection from the tank sides. To resolve this underestimation, later irradiance values were measured using the 4π-probe which was calibrated against the Macam SD101QCos 2π-probe. Earlier values, obtained using the 2π-probe, were converted to corrected values using a calibration equation calculated from both 4π and 2π measurements.

Phytoplankton primary productivity was measured as O_2 evolution, measured by Winkler titration, following the method of Carpenter (1965, 1966), following WOCE precautions and calculation procedures. Incubations took place in 125-ml soda glass bottles with volumes predetermined gravimetrically. A 25 l field sample was mixed well using a plastic pipe and used to rinse each bottle with approximately 30 ml of sample water. Each soda glass bottle was filled using a siphon, ensuring that each bottle was overfilled by at least three times it's volume to displace any atmospheric O_2. The 25 l field sample was mixed with a plastic pipe after every three bottles filled to ensure homogeneity. During the course of sub-sampling, between three and five bottles were fixed immediately with 1 ml 3M MnCl followed by 1 ml 8 M NaOH/4 M NaI using rapid delivery pipettes with the tip underneath the sample surface to avoid introduction of atmospheric O_2. These bottles were used to determine the initial O_2 concentration. The remaining bottles were placed, in triplicate, at different light levels, from 10 to 1200 μmol m^{-2} s^{-1}, inside the water bath. Triplicate bottles were also covered in aluminium foil to measure community respiration. Incubation times were in the region 4-8 h in spring and summer. Overnight incubations were necessary in winter when phytoplankton biomass was low. After incubation, each bottle was fixed, shaken well and the precipitate allowed to settle halfway down the bottle. The bottle was shaken again and the precipitate allowed to settle to the bottom third of the bottle.

A computer controlled Metrohm 665 Dosimat automated burette system (Bryant *et al.*, 1976; Williams & Jenkinson, 1982) was used to determine O_2 concentration using the Winkler Titration method. A 1-ml burette was used to automatically titrate sodium thiosulphate solution to a photometric endpoint using a photometer. The photometer used two wavelengths of light: one which was adjusted to the absorption maximum of iodine, and the other, independent of the contents of iodine to estimate the transmission at the endpoint of the titration so that titration times were shortened.

Before O_2 determination, the burette system was flushed between three and four times to displace any air bubbles. The sodium thiosulphate solution was standardised before each set of titrations by pipetting 10 ml of the solution into a clean bottle and nearly filling with distilled water. 2.2 ml 5M H_2SO_4 was then added followed by 1 ml 3M MnCl followed by 1 ml 8M NaOH/4 M NaI solution. This was then mixed, using a magnetic stirrer, and titrated to the end point. The standard was measured at least three times to ensure an accurate standard determination.

A blank was also determined to correct for O_2 present in the Winkler reagents. 1 ml KIO_3 was pipetted into a clean bottle and nearly filled with distilled water. 2.2 ml 5M H_2SO_4 was then added followed by 1 ml 3M MnCl and by 1 ml 8M NaOH/4 M NaI. This was mixed and titrated to the end point. A second 1 ml of KIO_3 was added and the liberated iodine again titrated to the endpoint. The difference represented the reagent blank. This procedure was repeated at least three times to ensure an accurate blank.

To measure the O_2 concentration of each sample, the bottle stopper was removed and 2.2 ml 5M H_2SO_4 was pipetted into the bottle. The top was replaced, taking care not to incorporate bubbles, and the sample shaken until the precipitate had dissolved. The stopper was then removed, the bottle wiped with a cloth and placed in the photometer section of the Metrohm automated burette system. The burette system titrated a predetermined concentration of $NaS_2O_35H_2O$ solution until the estimated photometric endpoint was reached. Each titration typically took 3 minutes. The difference in the concentration of O_2 in mg l^{-1} was then used to calculate chlorophyll *a* based rates of net photosynthesis and respiration using the following equation:

$$\text{Net } O_2 \text{ exchange } (\mu\text{mol } O_2 \text{ (mg chl } a)^{-1} \text{ h}^{-1}) = (((C\text{-}I)/t).32)/(\text{chl } a/1000) \qquad \text{(Eq. 3.6)}$$

Where:

C= O_2 concentration of sample (mg l^{-1})

I = Initial (pre-incubation) O_2 concentration (mg l^{-1})

t = time duration of incubation (h)

chl *a* = chlorophyll *a* concentration of sample (mg l^{-1})

It was assumed that the majority of O_2 consumption would arise from phytoplankton. However, as the samples were neither screened nor axenic, zooplankton and bacteria would also have contributed to respiration. Therefore community respiration was measured and so the resulting calculation does not strictly result in a measurement of net phytoplankton production. However, with this in mind we assume that the majority of respiration was contributed by the phytoplankton and so we use the term net production from here on.

The model of Platt *et al.* (1980):

$$P_s = P_m.((1-EXP(-\alpha.(I/P_m))).(EXP(-\beta.(I/P_m))))+R \qquad \text{(Eq. 3.7)}$$

Where:

P_s = potential net rate of light saturated photosynthesis if no photoinhibition was present

P_m = light saturated photosynthetic rate (µmol O_2 (mg chl *a*)$^{-1}$ h^{-1})

α = initial slope of curve (µmol O_2 (mg chl *a*)$^{-1}$ mol photon^{-1}m^{-2})

I = irradiance (µmol $m^{-2}s^{-1}$)

β = photoinhibition factor (µmol O_2 (mg chl *a*)$^{-1}$ mol photon^{-1}m^{-2})

R = respiration rate (µmol O_2 (mg chl *a*)$^{-1}$ h^{-1})

was fitted to these data and the Solver application in Microsoft Excel was used to minimise the residual sum of squares to estimate the curve parameters α, β, P_s and R. This model was chosen as it resulted in the lowest residual sum of squares when compared to other models on all but one occasion.

3.62 Photosynthesis-irradiance-depth-time (PIZT) model

To estimate the river column productivity over time and depth and to assess the relative contribution of environmental factors in controlling river column productivity, a modelling approach similar to that of Walsby (1997) was used. A spreadsheet (PIZT; Photosynthesis, Irradiance, Depth (Z) and Time) calculated photon irradiance at depth intervals of 0.1 m and time

intervals of 0.5 h. By combining the estimated photon irradiance at the given time and depth with the modelled P vs I response (Section 3.61) a daily average rate of photosynthesis was calculated for each depth interval (depth-average photosynthesis) and for the column assuming the river was of different depth (column-average photosynthesis).

Total radiation was measured every hour with a pyranometer at Leconfield (TA020435), 90 km away from Cromwell and 44 km away from Acaster. The average daily irradiance (W m^{-2}) used in the model was calculated for the thirty days prior to the photosynthesis measurements to calculate an average monthly irradiance. Preliminary investigations showed that a thirty day average resulted in a characteristic monthly irradiance response as reported by Kirk (1994). These values were converted to PAR (400-700 nm, W m^{-2}) using a ratio of 0.45 (Kirk 1994), which is within the range modelled by Baker and Frouin (1987) for different solar angles and atmospheric water vapour contents. PAR was converted to μmol m^{-2} s^{-1} (photon irradiance) using a value of 4.6 μmol photon W^{-1} s^{-1} (Morel & Smith 1974, Baker & Frouin 1987).

The total daily PAR (Q_s), averaged over thirty days, was converted to a time-course over 24 hours assuming that cloud cover was uniform throughout the day. The day of year was used to calculate solar declination (δ):

$$\delta = 0.39637 - 22.913\cos\psi + 4.02543\sin\psi - 0.3872\cos 2\psi + 0.052\sin 2\psi \qquad \text{(Eq. 3.8)}$$

where ψ is the day of year expressed as degrees.

Daylength, N (hours) was calculated from the declination (δ) and latitude (λ):

$$N = 0.133\cos^{-1}(-\tan\lambda\tan\delta) \qquad \text{(Eq. 3.9)}$$

The diurnal variation in photon irradiance at time t (E_t) was calculated from:

$$E_t = Q_s / N(1+\cos(Nt)) \qquad \text{(Eq. 3.10)}$$

where t is hours from noon.

The reflection losses for diffuse and direct radiation at the water surface were calculated differently. The reflection by diffuse radiation was taken to be 6.6% and independent of zenith angle, 2_a, (Baker & Frouin, 1987) while reflection of direct radiation was dependent on 2_a. The

zenith angle in air at different time of day was calculated from the time of day expressed as degrees 9:

$$\theta_a = 90 - (a \sin(\sin\gamma \sin\delta - \cos\gamma \cos\delta \cos\tau) \qquad \text{(Eq. 3.11)}$$

Reflection of direct radiation for a smooth surface was calculated from zenith angle using equations 46 and 47 in Gregg & Carder (1990) assuming a constant wind velocity of 4 m s^{-1} to account for the broken surface of rivers caused by turbulence.

Although the proportion of diffuse to total radiation will vary, particularly with zenith angle and atmospheric clarity, diffuse radiation was taken to be equal to 56% of total radiation throughout the day, which is the average values in the model of Gregg & Carder (1990).

3.7 Estimation of *in situ* rates of growth and loss

3.71 *In situ* growth and loss estimation

The exponential rate of change of chlorophyll *a* concentration with distance (km^{-1}) was calculated from a linear regression of the natural logarithm of chlorophyll *a* concentration at three sites on the Trent (Cavendish Bridge, Gunthorpe, Cromwell; Fig. 2.1) against distance. Distances of sampling sites from the source were calculated using 1:25000 Ordnance Survey maps and an electronic map measurer. Distances were measured five times and the average recorded.

The exponential rate of change of chlorophyll *a* concentration with distance was converted to a rate of increase or decrease per day, i.e. rate of growth or loss, by multiplying by the river velocity (km d^{-1}). River velocity was estimated from the quotient of average daily discharge (m^3 d^{-1}) and cross-sectional area (m^2) which were provided by the Environment Agency. Estimates were made for Shardlow (SK448300), where the samples for Cavendish Bridge were taken, Colwick (SK620399), 10.1 km upstream of Gunthorpe and for North Muskham (SK808610), 0.75 km upstream of Cromwell.

Cross-sections of the river at Shardlow, Colwick and North Muskham showed the channel to be essentially square-sided, so cross-sectional area was calculated as the product of river width and depth depending on stage height. An average velocity was then calculated for the stretch of river from Shardlow to North Muskham.

3.72 Isolation of phytoplankton into culture

Algae to be used in experiments to measure growth rates were isolated from the Ouse and Trent. A sample taken in spring was centrifuged to obtain a concentrated number of cells. This concentrated sample was mixed with distilled water, centrifuged again and the supernatant

discarded. This was repeated four to six times to reduce the number of bacteria present. Single cells were isolated using the method of Hoshaw and Rosowski (1973). The cell concentrate was then placed on a petri dish and surrounded by up to eight droplets of distilled water. The drop containing the cells was observed through a binocular microscope under x 125 power. A capillary pipette, produced by drawing a soda glass pipette over a bunsen flame (Guillard, 1973), was used to pick up desired cells. The cells were then placed in one of the drops of distilled water. This process was repeated, passing cells to other drops of distilled water, until a single desired cell was obtained. This cell was placed on a labelled petri dish containing c. 40 ml Chu 10F medium, developed from the recipe for Chu 10 (Chu, 1942), with twice the stated silica concentration and with 1.5 % w/w agar. The petri dish was incubated at 15°C on a 16:8 L:D cycle to allow growth to take place. After a colony was established on the dish, the colony was placed in a flask containing Chu 10F and allowed to grow under the conditions mentioned above. Cultures were typically sub-cultured to fresh flasks once to twice per month. Using this method, two species of centric diatom were isolated: *Cyclotella meneghiniana* Kütz and *Cyclostephanos invisitatus* Hohn et Hellerman from the Trent and one species of Chlorophyta: *Scenedesmus intermedius* Chodat from the Ouse.

3.73 Rates of growth and respiration as a function of temperature

Triplicate culture bottles were placed in constant temperature water baths at 5, 10, 15 and 20 °C. The bottles were illuminated from below by eight Philips 58 W fluorescent tubes which produced between 75 and 85 μmol m^{-2} s^{-1} (PAR, measured with a Biospherical QSP-200 4π-probe and QSP 170A meter) for sixteen hours a day, followed by eight hours in the dark. Using this range of light levels, the cultures at 5 and 10°C would not grow so Kodak neutral density filters were placed above the fluorescent lights to reduce light intensity to between 30 and 40 μmol m^{-2} s^{-1}. Each bottle was aerated by pumping an external supply of air through an aquarium air-stone using a Whisper 1000 air-pump. The aeration promoted gas exchange, sample mixing and reduced settling of the diatoms.

A 1 ml sub-sample was taken every day for samples growing under 15 and 20 °C and every other day for samples growing under 5 and 10 °C. This sample was preserved with 0.01 ml Lugol's iodine and cells counted using the method described in Section 3.42. Cells were counted until at least three events had been sampled during the exponential phase. Growth rate was determined as the slope of the natural log of cell number against time and calculated by linear regression.

During the exponential growth phase, material was taken to measure rates of dark respiration of the four algal species using the method described in Section 3.61 and using the water baths mentioned above. Material was diluted to around 150 μg l^{-1} chlorophyll *a* using Chu 10F medium, mixed well and then siphoned into 125-ml soda glass bottles. Three initial samples were fixed and

three further samples were covered in aluminium foil and incubated at the temperature experienced during the previous growth experiment, i.e. a species grown at 5 °C would be incubated at 5 °C to measure respiration. A sample was also taken to measure chlorophyll *a* concentration (Section 3.51). Samples were incubated for between two and four hours. After incubation, oxygen exchange was measured by the Winkler titration method described in Section 3.61.

3.74 Grazing rate estimation

Grazing rates were determined using the method of Landry and Hassett (1982). The method measures the change in either cell density or chlorophyll *a* concentration using a series of dilutions of natural river water. The method makes three assumptions. The first being that growth of phytoplankton individuals is not directly affected by presence or absence of other phytoplankton *per se*. Secondly, the probability of a cell being consumed is a direct function of the rate of encounter with consumers. Thirdly, the change in phytoplankton density (P) over time (t) is represented by the equation:

$$P_t = P_0 e^{(k-g)t} \qquad \text{(Eq. 3.12)}$$

Where k and g are instantaneous coefficients of population growth and grazing mortality, respectively.

In this study, the change in chlorophyll *a* concentration was measured. Sample water was diluted with the same sample water having passed through a 0.45-μm membrane filter. Samples were diluted in triplicate at 1:0, 3:1, 1:1 and 1:3 unfiltered:filtered sample. The flasks were then placed in an incubator at *in situ* temperatures at a photon irradiance of around 82 μmol m^{-2} s^{-1}, measured using a Macam SD101QCos 2π PAR sensor connected to a Macam Q102 radiometer 2π-sensor. Initial samples were taken for each dilution and chlorophyll *a* determined (Section 3.51). The flasks were incubated for between 24 and 48 h. Each flask was static but was shaken manually three times a day. The chlorophyll *a* concentration of the contents of each flask was then determined and the change from the initial noted. The apparent growth rate of each flask was determined using the equation:

$$\text{Growth rate} = (1/t).\ln(\text{chl } a_{tn}/\text{chl } a_{t0}) \qquad \text{(Eq. 3.13)}$$

Where:

T = incubation time (d)

chl a_{tn} = chlorophyll *a* concentration at end of incubation ($\mu g\ l^{-1}$)

chl a_{t0} = chlorophyll *a* concentration at start of incubation ($\mu g\ l^{-1}$).

The apparent growth rate was plotted against the dilution expressed as a fraction. The intercept with the y-axis was estimated as the apparent phytoplankton growth rate (day^{-1}). The gradient of the curve was estimated as the grazing rate (day^{-1}).

On occasions, the data fitted a straight line. However, on other occasions the data were widely scattered and on other occasions a positive gradient was shown (Appendix 1). As a result of these data the results should be treated with caution.

3.8 Estimation of phytoplankton carbon flux

The flux of phytoplankton was estimated for the Trent at Cavendish Bridge, Gunthorpe and Cromwell (Fig 2.1) and the Ouse at Acaster (Fig. 2.12). Average weekly carbon flux was calculated using the concentration of chlorophyll *a* and the average weekly discharge of the river at each site (measured by the EA) and an estimation of the carbon to chlorophyll ratio at Cromwell. The carbon to chlorophyll ratio was calculated as the gradient of the line of best fit of chlorophyll *a* concentration against POC concentration (LOIS CORE data) as described by Descy and Gosselain (1994), for Cromwell only. An estimation of the carbon to chlorophyll ratio was not calculated for Cavendish Bridge and Gunthorpe as POC data were not available and not for Acaster as no significant relationship between chlorophyll and POC data existed. When a gap in chlorophyll *a* data occurred, data were interpolated to give a value for weekly chlorophyll *a* concentration. The average, weekly phytoplankton carbon flux was then calculated using the following equation:

$$\text{Flux (mg C wk-}^{1}\text{)} = (\text{chl } a.R_{c:c}).Q \qquad \text{(Eq. 3.14)}$$

Where chl *a* = chlorophyll *a* concentration ($\mu g\ l^{-1}$; equivalent to $mg\ m^{-3}$)

$R_{c:c}$ = carbon to chlorophyll ratio ($mg\ mg^{-1}$)

Q = Discharge $m^3\ wk^{-1}$

Using these data, an annual flux estimate was calculated for all four sites from June 1995 to May 1996 and from June 1996 to May 1997.

3.9 Computing and statistics

Data were stored and analysed and models formulated using Microsoft Excel. Microsoft Word was used for text and Microsoft Paint application was used to produce diagrams. Variables used for correlation and in parametric tests were tested for normality using the Kolmogorov-Smirnov test function in Minitab 8.0. Data which deviated significantly from normality ($P>0.05$) was log transformed. Other statistical analysis was performed using Microsoft Excel.

4 SPECIES COMPOSITION, ABUNDANCE AND BIOMASS

4.1 Species composition and phytoplankton density

4.11 River Trent

Data were collected in order to assess the seasonal change in the size and composition of the phytoplankton population. Measurements concentrated upon phytoplankton density and the composition of the population during periods of rapid increase and subsequent decrease of the phytoplankton population.

At the tidal limit of the Trent at Cromwell, phytoplankton density increased as river discharge decreased in spring, reaching maximal concentrations of 45270, 53000 and 39500 individuals ml^{-1} on 10 May 1995, 29 April 1996 and 2 June 1997, respectively (Fig. 4.1). High phytoplankton density in spring was often interrupted by spring floods (Fig. 4.1). Density declined during summer to between 3000 and 6000 individuals ml^{-1} even though discharge was low (Fig. 4.1) and fell to winter minima of 60, 200 and 100 individuals ml^{-1} on 16 October 1995, 15 January 1996 and 20 January 1997, respectively. Winter minima corresponded with an increase in discharge and sporadic flood events (Fig 4.1) as well as low temperature and light availability.

For the Trent at Cromwell, 104 taxa were recorded from April 1995 to August 1997; 38 Bacillariophyta (Table 4.1), 50 Chlorophyta (Table 4.2), 4 Chrysophyta (Table 4.3), 3 Cryptophyta (Table 4.4), 5 Cyanophyta (Table 4.5), 2 Euglenophyta (Table 4.6), 1 Pyrrophyta (Table 4.7), and 1 Xanthophyta (Table 4.8). The largest proportional contribution of Chlorophya to the phytoplankton, dominated by the genera *Ankistrodesmus*, *Scenedesmus* and *Chlorella*, occurred during late summer, contributing maxima of 88, 87 and 78 % on 17 October 1995, 16 September 1996 and 20 May 1997, respectively (Fig. 4.2). Minimal contribution of Chlorophyta to the phytoplankton was recorded during spring with contributions falling to 10, 12 and 12 % on 11 April 1995, 15 May 1996 and 13 April 1997, respectively (Fig. 4.2).

Centric diatoms of the genus *Stephanodiscus, Cyclotella* and *Cyclostephanos* comprised the largest proportion of the population in spring, with maxima of 83, 81.6 and 81.7 % of the population on 9 May 1995, 15 May 1996 and 16 April 1997 (Fig. 4.2). Centric diatoms were least important in autumn and winter with contributions to the phytoplankton under 1% on 17 October 1995, 23 September and 15 October 1996. A minimal contribution, during spring, of 16% was recorded on 20 May 1997. This coincided with a spring flood event (Fig 4.1). Maximal concentrations of centric diatoms during spring coincided with spring minimal concentrations of SiO_2-Si of 0.04, 0.01 and 0.21 mg l^{-1} on 10 May 1995, 14 May 1996 and 15 April 1997, respectively (Fig. 4.3). A significant, negative correlation existed between SiO_2-Si concentration and centric diatom density during spring ($r=-0.71$, $P=0.001$, $n=24$).

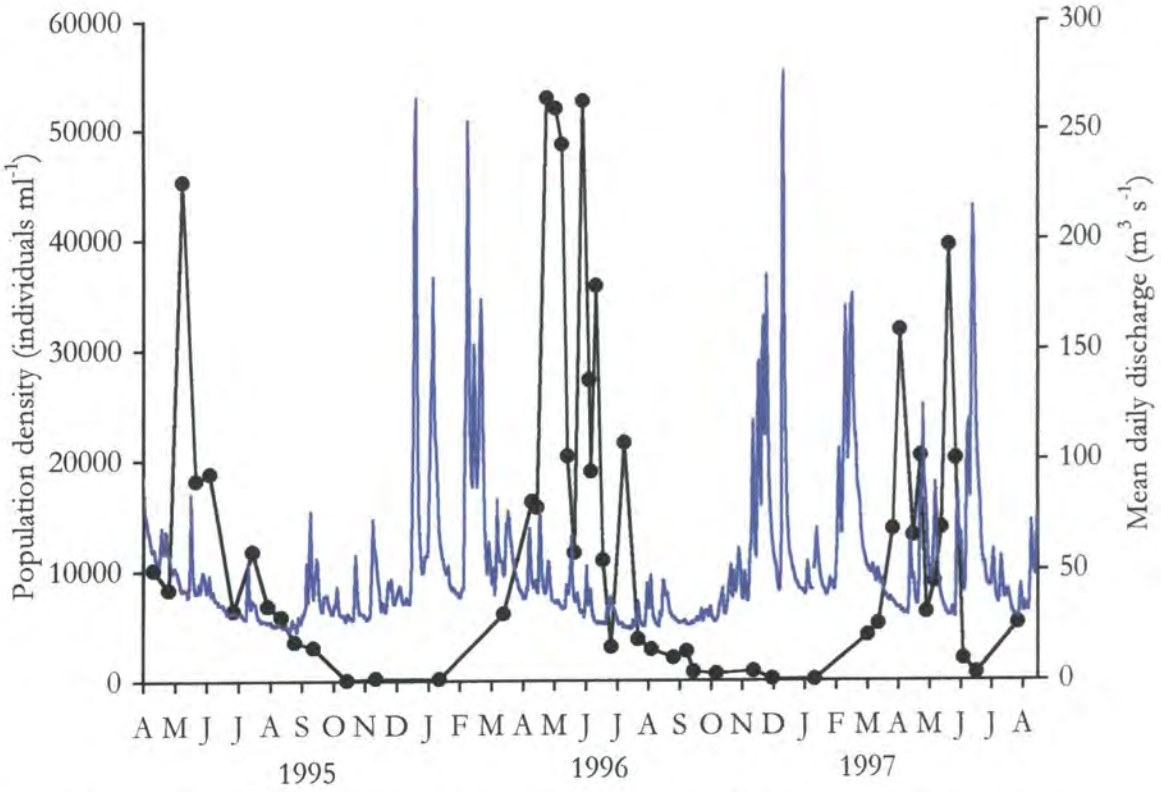

Figure 4.1 Temporal change in phytoplankton density (black line) and discharge (blue line) for the Trent at Cromwell.

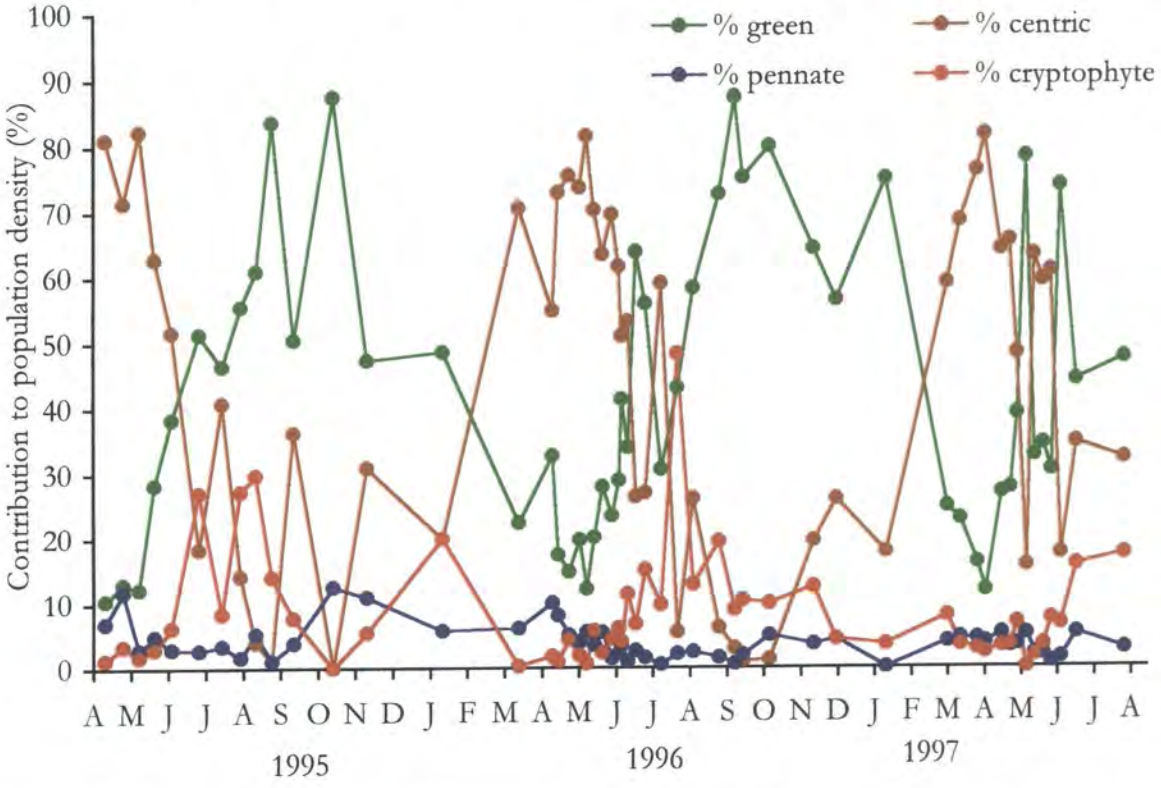

Figure 4.2 Temporal change in representation of algal to the flora of the Trent at Cromwell. Data are shown for groups which represented over 5% of the population for over 5% of the time.

Table 4.1 Bacillariophyta recorded for the Trent at Cromwell.

CODE	Genus	Species	Authority
13010660	*Achnanthes*	*lanceolata*	(Bréb.) Grunov 1880
13080010	*Asterionella*	*formosa*	Hassall
12030064	*Aulacoseira*	*granulata*	(Ehrenb.) Simonsen 1979
12060040	*Cyclostephanos*	*invisitatus*	(Hohn et Hellermann) Theriot, Stoermer et Hak. 1987
12070020	*Cyclotella*	*antiqua*	W.Sm.
12070040	*Cyclotella*	*atomus*	Hust. 1937
12070142	*Cyclotella*	*comta*	(Ehrenb.) Kütz.
12070273	*Cyclotella*	*kuetzingiana*	Thwaites
12070300	*Cyclotella*	*meneghiniana*	Kütz.
12070370	*Cyclotella*	*pseudostelligera*	Hust. 1939
12070400	*Cyclotella*	*radiosa*	(Grunov) Lemmerm. 1900
12070470	*Cyclotella*	*stelligera*	Cleve et Grun in Van Heurck 1882
12070560	*Cyclotella*	*woltereckii*	Hust. 1923
13220000	*Cymbella*	sp.	
13260000	*Diatoma*	sp.	
13260070	*Diatoma*	*vulgare*	Bory 1824
13460040	*Fragilaria*	*crotonensis*	Kitton 1869
13500290	*Gomphonema*	*olivaceoides*	Hust. 1950
13510000	*Gyrosigma*	sp.	
12110080	*Melosira*	*varians*	Agardh 1827
12110080	*Melosira*	*varians*	Agardh 1827
13580000	*Navicula*	sp.	
13584250	*Navicula*	*viridula*	(Kütz.) Ehrenb. 1836
13610020	*Nitzschia*	*acicularis*	(Kütz.) W.Sm.
13611260	*Nitzschia*	*palea*	(Kütz.) W.Sm.
13610000	*Nitzschia*	sp.	
13760000	*Sellaphora*	sp.	
12170020	*Skeletonema*	*potamos*	(Weber) Hasle 1976
12170020	*Skeletonema*	*potamos*	(Weber) Hasle 1976
12190090	*Stephanodiscus*	*hantzschii*	Grunov in Cleve et Grunov
12190160	*Stephanodiscus*	*minutulus*	(Kütz.) Cleve et Moller 1986
12190200	*Stephanodiscus*	*parvus*	Stoermer et Hak. 1984
12190230	*Stephanodiscus*	*tenuis*	Hust. 1939
13850010	*Synedra*	*acus*	Kütz. 1844
13850290	*Synedra*	*ulna*	(Nitzsch) Ehrenb. 1836
12200120	*Thalassiosira*	*guillardii*	Hasle
12200220	*Thalassiosira*	*pseudonana*	Hasle et Heimdal 1970
12200280	*Thalassiosira*	*weissfloggii*	(Grunov) Fryxell et Hasle 1977

Table 4.2 Chlorophyta recorded for the Trent at Cromwell.

CODE	Genus	Species	Authority
17010010	*Actinastrum*	*hantzschii*	Lagerheim
17040040	*Ankistrodesmus*	*falcatus*	(Corda) Ralfs
16180150	*Chlamydomonas*	*tetragonia*	(Bohlin) Ettl
16180000	*Chlamydomonas*	sp.	
17130000	*Chlorella*	sp.	
27040043	*Closterium*	*acutum var. variabile*	Bréb. in Ralfs 1848
17210030	*Coelastrum*	*microporum*	Nägeli
27050000	*Cosmarium*	sp.	
17240010	*Crucigenia*	*fenestrata*	(Schmidle) Schmidle
17240020	*Crucigenia*	*quadrata*	Morren
17240030	*Crucigenia*	*tetrapedia*	(Kirchner) W. et G.S.West
17250010	*Crucigeniella*	*apiculata*	(Lemmerm.) Komárek
17250030	*Crucigeniella*	*rectangularis*	(Nägeli) Komárek
17300030	*Dictyosphaerium*	*pulchellum*	Wood
17320020	*Didymogenes*	*palatina*	Schmidle
25010010	*Elakatothrix*	*gelatinosa*	Wille
16260010	*Eudorina*	*elegans*	Ehrenb.
16330020	*Gonium*	*sociale*	(Dujardin) Warming
17440020	*Granulocystopsis*	*pseudocoronata*	(Korshikov) Hindák
17500090	*Kirchneriella*	*subcapitata*	Korshikov
25030010	*Koliella*	*longiseta*	(Vischer) Hindák
17530040	*Lagerheimia*	*genevensis*	(Chodat) Chodat
17530070	*Lagerheimia*	*wratislaviensis*	Schröder
17550010	*Micractinium*	*pusillum*	Fresenius
17560040	*Monoraphidium*	*griffithii*	(Berk.) Komárek-Legnerová
17560020	*Monoraphidium*	*contortum*	(Thur.) Komárek-Legnerová
16470010	*Pandorina*	*morum*	(O.F.Müll.) Bory
17680030	*Pediastrum*	*boryanum*	(Turpin) Menegh.
17680050	*Pediastrum*	*duplex*	Meyen
17680090	*Pediastrum*	*tetras*	(Ehrenb.) Ralfs
17820020	*Scenedesmus*	*acuminatus*	(Lagerheim) Chodat
17820200	*Scenedesmus*	*ecornis*	(Ehrenb. ex Ralfs) Chodat
17820240	*Scenedesmus*	*intermedius*	Chodat
17820270	*Scenedesmus*	*obliquus*	(Turpin) Kütz.
17820330	*Scenedesmus*	*protuberans*	F.E. Fritsch et Rich
17820350	*Scenedesmus*	*quadricauda*	(Turpin) Bréb.
17830020	*Schroederia*	*planktonica*	(Skuja) Philipose
17840020	*Selenastrum*	*gracile*	Reinsch
16680010	*Spermatozopsis*	*exsultans*	Korshikov
17900020	*Sphaerocystis*	*schroeteri*	Chodat
27380610	*Staurastrum*	*furcigerum*	Bréb.
24340010	*Stichococcus*	*bacillaris*	Nägeli
17930010	*Tetraedron*	*caudatum*	(Corda) Hansg.
17930030	*Tetraedron*	*incus*	(Teiling) G.M.Sm.
17930052	*Tetraedron*	*minimum*	(A.Braun) Hansg.
16760010	*Tetraselmis*	*cordiformis*	(N.Carter) Stein
16770010	*Tetraspora*	*gelatinosa*	(Vaucher) Desv.
17940070	*Tetrastrum*	*staurogeniaeforme*	(Schröder) Lemmerm.
04100090	*Trachelomonas*	*volvocina*	Ehrenb.
10350000	*Trachychloron*	sp.	

Table 4.3 Chrysophyta recorded for the Trent at Cromwell.

Code	Genus	Species	Authority
09280020	*Dinobryon*	*divergens*	(Imhof) Lemmerm.
09380010	*Mallomonas*	*acaroides*	Perty
09380000	*Mallomonas*	sp.	
09660010	*Synura*	*petersenii*	Korshikov

Table 4.4 Cryptophyta recorded for the Trent at Cromwell.

Code	Genus	Species	Authority
05020000	*Chroomonas*	sp.	
05040050	*Cryptomonas*	*ovata*	Ehrenb.
05100010	*Rhodomonas*	*lacustris*	Pascher et Ruttner

Table 4.5 Cyanophyta recorded for the Trent at Cromwell.

Code	Genus	Species	Authority
01020000	*Anabaena*	sp.	
01460000	*Merismopedia*	sp.	
01530010	*Oscillatoria*	*agardhii*	Gomont
01530160	*Oscillatoria*	*limnetica*	Lemmerm.
01530000	*Oscillatoria*	sp.	

Table 4.6 Euglenophyta recorded for the Trent at Cromwell.

Code	Genus	Species	Authority
04020150	*Euglena*	*viridis*	Ehrenb.
04070000	*Phacus*	sp.	

Table 4.7 Pyrrophyta recorded for the Trent at Cromwell.

Code	Genus	Species	Authority
06090000	*Glenodinium*	sp.	

Table 4.8 Xanthophyta recorded for the Trent at Cromwell.

Code	Genus	Species	Authority
10070010	*Centritractus*	*belonophorus*	Lemmerm.

Other algal groups contributed little to the phytoplankton over the sampling period. The occurrence of Cryptophytes was sporadic and reached maximal concentrations of 48% on 30 July 1996 when the contribution of Chlorophyta and centric diatoms to the population was low (Fig 4.2). Cyanophytes contributed a maximum of 11% to the phytoplankton on 23 September 1996. Other groups contributed less than 2% to the phytoplankton over the sampling period.

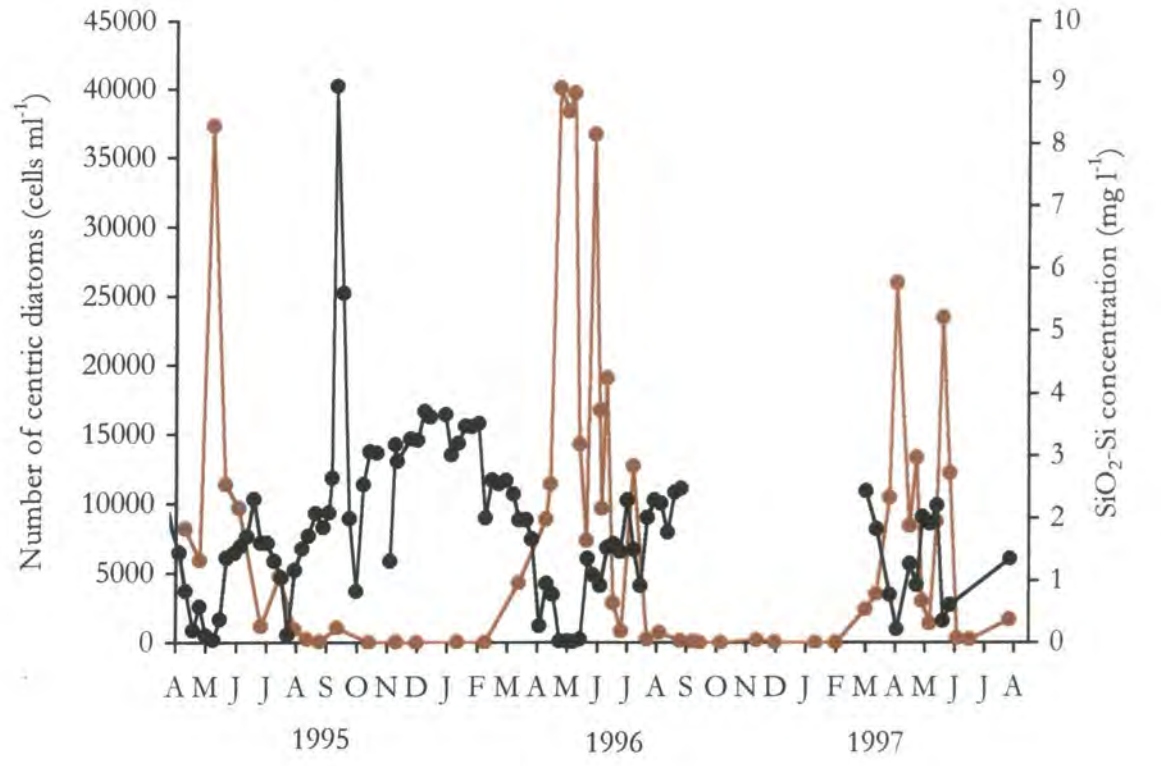

Figure 4.3 Temporal change in number of centric diatoms (brown line) and SiO_2-Si concentration (black line) for the Trent at Cromwell.

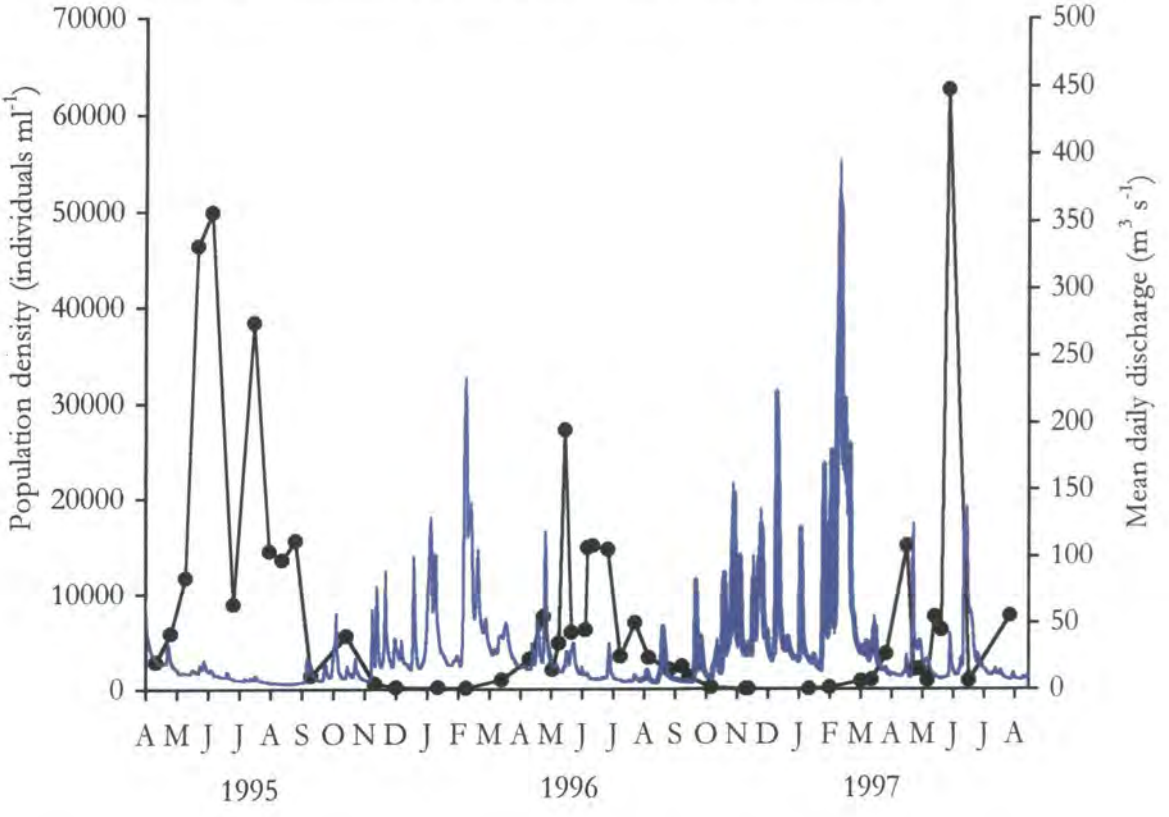

Figure 4.4 Temporal change in phytoplankton density (black line) and discharge (blue line) for the Ouse at Acaster.

4.12 Ouse

As discharge decreased at the beginning of each spring, phytoplankton density increased and reached maximal concentrations of 49920, 27320 and 62700 individuals ml^{-1} on 5 June 1995, 10 June 1996 and 21 May 1997, respectively (Fig. 4.4). Summer populations declined to around 2000 to 6000 individuals ml^{-1} and declined further to winter minima of 210, 40 and 60 individuals ml^{-1} on 5 December 1995, 21 November 1996 and 21 January 1997, respectively. These minima corresponded with high discharge events (Fig. 4.4) and low temperature and low light availability.

Over the 29 month sampling period, 102 taxa were recorded; 39 Bacillariophyta (Table 4.9), 47 Chlorophyta (Table 4.10), 6 Chrysophyta (Table 4.11), 4 Cryptophyta (Table 4.12) 2 Cyanophyta (Table 4.13), 2 Euglenophyta (Table 4.14), 1 Haptophyta (Table 4.15) and 1 Pyrrophyta (Table 4.16). Chlorophyta, mainly *Ankistrodesmus*, *Scenedesmus* and *Chlorella*, usually dominated the phytoplankton in summer or autumn and the largest proportional contribution to the population occurred on 17 October 1995, 3 September 1996 and 10 June 1997 where they contributed 49, 45 and 51 % of the phytoplankton population, respectively (Fig. 4.5). The least proportional contribution of Chlorophyta to the phytoplankton population occurred during spring with contributions falling to 20, 7 and 14 % on 11 April 1995, 21 May 1996 and 14 April 1997, respectively (Fig. 4.5).

The phytoplankton comprised mainly centric diatoms during spring with maximal contribution to the phytoplankton population increasing to 53, 85 and 66% of the population in 22 May 1995, 21 May 1996 and 29 April 1997, respectively (Fig. 4.5). Centric diatoms of the genus *Stephanodiscus*, *Cyclotella* and *Cyclostephanos* dominated during these occasions. Centric diatoms comprised minima of 1 and 0% of the population on 1 August 1995 and 21 November 1996, respectively. A minimum contribution in summer of 0% was recorded on 3 June 1997 (Fig. 4.5).

Spring minimum SiO_2-Si concentrations of 0.01, 0.02 and 0.01 mg l^{-1} corresponded with maximal centric diatom concentrations of 49920, 27310 and 62700 individuals ml^{-1} on 22 May 1995, 21 May 1996 and 29 April 1997, respectively (Fig. 4.6). A significant, negative relationship existed between centric diatom abundance and SiO_2-Si concentration during the spring months ($r=-0.63$, $P<0.01$, $n=19$).

Other algal groups contributed little to the phytoplankton over the sampling period although Cryptophytes reached maximal contribution to the phytoplankton of 33% on 21 November 1996 (Fig. 4.5) and were also important on 13 February 1996 and 21 January 1997 (Fig. 4.5). Other groups showed sporadic peaks in their contribution to the phytoplankton but no steady pattern was obvious. Amongst these, the best represented were Cyanophytes and Chrysophytes, reaching maximal contribution of 14% and 21% respectively on 19 November 1996 (Fig. 4.5).

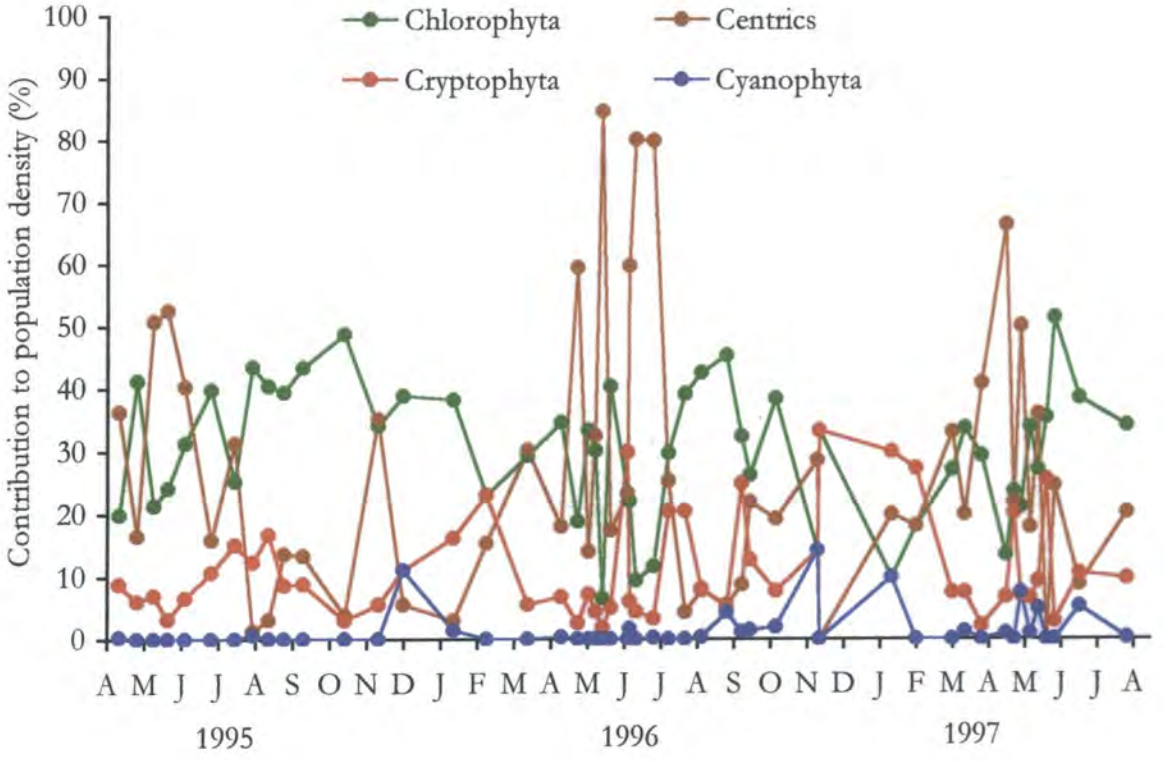

Figure 4.5 Temporal change in representation of algal to the flora of the Ouse at Acaster. Data are shown for groups which represented over 5% of the population for over 5% of the time.

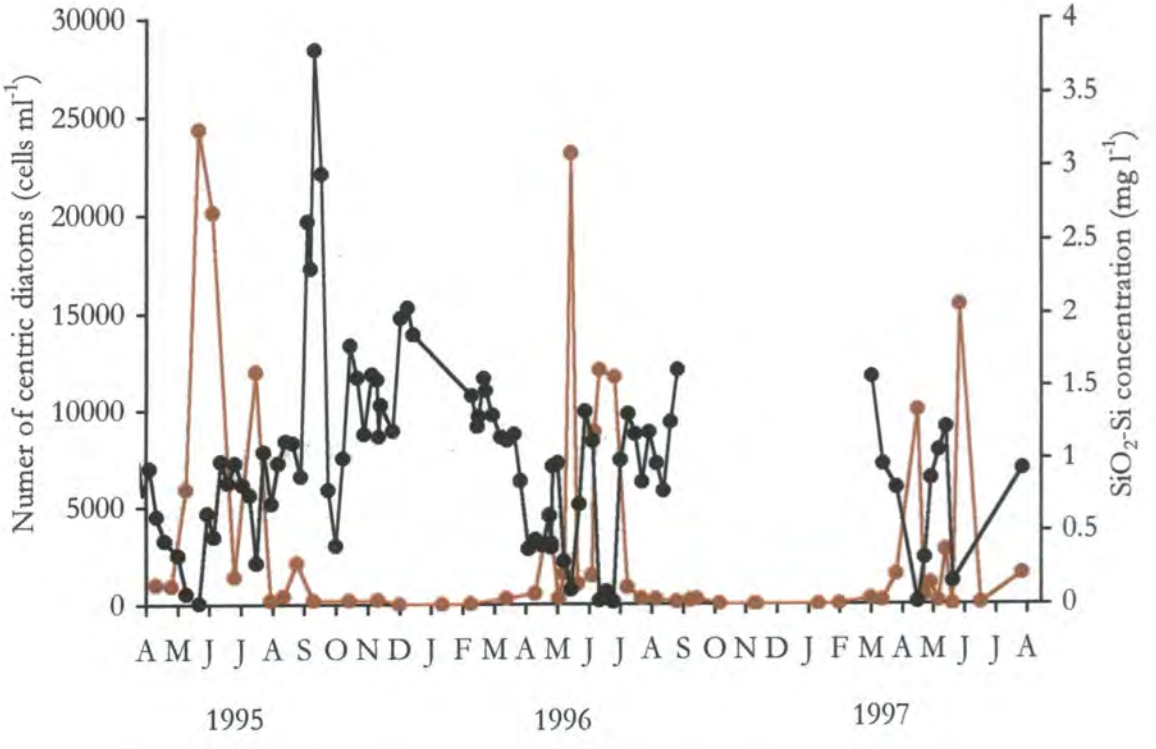

Figure 4.6 Temporal change in number of centric diatoms (brown line) and SiO_2-Si concentration (black line) for the Ouse at Acaster.

Table 4.9 Bacillariophyta recorded for the Ouse at Acaster.

CODE	Genus	Species	Authority
13080010	*Asterionella*	*formosa*	Hassall
12030064	*Aulacoseira*	*granulata*	(Ehrenb.) Simonsen 1979
13160000	*Cocconeis*	sp.	
12060040	*Cyclostephanos*	*invisitatus*	(Hohn et Hellermann) Theriot, Stoermer et Hak. 1987
12070020	*Cyclotella*	*antiqua*	W.Sm.
12070040	*Cyclotella*	*atomus*	Hust. 1937
12070142	*Cyclotella*	*comta*	(Ehrenb.) Kütz.
12070273	*Cyclotella*	*kuetzingiana*	Thwaites
12070300	*Cyclotella*	*meneghiniana*	Kütz.
12070370	*Cyclotella*	*pseudostelligera*	Hust. 1939
12070400	*Cyclotella*	*radiosa*	(Grunov) Lemmerm. 1900
12070470	*Cyclotella*	*stelligera*	Cleve et Grun in Van Heurck 1882
12070560	*Cyclotella*	*woltereckii*	Hust. 1923
13220000	*Cymbella*	sp.	
13260000	*Diatoma*	sp.	
13460040	*Fragilaria*	*crotonensis*	Kitton 1869
13470082	*Fragilariforma*	*virescens var. capitata*	(Ralfs) D.M.Williams et Round 1988
13510000	*Gyrosigma*	sp.	
12110080	*Melosira*	*varians*	Agardh 1827
13570000	*Meridion*	sp.	
13580720	*Navicula*	*confervacea*	(Kütz.) Grunov
13580000	*Navicula*	sp.	
13584250	*Navicula*	*viridula*	(Kütz.) Ehrenb. 1836
13610020	*Nitzschia*	*acicularis*	(Kütz.) W.Sm.
13611260	*Nitzschia*	*palea*	(Kütz.) W.Sm.
13610000	*Nitzschia*	sp.	
13660000	*Pinnularia*	sp.	
12170020	*Skeletonema*	*potamos*	(Weber) Hasle 1976
12190090	*Stephanodiscus*	*hantzschii*	Grunov in Cleve et Grunov
12190160	*Stephanodiscus*	*minutulus*	(Kütz.) Cleve et Moller 1986
12190200	*Stephanodiscus*	*parvus*	Stoermer et Hak. 1984
12190230	*Stephanodiscus*	*tenuis*	Hust. 1939
13840000	*Surirella*	sp.	
13850010	*Synedra*	*acus*	Kütz. 1844
13850290	*Synedra*	*ulna*	(Nitzsch) Ehrenb. 1836
13860022	*Tabellaria*	*flocculosa var. asterionelloides*	(Roth) Kütz.
12200120	*Thalassiosira*	*guillardii*	Hasle
12200220	*Thalassiosira*	*pseudonana*	Hasle et Heimdal 1970
12200280	*Thalassiosira*	*weissfloggii*	(Grunov) Fryxell et Hasle 1977

Table 4.10 Chlorophyta recorded for the Ouse at Acaster.

Code	Genus	Species	Authority
17010010	*Actinastrum*	*hantzschii*	Lagerheim
17040040	*Ankistrodesmus*	*falcatus*	(Corda) Ralfs
16180080	*Chlamydomonas*	*monadinia*	Stein
16180000	*Chlamydomonas*	sp.	
17130000	*Chlorella*	sp.	
16190010	*Chlorogonium*	*elongatum*	(Dang.) Dang.
27040043	*Closterium*	*acutum var. variabile*	Bréb. in Ralfs 1848
27040460	*Closterium*	*moniliferum*	(Bory) Ehrenb. ex Ralfs 1848
17190010	*Coccomyxa*	*confluens*	(Kütz.) Fott
17210030	*Coelastrum*	*microporum*	Nägeli
17240020	*Crucigenia*	*quadrata*	Morren
17240030	*Crucigenia*	*tetrapedia*	(Kirchner) W. et G.S.West
17250030	*Crucigeniella*	*rectangularis*	(Nägeli) Komárek
17300030	*Dictyosphaerium*	*pulchellum*	Wood
16260010	*Eudorina*	*elegans*	Ehrenb.
17410010	*Golenkinia*	*paucispina*	W. et G.S.West
17410020	*Golenkinia*	*radiata*	(Chodat) Wille
16330020	*Gonium*	*sociale*	(Dujardin) Warming
16350020	*Haematococcus*	*pluvialis*	Flot.
17490020	*Keratococcus*	*suecicus*	Hindák
25030010	*Koliella*	*longiseta*	(Vischer) Hindák
17520010	*Korshikoviella*	*michailovskoensis*	(Elenkin) Silva
17530010	*Lagerheimia*	*chodatii*	Bernard
17550010	*Micractinium*	*pusillum*	Fresenius
17560020	*Monoraphidium*	*contortum*	(Thur.) Komárek-Legnerová
17640010	*Oocystella*	*marssonii*	Lemmerm.
17640030	*Oocystella*	*solitaria*	(Wittrock) Hindák
17640020	*Oocystella*	*parva*	W. et G.S. West
16470010	*Pandorina*	*morum*	(O.F.Müll.) Bory
17680030	*Pediastrum*	*boryanum*	(Turpin) Menegh.
17680050	*Pediastrum*	*duplex*	Meyen
17820010	*Scenedesmus*	*aculeotatus*	Reinsch
17820020	*Scenedesmus*	*acuminatus*	(Lagerheim) Chodat
17820040	*Scenedesmus*	*acutus*	Meyen
17820080	*Scenedesmus*	*armatus*	(Chodat) Chodat
17820200	*Scenedesmus*	*ecornis*	(Ehrenb. ex Ralfs) Chodat
17820270	*Scenedesmus*	*obliquus*	(Turpin) Kütz.
17820280	*Scenedesmus*	*obtusus*	(Turpin) Kütz.
17820350	*Scenedesmus*	*quadricauda*	(Turpin) Bréb.
17840020	*Selenastrum*	*gracile*	Reinsch
17900020	*Sphaerocystis*	*schroeteri*	Chodat
24340010	*Stichococcus*	*bacillaris*	Nägeli
17930010	*Tetraedron*	*caudatum*	(Corda) Hansg.
17930030	*Tetraedron*	*incus*	(Teiling) G.M.Sm.
17930080	*Tetraedron*	*trigonum*	(Nägeli) Hansg.
04100090	*Trachelomonas*	*volvocina*	Ehrenb.
17970000	*Treubaria*	sp.	

Table 4.11 Chrysophyta recorded for the Ouse at Acaster.

Code	Genus	Species	Authority
09060000	*Chromulina*	sp.	
09140000	*Chrysococcus*	sp.	
09280020	*Dinobryon*	*divergens*	(Imhof) Lemmerm.
09360000	*Kephyrion*	sp.	
09450000	*Ochromonas*	sp.	
09660010	*Synura*	*petersenii*	Korshikov

Table 4.12 Cryptophyta recordede for the Ouse at Acaster.

Code	Genus	Species	Authority
05020000	*Chroomonas*	sp.	
05040050	*Cryptomonas*	*ovata*	Ehrenb.
06170000	*Peridinium*	sp.	
05100010	*Rhodomonas*	*lacustris*	Pascher et Ruttner

Table 4.13 Cyanophyta recorded for the Ouse at Acaster.

Code	Genus	Species	Authority
01020000	*Anabaena*	sp.	
01530000	*Oscillatoria*	sp.	

Table 4.14 Euglenophyta recorded for the Ouse at Acaster.

Code	Genus	Species	Authority
04020150	*Euglena*	*viridis*	Ehrenb.
04070000	*Phacus*	sp.	

Table 4.15 Haptophyta recorded for the Ouse at Acaster.

Code	Genus	Species	Authority
08010010	*Chrysochromulina*	*parva*	Lackey

Table 4.16 Pyrrophyta recorded for the Ouse at Acaster.

Code	Genus	Species	Authority
06120000	*Gymnodinium*	sp.	

4.2 Phytoplankton biomass

4.21 Chlorophyll *a* concentration and phytoplankton density

Chlorophyll *a* concentration was used as a surrogate measure of phytoplankton biomass using the method of Marker (1994; Section 3.51). A significant, positive correlation existed between chlorophyll *a* concentration and phytoplankton density for both Cromwell ($r=0.92$, $P<0.001$, $n=51$) and Acaster ($r=0.71$, $P<0.001$, $n=49$; Fig. 4.7). The relationship explained 85% of the variation at Cromwell and 50% of the variation at Acaster. The gradient of the line of linear regression was used to calculate an average chlorophyll *a* content per phytoplankton individual of 2.8 pg chl *a* individual^{-1} at Cromwell, which was twice that at Acaster where individuals on average contained 1.4 pg chl *a* individual^{-1}. This result could be explained by a poorer light climate or larger individuals at Cromwell compared to Acaster.

Phytoplankton biomass in both the Trent and Ouse showed spatial and temporal variation. Intra-site variability was checked by comparing the chlorophyll *a* concentration at three positions across the river at three sites on the Trent and three sites on the Ouse system (Section 3.51). No significant difference in chlorophyll *a* concentration occurred between samples taken at different positions of the channel at Thornton Manor on 28 June 1995, Kelham on 12 September 1995 or Cavendish Bridge on 5 June 1996 (Fig. 4.8). However, variation was evident at Boroughbridge on 17 July 1995, Clifton on 1 August 1995 and Gunthorpe on 14 August 1995. At Boroughbridge, the middle of the river had significantly higher concentrations of chlorophyll *a* than both the left (ANOVA, $P=0.0015$) and right side (ANOVA, $P=0.0012$; Fig. 4.8) of the river. At Clifton, the left side of the river had significantly lower concentration of chlorophyll *a* than the right side (ANOVA, $P=0.042$). At Gunthorpe, the right side of the river had lower concentrations of chlorophyll *a* than both the middle (ANOVA, $P=0.014$) and the left side (ANOVA, $P=0.029$; Fig. 4.8) of the channel.

4.22 Temporal variation in chlorophyll *a*

4.221 Trent system

The concentration of chlorophyll *a* in the Trent showed large temporal variation, but a similar seasonal pattern each year (Fig. 4.9a). The main period of increase in chlorophyll *a* occurred between March and June as river discharge decreased although at Cavendish Bridge, the most upstream site, the maximum of 107 $\mu g\ l^{-1}$ occurred on 16 July 1995 (Fig. 4.9a). Essentially a single chlorophyll *a* maximum occurred each year. This spring peak in chlorophyll *a* was often disrupted by short periods of low chlorophyll *a* which corresponded to spring floods (Section 4.25).

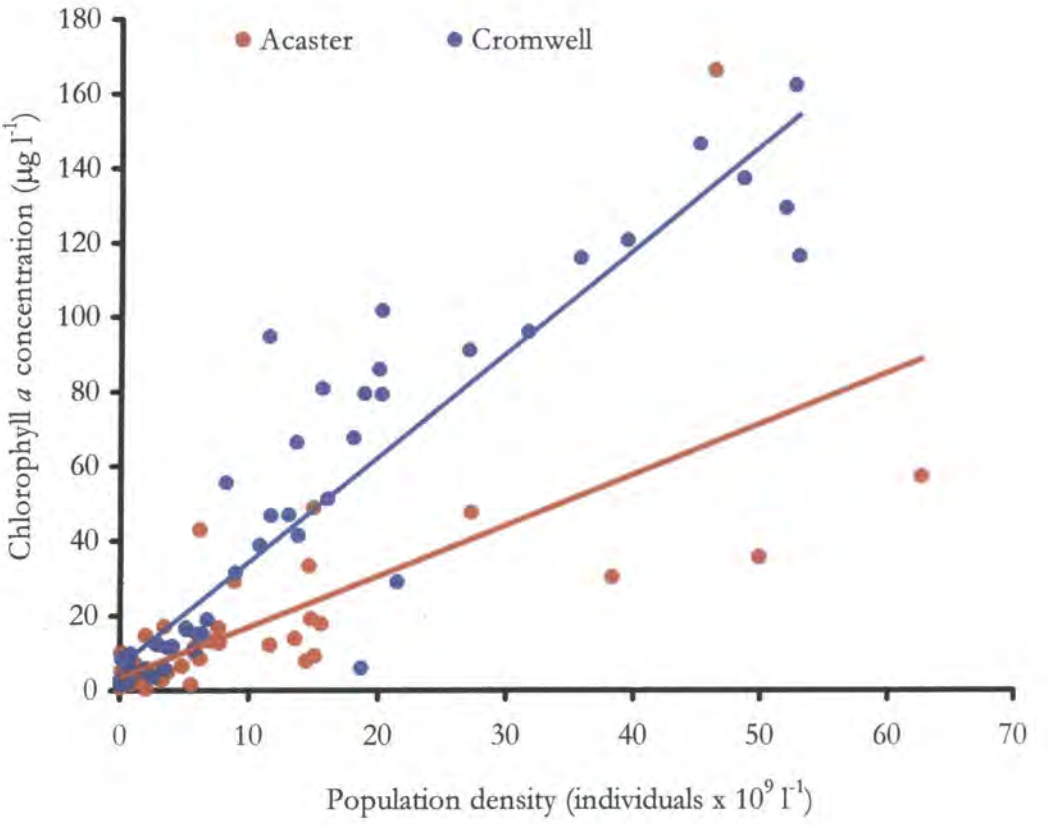

Figure 4.7 Relationship between chlorophyll *a* concentration and phytoplankton population density for the Trent at Cromwell (blue line) and Ouse at Acaster (red line). The gradient of the line of linear regression was used estimate a chlorophyll *a* content of 2.8 pg chl *a* individual^{-1} for Cromwell ($r=0.92$, $P<0.001$) and 1.37 pg chl *a* individual^{-1} for Acaster ($r=0.71$, $P<0.001$).

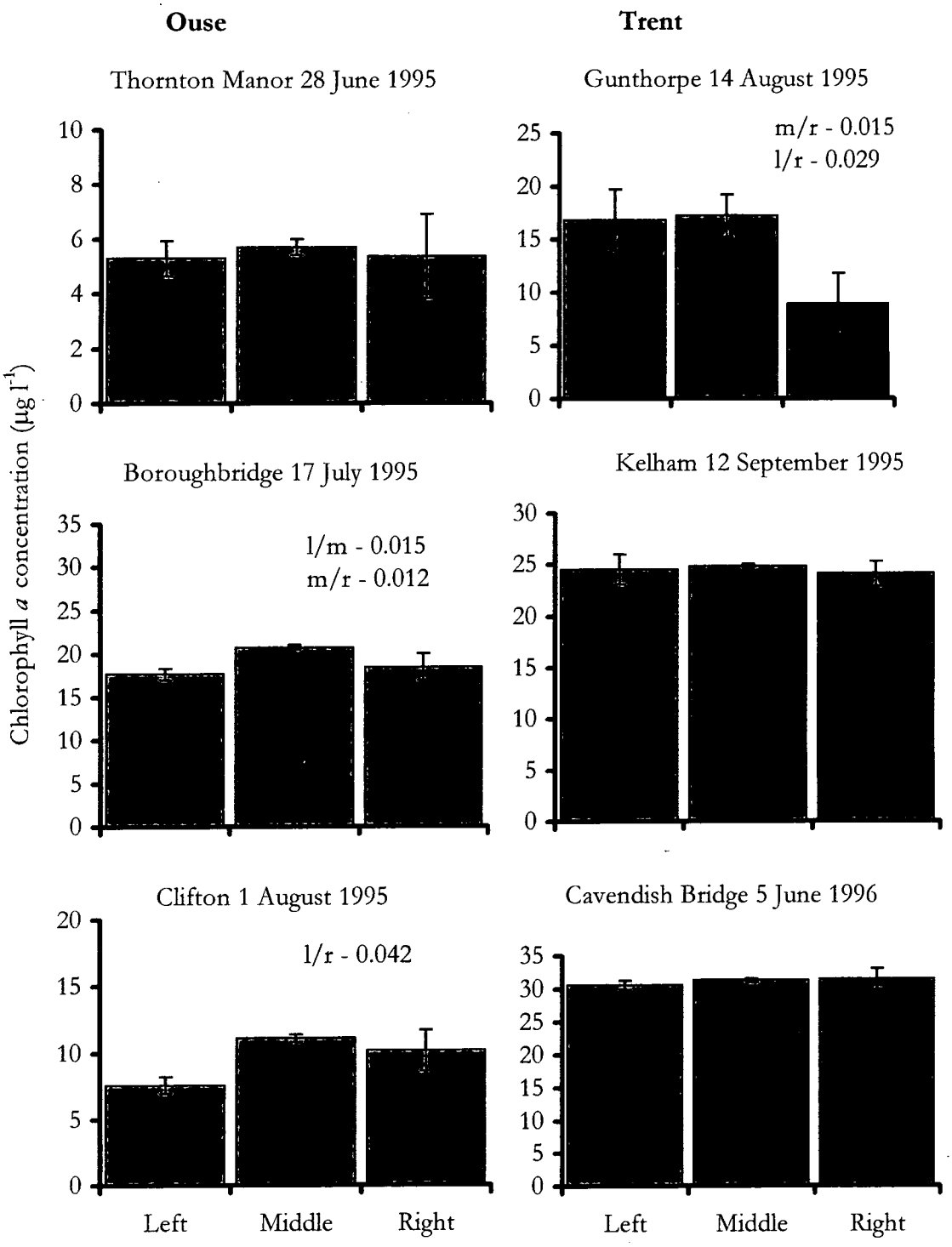

Figure 4.8 Spatial variation in chlorophyll *a* concentration at three sites on the Ouse system and three on the Trent system. Three samples were taken from three positions across the river channel at two minute intervals (see section 3.6 for full explanation). Positions refer to position across channel looking downstream. The significance of difference (ANOVA) is indicated where appropriate. L/m=left and middle, m/r=middle and right, l/r=left and right of channel.

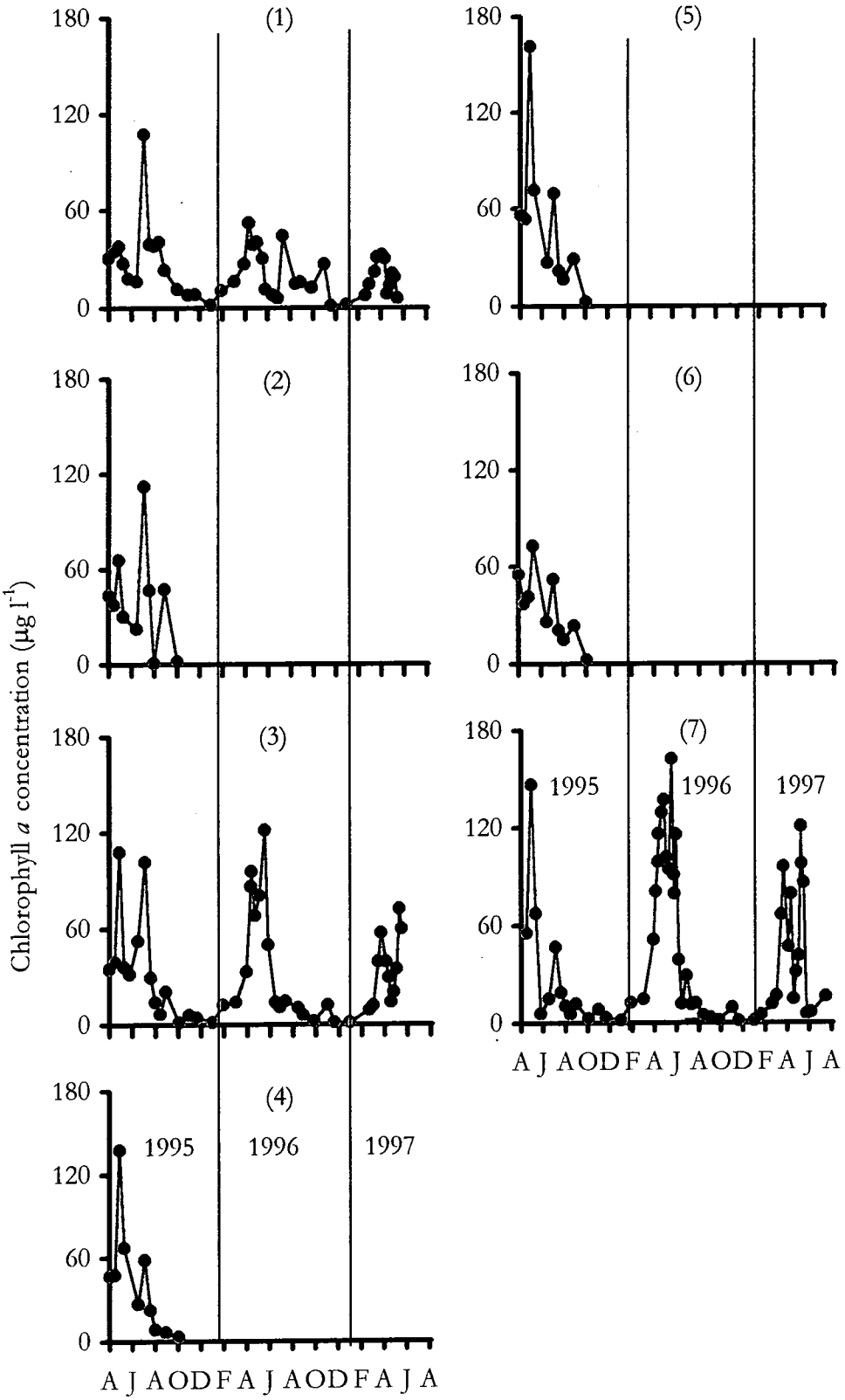

Figure 4.9a Time series of chlorophyll *a* concentration for the Trent from April 1995 to August 1997. Charts are in ascending order of position downstream as indicated by panel number (1, Cavendish Bridge; 2, Wilford; 3, Gunthorpe; 4, Kelham; 5, South Muskham; 6, Newark; 7, Cromwell).

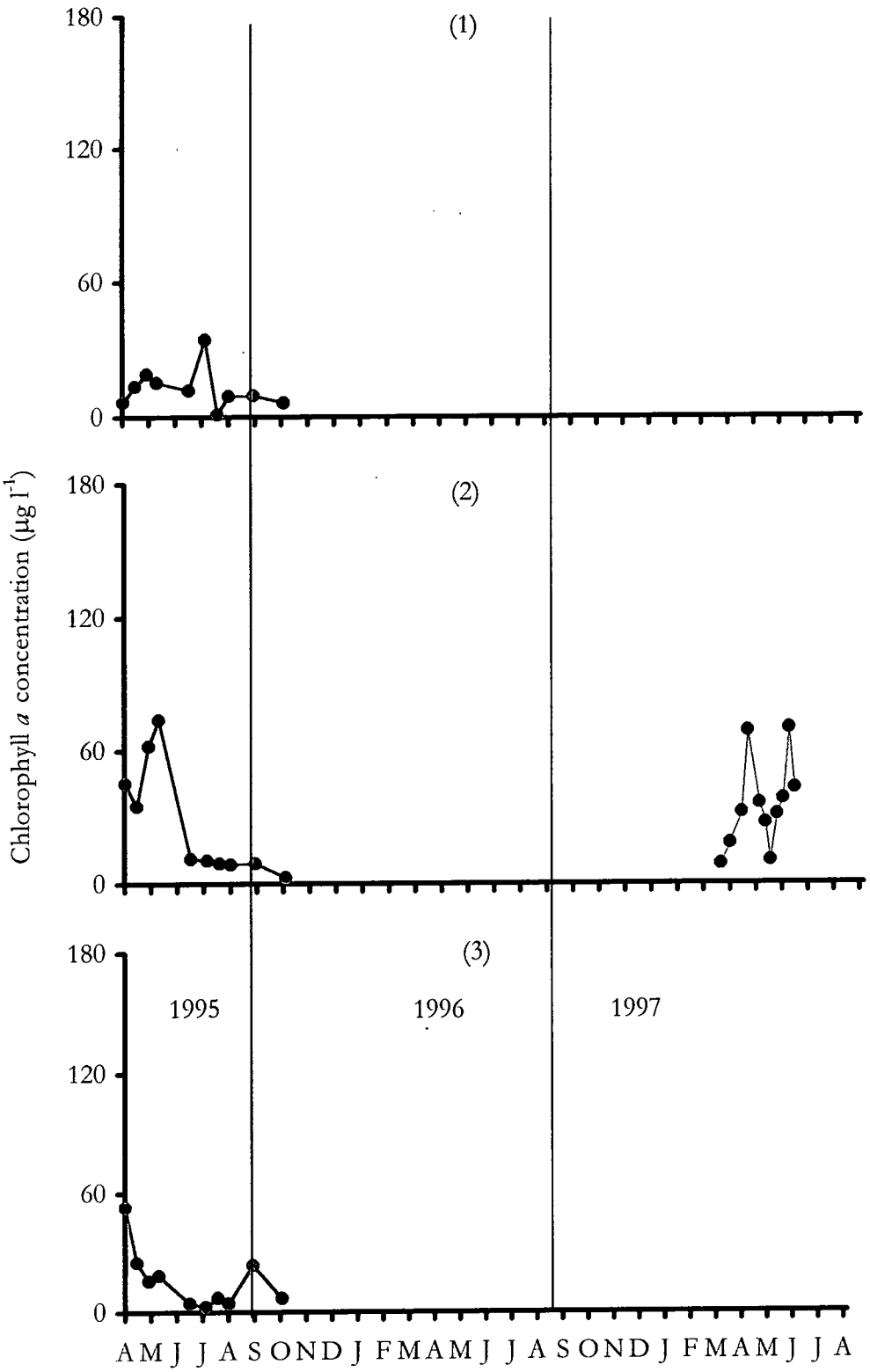

Figure 4.9b Time series of chlorophyll *a* concentration for the Trent tributaries from April 1995 to August 1997. Charts are in ascending order of position of entry of tributary downstream of the Trent as indicated by panel number (1, Derwent; 2, Soar; 3, Devon).

At Cromwell, the tidal limit, where the seasonal amplitude was greatest, the annual maxima reached 147, 162 and 121 $\mu g\ l^{-1}$ on 10 May 1995, 4 June 1996 and 2 June1997, respectively (Fig. 4.9a) at times when river velocity was low (between 0.16 and 0.23 m s^{-1}). The maxima then declined rapidly and were followed by a small peak during July. By August, the concentration of chlorophyll *a* had fallen to 6, 12 and 16 $\mu g\ l^{-1}$ on 27 August 1995, 12 August 1996 and 11 August 1997, respectively (Fig. 4.9a). Annual minima (c. 1.5 $\mu g\ l^{-1}$) occurred in December or January at all sites studied over the winter period.

The tributaries to the Trent showed a similar pattern in chlorophyll *a*. The Derwent and Devon were only sampled during April to October 1995 whereas the Soar was sampled additionally from April to August 1997. The Derwent increased from under 20 $\mu g\ l^{-1}$ to a maximum chlorophyll *a* concentration of 35 $\mu g\ l^{-1}$ on 17 July 1995, after which concentrations fell below 10 $\mu g\ l^{-1}$ (Fig 4.9b). The chlorophyll *a* maximum in the Devon reached 53 $\mu g\ l^{-1}$ on 11 April 1995 then fell below 10 $\mu g\ l^{-1}$ until 12 September when there was a secondary peak reaching 24 $\mu g\ l^{-1}$, after which concentrations again fell below 10$\mu g\ l^{-1}$ (Fig. 4.9b). During 1995 the Soar had a maximum concentration of 73 $\mu g\ l^{-1}$ on 22 May which rapidly declined to concentrations below 10 $\mu g\ l^{-1}$ (Fig. 4.9b). During 1997, two maxima were recorded; 69 $\mu g\ l^{-1}$ on 14 April and 70 $\mu g\ l^{-1}$ on 2 June (Fig. 4.9b). On other dates, concentrations did not increase above 10 $\mu g\ l^{-1}$.
Overall, the seasonal pattern in chlorophyll *a* was similar for both the main river and the tributaries. High concentrations of chlorophyll *a* in the Trent system were recorded during spring. Concentrations declined during summer and fell to minima during winter.

4.222 Ouse system

Chlorophyll *a* concentration in the Ouse showed a similar seasonal pattern each year (Fig. 4.10). During spring, chlorophyll *a* reached maximum concentrations of 166, 48 and 57 $\mu g\ l^{-1}$ on 21 May 1995, 20 May 1996 and 9 June 1997, respectively, with the concentration at Clifton, 9.2 km upstream of Acaster, reaching a maximum of 169 $\mu g\ l^{-1}$ on 21 May 1995 (Fig. 4.10). Concentrations then declined to between 2 and 7 $\mu g\ l^{-1}$ in summer at Acaster and down to around 16 $\mu g\ l^{-1}$ at Clifton with winter minima at Acaster falling below 2 $\mu g\ l^{-1}$ (Fig. 4.10).

The seasonal pattern in the Ure and Nidd was similar to that of the Ouse. Concentrations in the Ure reached spring maxima of 184, 82 and 55 $\mu g\ l^{-1}$ on 21 May 1995, 2 July 1996 and 2 June 1997, respectively (Fig. 4.10). Concentrations then fell in summer to between 1 and 5 $\mu g\ l^{-1}$ and declined further to winter minima below 1$\mu g\ l^{-1}$ (Fig. 4.10).

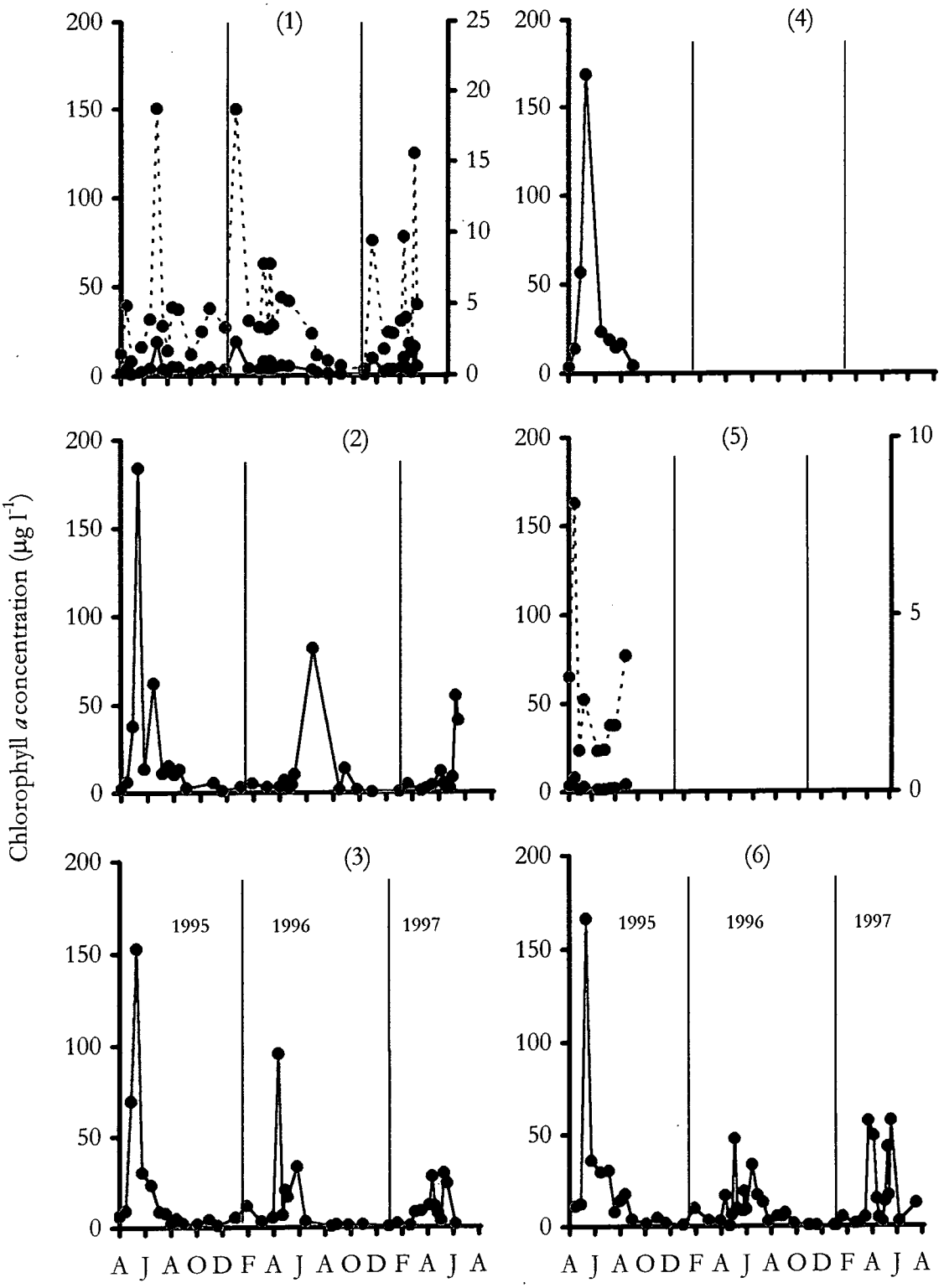

Figure 4.10 Times series of chlorophyll *a* concentration for the rivers of the Ouse system from April 1995 to August 1997. Charts are in order of ascending latitude, indicated by panel number (1, Swale at Thornton Manor; 2, Ure at Boroughbridge; 3, Nidd at Skip Bridge; 4, Ouse at Clifton; 5, Foss at York; 6, Ouse at Acaster). Broken lines refer to secondary y-axis for the Swale and Foss.

Spring concentrations in the Nidd reached maxima of 153, 96 and 30 $\mu g\ l^{-1}$ on 21 May 1995, 27 April 1996 and 2 June 1997, respectively, and declined in summer to concentrations between 1 and 4 $\mu g\ l^{-1}$ before declining further in winter to below 1 $\mu g\ l^{-1}$ (Fig. 4.10). The seasonal pattern was slightly different in the Swale with maximum concentrations not exceeding 19 $\mu g\ l^{-1}$, almost ten times lower than in the other main rivers in this system (Fig. 4.10). During 1995, the seasonal pattern was similar to the pattern for other rivers in the Ouse system. A maximum chlorophyll *a* concentration of 18.8 $\mu g\ l^{-1}$ was measured on 16 July 1995 but during 1996, the maximum of 18.7 $\mu g\ l^{-1}$ occurred in February during a flood and in 1997, a maximum concentration of 15.6 $\mu g\ l^{-1}$ occurred during June (Fig. 4.10). Minimum concentrations occurred on 24 April 1995, 18 November 1996 and 21 January 1997 with concentrations falling below 1$\mu g\ l^{-1}$ (Fig. 4.10). Concentrations in the Foss were also low with a spring maximum of only 8 $\mu g\ l^{-1}$ on 26 April 1995 which declined during summer and autumn to concentrations below 5 $\mu g\ l^{-1}$ (Fig 4.10).

4.23 Spatial variation in chlorophyll *a*

4.231 Trent system

At the time of the annual maximum at the tidal limit of the Trent at Cromwell, chlorophyll *a* concentration increased markedly downstream. The spatial pattern of chlorophyll *a* with distance downstream is discussed fully in Section 6.1

Seasonal monitoring of the tributaries during 1995 showed relatively low phytoplankton chlorophyll *a* concentrations for the Derwent and Devon (Fig. 4.9b), but concentrations for the Soar (Fig. 4.9b) similar in magnitude and seasonal pattern for the Trent at Cromwell (Fig. 4.9a). On the whole, tributaries did not provide a major input of phytoplankton chlorophyll *a* to the main river.

4.232 Ouse system

It is evident that the feeder rivers of the Swale-Ouse, primarily the Ure and Nidd, contributed most of the chlorophyll *a* to the Ouse (Fig. 4.10). Few sites along the Swale-Ouse were sampled. This makes the investigation for the evidence of *in situ* growth of chlorophyll *a* with distance difficult. However, it is hypothesised that concentrations of chlorophyll *a* in the Ure and Nidd were responsible for concentrations found downstream at Clifton and Acaster as concentrations carried by the Swale and input from the Foss were small. This can be assumed by looking at Figure 4.10. This shows that periods of high chlorophyll *a* at Clifton and Acaster occurred during high concentrations in the Ure and Nidd. As concentrations were always low in the Swale and Foss during the sampling period (Fig. 4.10) it is assumed that these rivers had a dilution effect upon the Ouse rather than contributing great amounts of chlorophyll *a*.

4.24 Relationship between chlorophyll *a* and discharge

Figure 4.11 shows the relationship between chlorophyll *a* concentration and discharge for the Trent and the Ouse. Data are categorised into seasonal events.

For the Trent at Cromwell, chlorophyll *a* concentration declined to below 30 $\mu g\ l^{-1}$ when discharge increased to around 60 $m^3\ s^{-1}$ (Fig. 4.11, top figure). For the Ouse at Acaster, when discharge increased to 60 $m^3\ s^{-1}$ chlorophyll *a* concentration declined to below 10 $\mu g\ l^{-1}$ (Fig. 4.11, bottom figure). The spring months were dominated by low discharge, high chlorophyll events, while the winter months were dominated by high discharge, low chlorophyll events. In contrast, low discharge events in summer coincided with low chlorophyll concentration (Fig. 4.11) which is discussed later in Sections 5.4 to 5.6. The overall relationship shows a discharge threshold after which chlorophyll *a* increases. For the Trent and Ouse this threshold is approximately 55 and 25 $m_3\ s^{-1}$, respectively (Fig 4.11).

4.25 Day to day variation in chlorophyll *a* for the Trent

To obtain data of finer temporal resolution, to include patterns which were missed by weekly sampling, a daily chlorophyll *a* sampling regime was implemented (Section 3.52). Figure 4.12 shows daily chlorophyll *a* concentration and discharge at Cromwell. As discharge decreased during mid-March to mid-April from 51 to 31 $m^3\ s^{-1}$, chlorophyll *a* concentration started to increase. Five major floods corresponded with a series of declines in chlorophyll *a* concentrations (Fig. 4.12). The first in this series of floods started on 25 April when discharge increased to a maximum of 66 $m^3\ s^{-1}$ and chlorophyll *a* fell from 108 to 32 $\mu g\ l^{-1}$. After this flood chlorophyll *a* concentration started to increase steadily as discharge decreased. Chlorophyll *a* increased to 121 $\mu g\ l^{-1}$, the spring maximum of 1997, until the second flood started on 6 May, reaching a maximum discharge of 131 $m^3\ s^{-1}$, causing chlorophyll *a* to fall to 10 $\mu g\ l^{-1}$. Chlorophyll *a* concentration increased slightly to 25 $\mu g\ l^{-1}$ until the next flood (starting 19 May) saw discharge increasing to 94 $m^3\ s^{-1}$, causing chlorophyll *a* to decline to 4 $\mu g\ l^{-1}$.

The 19-day gap between the peak of the third flood and just before the start of the fourth flood saw a decrease in discharge from 94 to 30 $m^3\ s^{-1}$. This respite allowed chlorophyll *a* concentration to increase, sometimes rapidly, with a nine-fold increase from 13 to 118 $\mu g\ l^{-1}$ over 8 days. This peak in chlorophyll *a* declined steadily to 54 $\mu g\ l^{-1}$ with no apparent increase in discharge.

The fourth flood, which started on 11 June, caused chlorophyll *a* to decline from 53 to 6 $\mu g\ l^{-1}$ during a flood which saw discharge increase to 95 $m^3\ s^{-1}$. The fourth flood was rapidly followed by the relatively large fifth flood (starting 21 June), where discharge increased to 220 $m^3\ s^{-1}$.

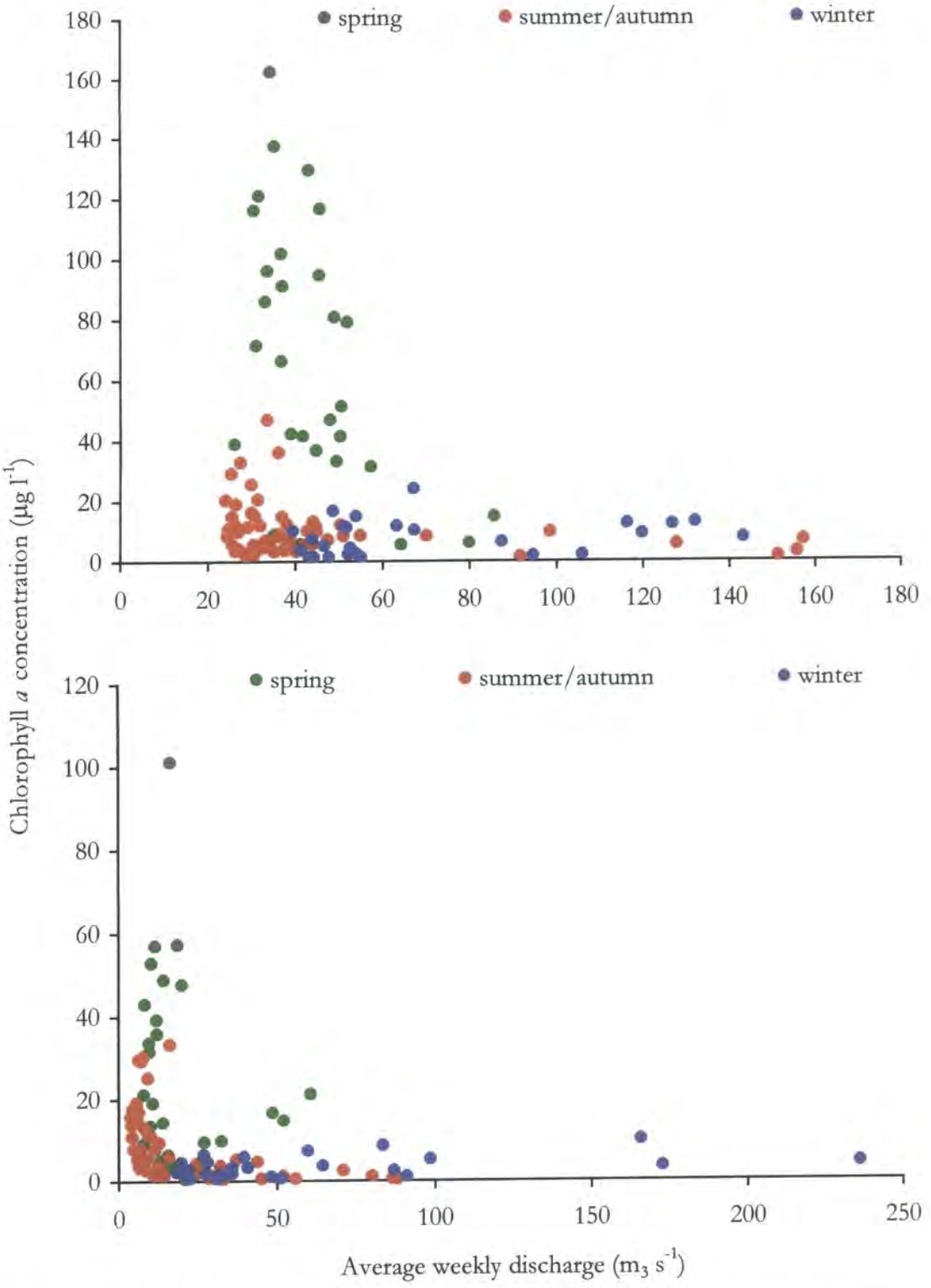

Figure 4.11 Seasonal relationship between chlorophyll *a* concentration and average weekly discharge for the Trent at Cromwell (top figure) and the Ouse at Acaster. Data have been categorised into events occuring in spring (March - May), summer /autumn (June - November) and winter (December - February).

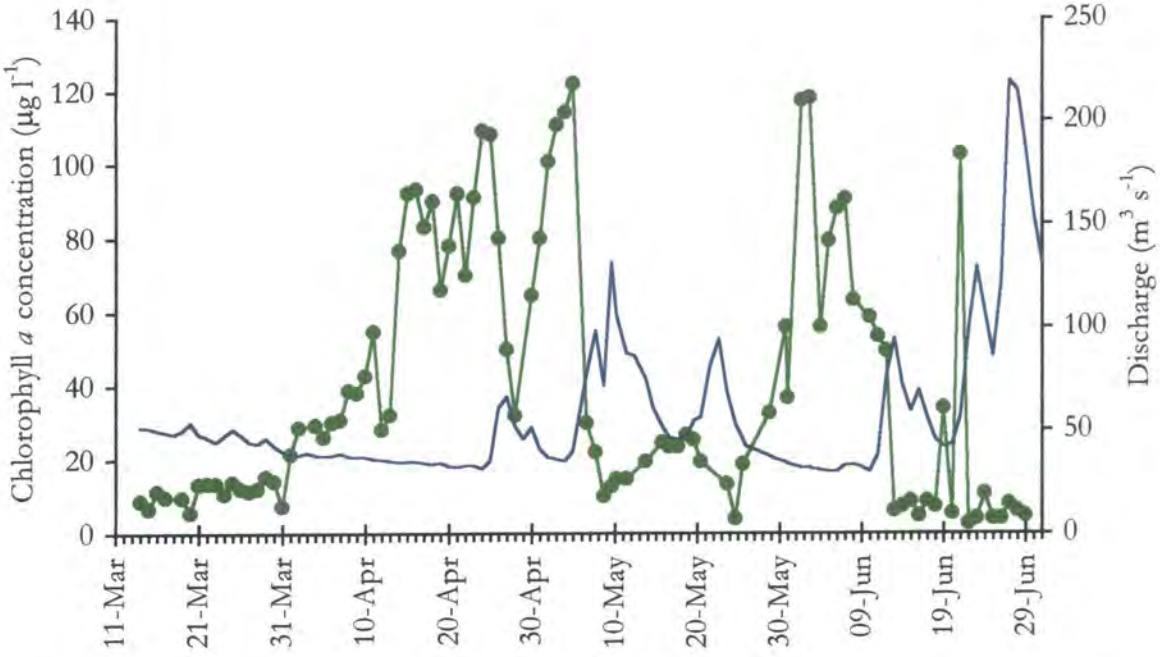

Figure 4.12 Day to day variation in chlorophyll *a* concentration (green line) and discharge (blue line) for the Trent at Cromwell. Samples were taken from 14 March to 29 June 1997.

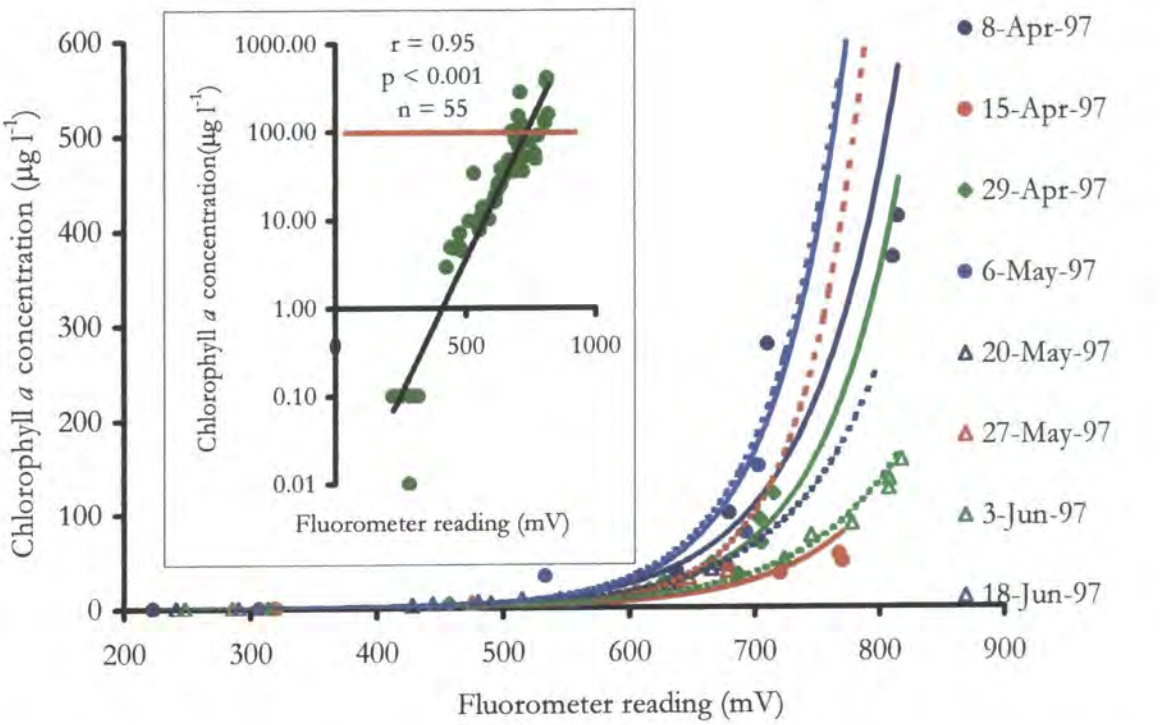

Figure 4.13 Calibration curves derived from fluorometer readings and calculated chlorophyll *a* concentration for *in situ* fluorometer deployed at the tidal limit of the Trent at Cromwell. r values ranged from 0.95 to 0.99. Inset shows line of best fit for all data. Red line shows maximum chlorophyll a concentration measured manually from April 1995 to August 1997.

During this event, chlorophyll *a* concentration remained low (< 11 $\mu g\ l^{-1}$) apart from two small peaks of 34 and 103 $\mu g\ l^{-1}$ on 19 and 21 June, respectively, when discharge fell to between 43 and 57 $m^3\ s^{-1}$.

4.26 Daily variation in chlorophyll *a* estimated from fluorometry

A fluorometer was deployed *in situ* and was calibrated on site during each sampling visit (Section 3.53). Figure 4.13 shows individual calibration curves with the inset showing all calibration points plotted together and the line of best fit. A significant relationship existed between chlorophyll *a* concentration and the mV reading given by the fluorometer, explaining 91% of the variation (Fig. 4.13, inset). However, individual calibrations were used to calculate chlorophyll *a* concentration as the equation calculated from the pooled data grossly overestimated the chlorophyll *a* concentration on many occasions. Figure 4.14 shows the output of the fluorometer during the period of deployment at the tidal limit of the Trent at Cromwell. Fluorometric determination of chlorophyll *a* showed a similar pattern of change and general magnitude to the day to day chlorophyll *a* with an increase in chlorophyll *a* concentration with decreasing discharge and with maximum concentrations interrupted by a series of five floods (Fig. 4.14). Data were not obtained between 12 May and 20 May 1997 (Fig. 4.14) as the large flood, starting 6 May 1997, damaged the fluorometer cable and readings were subsequently not logged.

The greater temporal resolution provided by the fluorometer revealed marked diel variation. The pattern of variation consisted of chlorophyll *a* minima during the early morning and maxima during the early evening. For example, on 23 April 1997, chlorophyll *a* concentration, estimated by the fluorometer, increased from a minimum of 63 $\mu g\ l^{-1}$ at 05:00 am to 100 $\mu g\ l^{-1}$ at 18:45 pm (Fig. 4.14).

Laboratory studies focused upon the fluorometric response of phytoplankton at different light intensities and incubated at different periods of time. Figure 4.15 shows the fluorometric response of *Cyclotella meneghiniana* and river water, both from the Trent after incubation at different intensities of light. The response of *C. meneghiniana* and the populations present in river water differed slightly. The fluorometric response of *C. meneghiniana* declined from the maximum response of 79.9 mv $(\mu g\ chl\ a)^{-1}$ at 19 $\mu mol\ m^{-2}s^{-1}$ until a minimum response of 56.8 mv $(\mu g\ chl\ a)^{-1}$ was measured at 1377 $\mu mol\ m^{-2}s^{-1}$ (Fig. 4.15a), the highest irradiance the cells were incubated at over the three hour experiment. The fluorometric response of natural populations incubated at five hours was similar to that of *C. meneghiniana.* There was a continual decrease from the maximum value of 26.4 mv $(\mu g\ chl\ a)^{-1}$ at 65 $\mu mol\ m^{-2}s^{-1}$ to the lowest value of 20.3 mv $(\mu g\ chl\ a)^{-1}$ at 643 $\mu mol\ m^{-2}s^{-1}$ (Fig. 4.15b).

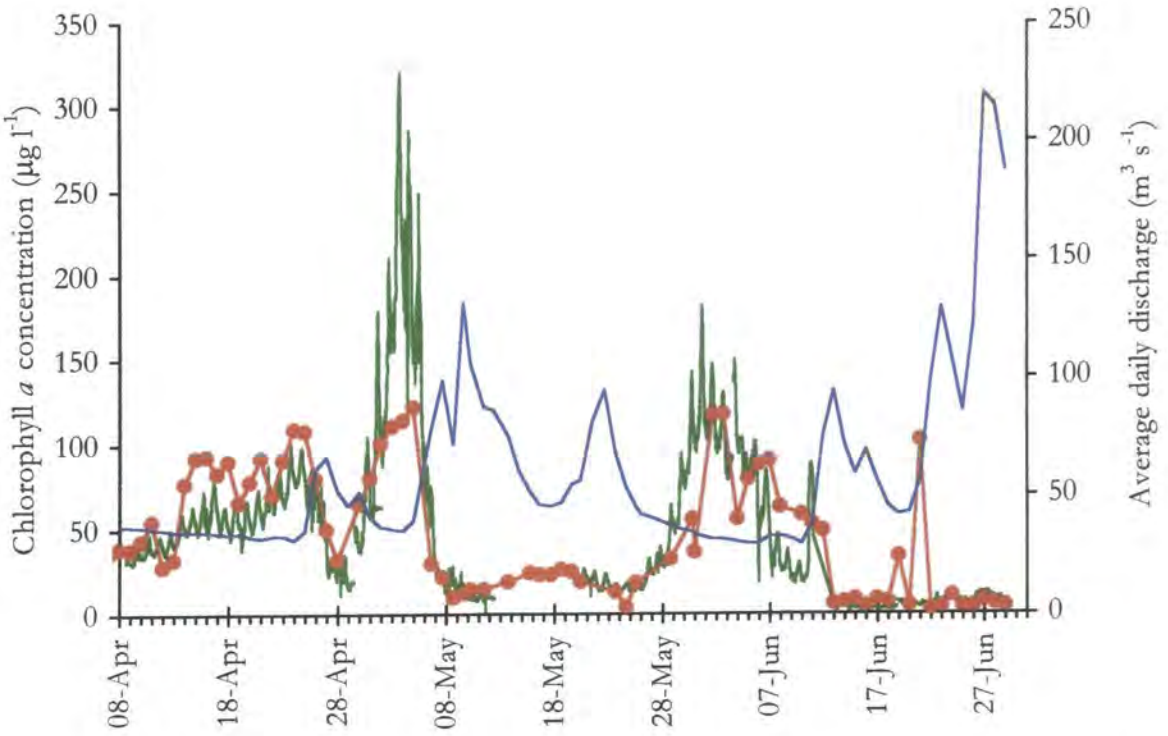

Figure 4.14 Fluorometer estimated chlorophyll *a* concentration (green line), daily chlorophyll *a* concentration (red line) and discharge (blue line) for the Trent at Cromwell from 8 April to 3 July 1997. Missing fluorometer estimated chlorophyll *a* data (12 May-21 May) are a result of a large flood event which damaged the fluorometer.

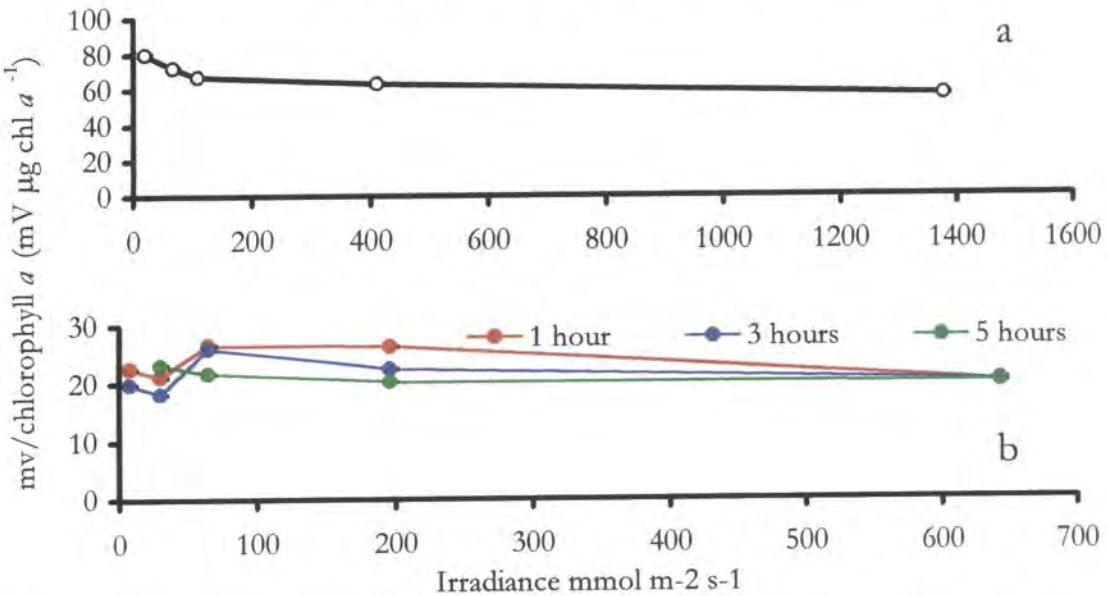

Figure 4.15 Fluorescence of *Cyclotella meneghiniana* in culture (top figure; a) and a river sample taken from the Trent at Cromwell on 14 August 1997 (bottom figure; b). *Cyclotella meneghiniana* was incubated for three hours and fluorescence readings taken. Samples taken from Cromwell were incubated for either one, three or five hours and readings then taken (see section 3.8). Fluorescence units (y-axis) are based on a chlorophyll *a* basis.

The fluorometric response of the natural population incubated at one and three hours differed slightly to the response of *C. meneghiniana* and natural populations incubated at five hours. The fluorometric response of natural populations incubated at one and three hours increased from 22.6 mv (μg chl *a*)$^{-1}$ at 8 μmol m^{-2}s^{-1} to 26.4 mv (μg chl *a*)$^{-1}$ at 65 μmol m^{-2}s^{-1} and from 19.8 mv (μg chl *a*)$^{-1}$ at 9 μmol m^{-2}s^{-1} to 26.0 mv (μg chl *a*)$^{-1}$ at 65 μmol m^{-2}s^{-1}, respectively (Fig. 4.15b). After 65 μmol m^{-2}s^{-1}, the fluorometric response decreased continually to 26.4 mv (μg chl *a*)$^{-1}$ at 196 μmol m^{-2}s^{-1} and then to 20.1 mv (μg chl *a*)$^{-1}$ at 643 μmol m^{-2}s^{-1} for populations incubated at one hour (Fig. 4.15b). For populations incubated for three hours, the fluorometric response declined to 22.5 mv (μg chl *a*)$^{-1}$ at 196 μmol m^{-2}s^{-1} and then 20.3 mv (μg chl *a*)$^{-1}$ at 643 μmol m^{-2}s^{-1} (Fig. 4.15b).

The overall response was a decrease in the fluorometric response at the three highest light levels with increasing incubation time. At the highest incubation irradiance, 643 μmol m^{-2}s^{-1}, the fluorometric response was very similar, around 20 mv (μg chl *a*)$^{-1}$ for populations incubated at one, three and five hours (Fig. 4.15b).

The laboratory studies suggest that the general fluorometric response of mixed natural populations decreased with an increase in irradiance and incubation time. However, when incubated for short periods of time, an optimum fluorometric response was observed at irradiances between 50 and 70 μmol m^{-2}s^{-1}. *In situ* fluorometric response of phytoplankton populations followed a daily pattern of early morning minima and early evening maxima. The day to day fluorometric response followed a similar pattern to daily estimated chlorophyll *a* measurements although fluorometry often overestimated chlorophyll *a* concentration. This suggests that chlorophyll *a* content of phytoplankon population was not the only factor influencing the fluorometric response of phytoplankton.

4.3 Discussion

A large amount of data have been collected concerning phytoplankton species, biomass and the periodicity of phytoplankton in the rivers of the Trent and Ouse system. The data show that species composition and overall phytoplankton biomass experienced large periodicity. High biomass, consisting primarily of centric diatoms was observed in spring and lower biomass, chiefly comprising green algae were observed in summer. Biomass minima were observed during winter when cell abundance was low. Both rivers showed similar patterns in periodicity although the pattern was more marked for the Trent.

Chlorophyll *a* was considered an adequate surrogate measure of biomass as a significant correlation existed between cell density and chlorophyll *a* concentration. However, a more significant correlation may have been obtained using a calculation of weight or biovolume instead of chlorophyll *a* concentration.

It was hypothesised that discharge was the controlling environmental variable influencing phytoplankton biomass in both rivers. Daily sampling in the Trent showed the importance that spring floods had upon the disruption of spring phytoplankton populations. Silica was also thought to influence phytoplankton development, primarily that of centric diatoms in the spring. However, this must be treated with caution as other factors may also be responsible.

Daily measurement of biomass using fluorometry offered positive and negative points. On the positive side, data of fine spatial resolution was obtained, showing the daily increase and decrease in phytoplankton biomass. The negative side was that although calibration of readings against chlorophyll *a* concentration were good, the results showed extremely high biomass maxima when compared with maxima compared with routine sampling. Laboratory investigations suggested that the influence of light interfered with the readings although the evidence was not conclusive.

Spatial variability was evident, particularly in the Trent where downstream increase in biomass was observed during spring. Cross channel variability occurred for sites on both the Trent and Ouse in summer. This suggested that the rivers were not homogeneous during periods of low discharge.

It is now useful to use this data when investigating phytoplankton and river productivity. The development of large populations have been proven in the Trent and Ouse, particularly at downstream sites. The next chapter investigates phytoplankton production and respiration at the tidal limits of these rivers in light of the previous data. The importance of the contribution of algal groups to river productivity and the effect of environmental variables upon the production and development of algal groups is the main theme considered.

4.4 Summary

1. Abundance of individuals increased as discharge decreased and reached maximal concentrations of 53000 and 62700 individuals ml^{-1} during spring for the Trent and Ouse, respectively. Abundance then declined during summer and declined further to winter minima during periods of high discharge.

2. A total of 85 taxa were recorded for the Trent and 82 taxa were recorded for the Ouse and at the tidal limits at Cromwell and Acaster, respectively. Chlorophyta comprised the majority these taxa.

3. In both the Trent and Ouse, centric diatoms comprised the majority of the phytoplankton population during spring, comprising a maximum of 83 and 85% of the population, respectively. Chlorophyta comprised the majority during the rest of the year, particularly during late summer, where they made up a maximum of 88 and 51% of the population for the Trent and Ouse, respectively. Other algal groups were generally unimportant.

4. A significant relationship existed between abundance of individuals and chlorophyll *a* concentration. At 2.8 pg chl *a* $individual^{-1}$, individuals at the tidal limit of the Trent at Cromwell contained twice the amount of chlorophyll *a* per cell than individuals at the tidal limit of the Ouse at Acaster.

5. As with phytoplankton abundance, chlorophyll *a* concentration showed a temporal pattern, reaching maximal concentrations of 162 and 166 $\mu g\ l^{-1}$ during spring in the Trent and Ouse, respectively. Concentrations declined in summer and declined further in winter to annual minima.

6. The tributaries Ure and Nidd were important as a source of chlorophyll *a* to the Ouse but tributaries were relatively unimportant for the Trent.

7. A significant relationship existed between discharge and chlorophyll *a* concentration although periods of low flow in summer exhibited lower concentrations than the relationship predicted. Daily sampling resulted in finer spatial resolution of data, which highlighted the impact of discharge upon chlorophyll *a*, particularly during spring.

8. Fluorometric data provided finer temporal resolution, showing a pattern of early morning minima and early evening maxima in chlorophyll *a* concentration. The difference between the daily maxima and minima was greatest during periods of high chlorophyll *a* concentration. A highly significant relationship between fluorometric readings and chlorophyll *a* existed, giving confidence to the fluorometric data. However, during the chlorophyll *a* maximum, fluorometry greatly overestimated chlorophyll *a* concentration when compared to manually collected data.

9. Laboratory studies indicated that although fluorometric response of phytoplankton sometimes reaches a maximum between 50 and 70 $\mu mol\ m^{-2}\ s^{-1}$, the general fluorometric response of phytoplankton decreased with increasing irradiance and increasing exposure time to higher irradiance. It was considered that factors, other than chlorophyll *a* concentration, also influenced the fluor9ometric response of phytoplankton.

5. PRODUCTION

5.1 Underwater light climate

5.11 Attenuation of photosynthetically active radiation (PAR)

5.111 Trent

Figure 5.1 shows the time series of light attenuation with depth (K_d) for three sites on the Trent: Cavendish Bridge, Gunthorpe and Cromwell. Essentially, the attenuation coefficient was similar in seasonal pattern and magnitude for the three sites studied with three major peaks in the K_d value occurring over the sampling period. Maximal K_d of 8.8, 8.9 and 9 m^{-1} on 12 February and 6.6, 4.9 and 5.0 m^{-1} on 20 November were recorded for Cavendish Bridge, Gunthorpe and Cromwell, respectively, during 1996 (Fig. 5.1). Maximal K_d of 2.4 and 2.6 m^{-1} on 6 May for Cavendish Bridge and Gunthorpe, respectively, and 5.4 m^{-1} on 2 June for Cromwell occurred during 1997 (Fig. 5.1). Measurements during the remaining period ranged from 1.4 to 2.4 m^{-1} at Cavendish Bridge, from 1.0 to 2.8 m^{-1} at Gunthorpe and between 0.9 and 2.9 m^{-1} at Cromwell.

Overall, a downstream pattern in K_d was observed with minimum K_d recorded decreasing and maximum values increasing with distance downstream. The two peaks in K_d for all three Trent sites during 1996 coincided with flood events. The discharge at Cromwell during the events on 12 February and 20 November 1996 was 159 and 82 $m^3 s^{-1}$, respectively (Fig. 5.1). During 1997, the K_d maxima on 6 May 1997 at Cavendish Bridge and Gunthorpe coincided with a flood event where the discharge was 96 $m^3 s^{-1}$ at Cromwell (Fig. 5.1). In contrast, during 1997, a peak in K_d at Cromwell coincided with a low flow event where discharge was 29 $m^3 s^{-1}$ on 2 June 1997 (Fig. 5.1). K_d minima were measured when discharge ranged from 26 to 56 $m^3 s^{-1}$ although there was no significant relationship between discharge and K_d. There was, however, a significant, positive relationship between K_d and chlorophyll *a* concentration for the three sites monitored on the Trent when K_d was below 4 m^{-1} ($r=0.66$, $P<0.001$, $n=96$; Fig. 5.3). This suggested that K_d was controlled primarily by phytoplankton density when values of K_d were low. The data where $K_d >$ 4 m^{-1}, which were not included in the relationship, coincided with high discharge events. Here, the attenuation coefficient was probably influenced primarily by non-algal suspended solids

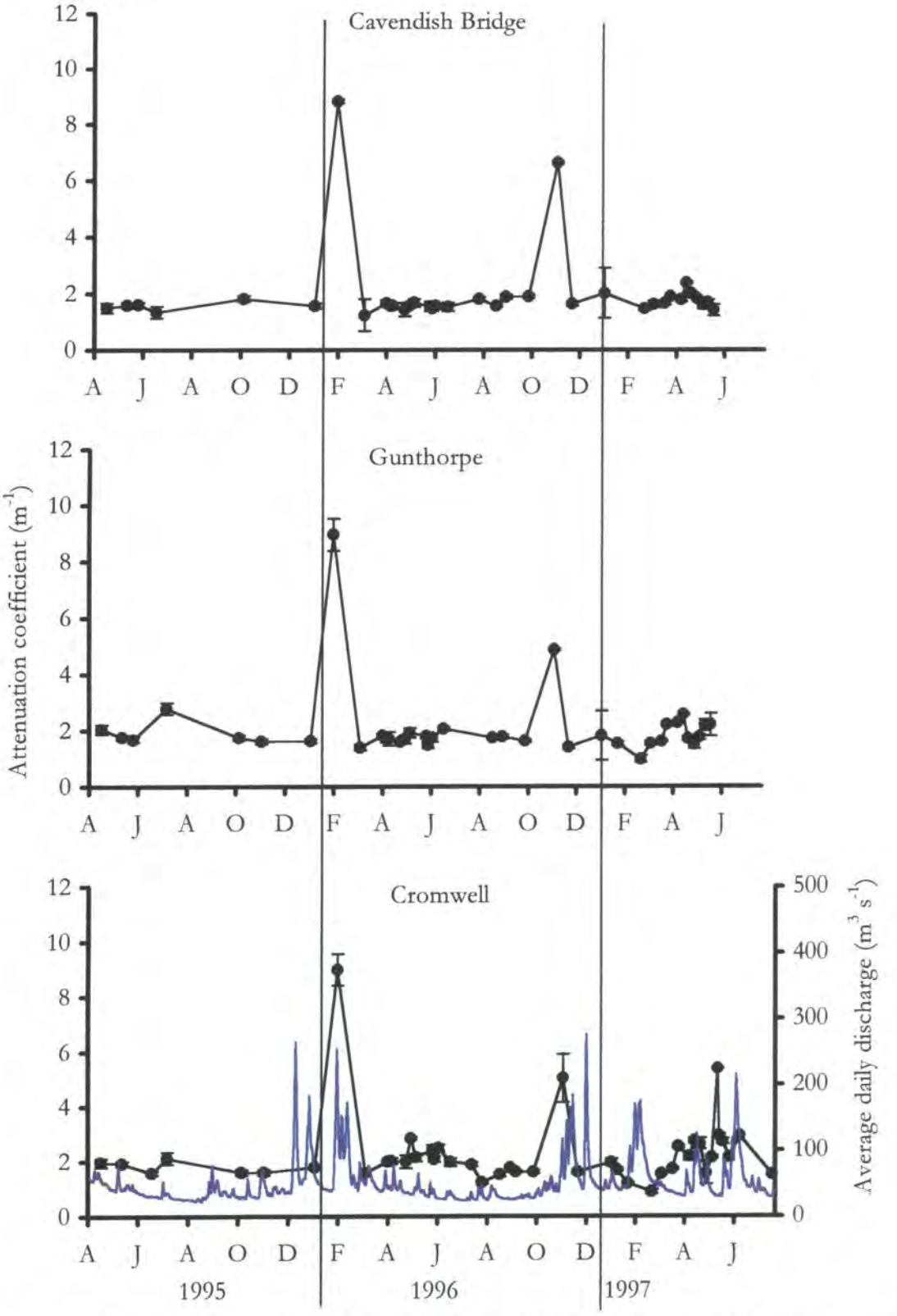

Figure 5.1 Time series of attenuation of photosynthetically active radiation (PAR, 400-700 nm) for three sites on the Trent. Sites are in ascending order of position down the river. Bars show standard deviation. Average daily discharge is shown for Cromwell.

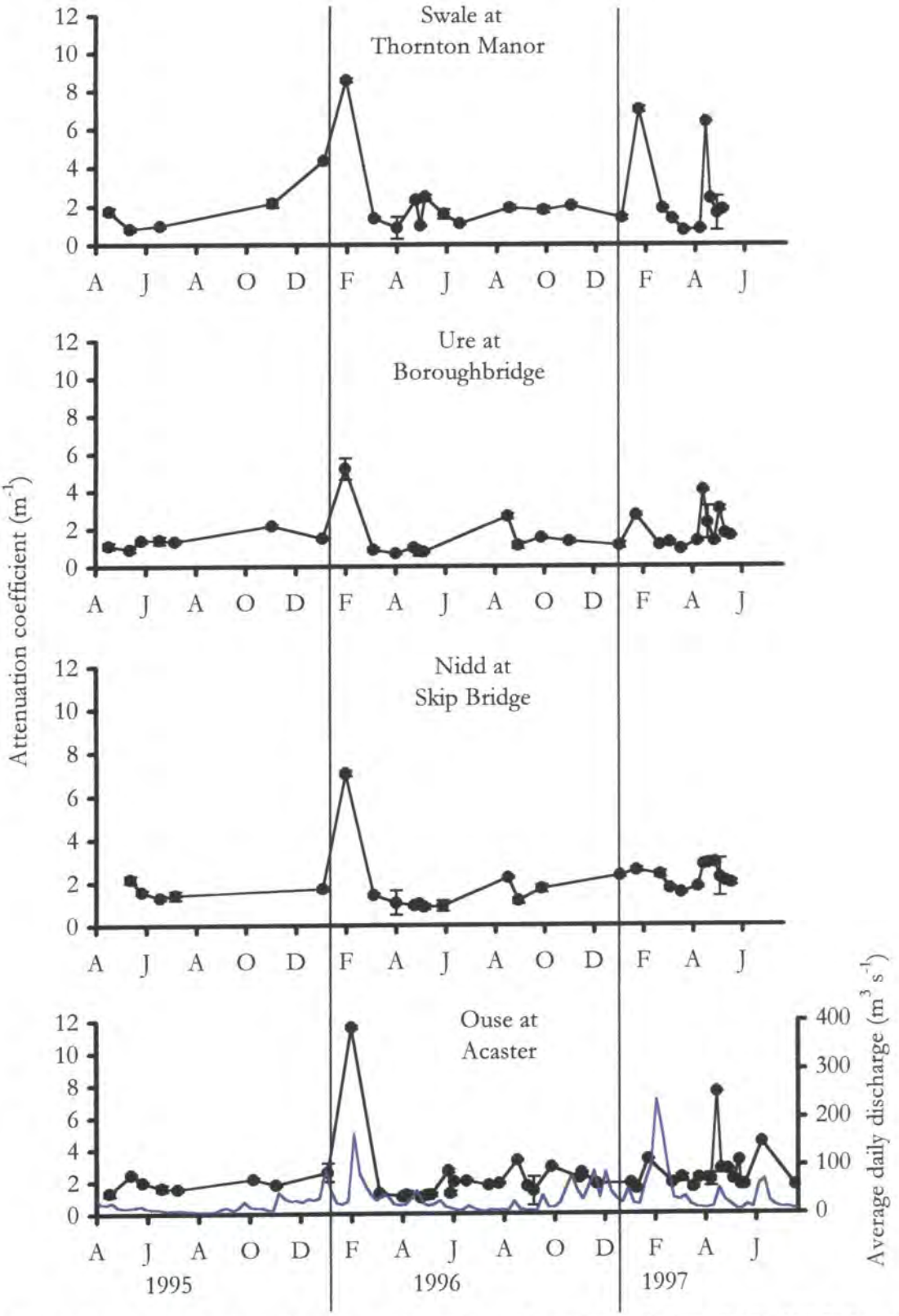

Figure 5.2 Time series of attenuation of photosynthetically active radiation (PAR, 400-700 nm) for four sites on the Ouse system. Charts are in ascending order of position downstream on the Ouse. Bars show standard deviation. Average daily discharge is shown for Acaster.

5.112 Ouse

Figure 5.2 shows the time series of the attenuation coefficient for four sites on the Ouse system; the Swale at Thornton Manor, Ure at Boroughbridge, Nidd at Skip Bridge and the Ouse at Acaster. For the Swale at Thornton Manor, three large peaks in K_d occurred. K_d maxima of 8.6, 7.0 and 6.4 m^{-1} were measured on 12 February 1996, 10 February 1997 and 5 May 1997, respectively (Fig. 5.2). Two major K_d peaks occurred for the other three sites. The flood event of 12 February coincided with the highest K_d measured over the sampling period with values of 5.2, 7.1 and 11.6 m^{-1} recorded for the Ure at Boroughbridge, Nidd at Skip Bridge and Ouse at Acaster, respectively (Fig. 5.2). The major peak in K_d during 1997 occurred during spring. At Boroughbridge on 6 May, at Skip Bridge on 20 May and at Acaster on 5 May 1997, K_d of 4.1, 2.9 and 7.6 m^{-1}, respectively were recorded (Fig. 5.2). K_d during the rest of the sampling period ranged from 0.7 to 4.4 m^{-1} at Thornton Manor, from 0.7 to 2.7 m^{-1} at Boroughbridge, from 0.9 to 2.6 m^{-1} at Skip Bridge and from 1.0 to 4.5 m^{-1} at Acaster (Fig. 5.2).

On the whole, the highest minimum and maximum K_d values were measured for the Ouse at Acaster. The highest minimum and maximum values for the tributaries to the Ouse were measured for the at Thornton Manor.

The K_d maxima for all four sites monitored on the Ouse system on 12 February 1996 coincided with a flood event where the discharge was 220 $m^3 s^{-1}$ at Acaster (Fig. 5.2). On this occasion, the highest K_d were recorded for each site. Other high K_d coincided with flood events where the discharge at Acaster was 80 and 90 $m^3 s^{-1}$ (Fig 5.2). The K_d maxima at Skip Bridge during 1997 coincided with a relatively low discharge event at Acaster of 22 $m^3 s^{-1}$ (Fig 5.2). This may be explained by the discharge from the Nidd coming from a different catchment area than from the Swale and Ure. As the Swale and Ure are the main tributaries to the Ouse it is expected that the pattern of discharge is similar whereas the pattern of the Nidd is different. Minima in K_d all coincided with relatively low discharge events, between 9 and 49 $m^3 s^{-1}$ (Fig 5.2) although there was no significant relationship between K_d and discharge. No significant relationship was observed between K_d and chlorophyll *a* concentration. This suggested that attenuation of light in the Ouse system was controlled primarily by non-phytoplanktonic constituents of the rivers, for example, dissolved and suspended organic materials.

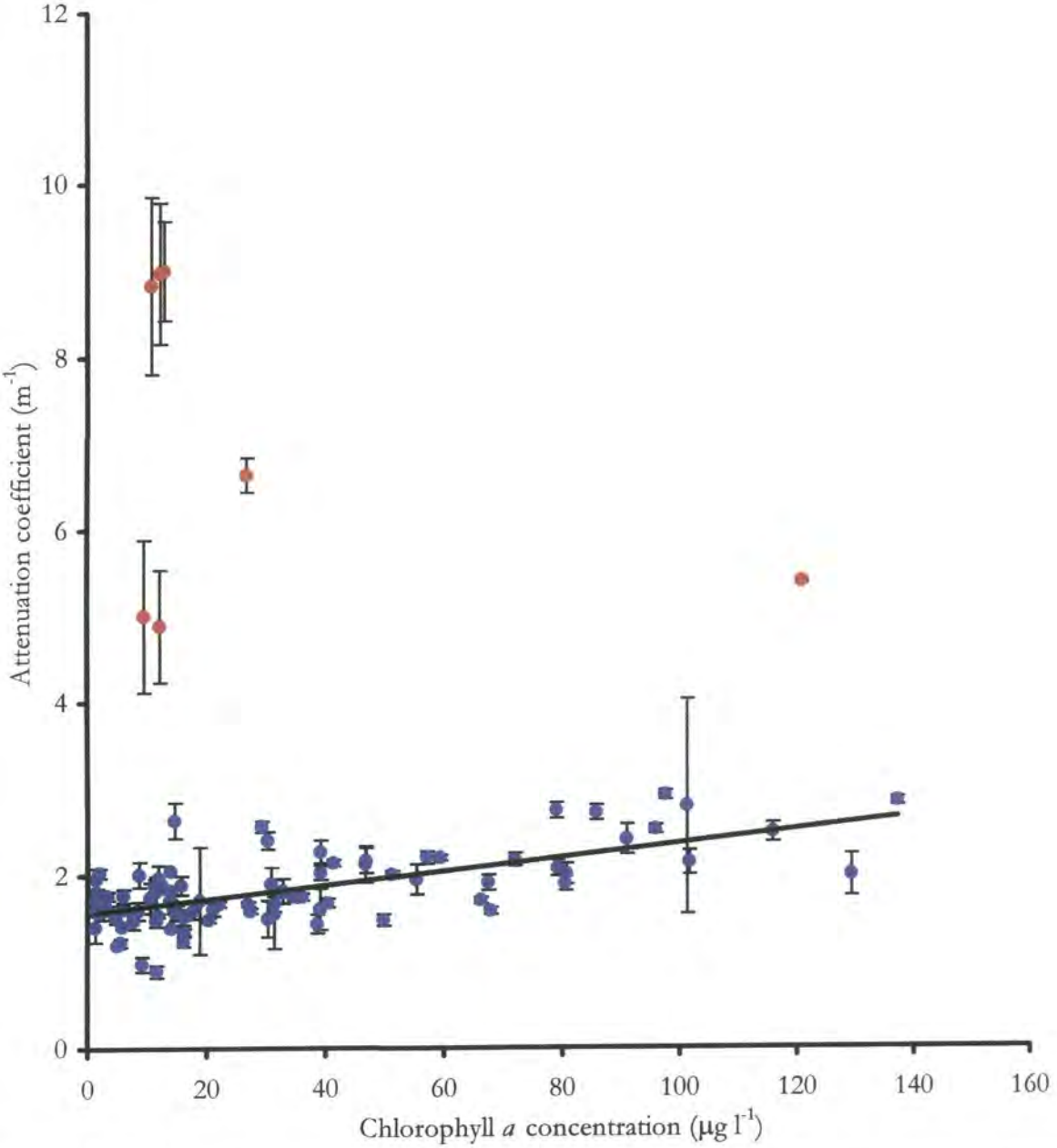

Figure 5.3 Relationship between attenuation coefficient and chlorophyll *a* concentration (blue circles) for the combined data from three sites on the Trent; Cavendish Bridge, Gunthorpe and Cromwell. A significant, positive relationship existed when the attenuation coefficient was below 4.0 m^{-1} ($r=0.66$, $P<0.001$, $n=96$). Data where $K_d>4.0$ m^{-1} were omitted from the analysis (red circles). Bars show standard deviationof K_d.

5.12 Spectroradiometric measurement of the underwater light climate

5.121 Trent

The pattern of attenuation of light from 300 to 700 nm showed a similar pattern for the three dates when measurements were taken with high K_d values in the blue spectrum and low K_d values in the red spectrum. This indicated that short wavelength radiation including UV-B (280-320 nm), UV-A (320-400 nm) and visible blue bands were much more rapidly attenuated than longer wavelength bands such as red light in these rivers. Overall, at Cromwell, attenuation over the range of wavelengths was greatest on 5 June, intermediate on 29 April and least on 11 February 1997.

On 11 February 1997, the maximum K_d value was 12.31 m^{-1} at 335 nm (Fig. 5.4). On 29 April, attenuation reading started at 315 nm and the maximum K_d value was 20.05 m^{-1} at 335 nm (Fig. 5.4). On 5 June 1997, maximum K_d was 15.41 m^{-1} where the K_d values began at 330 nm (Fig. 5.4). A seasonal increase in attenuation can be seen between 650 and 700 nm. Maximal K_d values of 1.04, 2.32 and 3.67 m^{-1} occurred on 11 February, 29 April and 5 June 1997, respectively, at 675 nm when chlorophyll *a* concentration was 5, 47 and 15 $\mu g\ l^{-1}$, respectively (Fig. 5.4, inset). A positive correlation ($r=0.97$, $P<0.01$, $n=6$) was observed between chlorophyll *a* concentration and attenuation coefficient at 675 nm for the Trent (Fig. 5.5).

Maximum K_d values at 675 during a chlorophyll *a* maximum and coinciding with low discharge events suggest that the attenuation of light in the red section of the spectrum was primarily controlled by phytoplankton density.

5.122 Ouse

The pattern of attenuation of light from 300 to 700 nm showed a similar pattern for the three dates measurements were taken with maximal K_d values in the blue spectrum and minimum K_d values in the red spectrum. K_d values in the blue section of the spectrum showed high seasonal variation.

At Acaster, attenuation over the range of wavelengths was greatest on 11 February 1997. From 310 to 465 nm, the attenuation was next highest on 5 June 1997 and lowest on 29 April 1997 (Fig. 5.4). For wavelengths greater than 465 nm, the pattern changed and K_d values were at a minimum for the three dates sampled on 5 June 1997 (Fig. 5.4).

On 11 February 1997, the maximum K_d value was 26.52 m^{-1} at 335 nm. On 29 April, a maximum K_d value of 15.09 m^{-1} was observed at 310 nm and a maximum K_d of 19.86 m^{-1} at 315 nm (Fig. 5.4). A seasonal change in attenuation can be seen for the 650 to 700 nm band (Fig 5.4, inset).

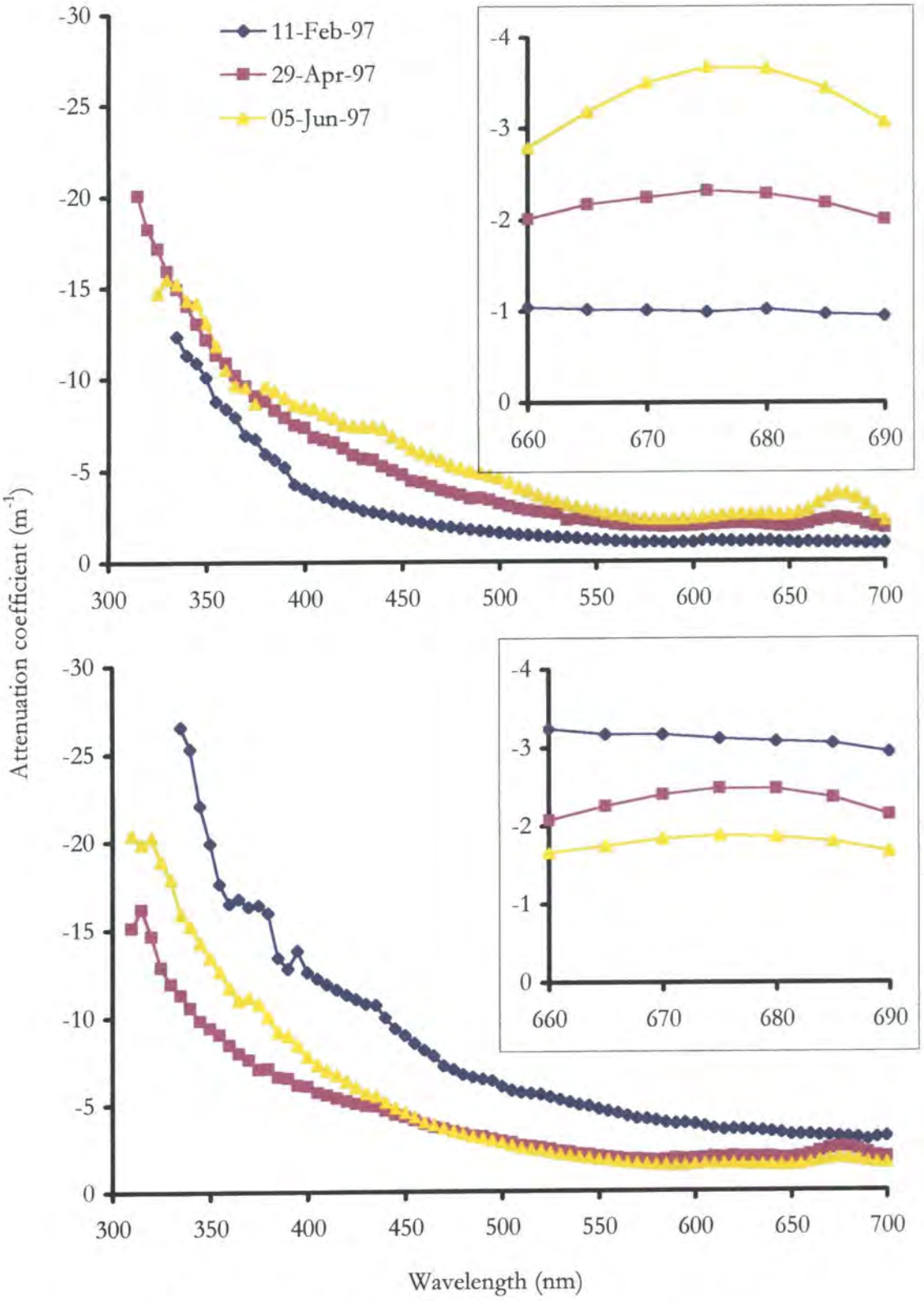

Figure 5.4 Spectroradiometric data for the tidal limits of the Trent at Cromwell (top figure) and Ouse at Acaster (bottom figure). Readings were taken over the range 300 - 700 nm on three occasions; 11 February, 29 April and 5 June 1997 (see section 3.3). Inset shows a section of the data from 660 - 690 nm.

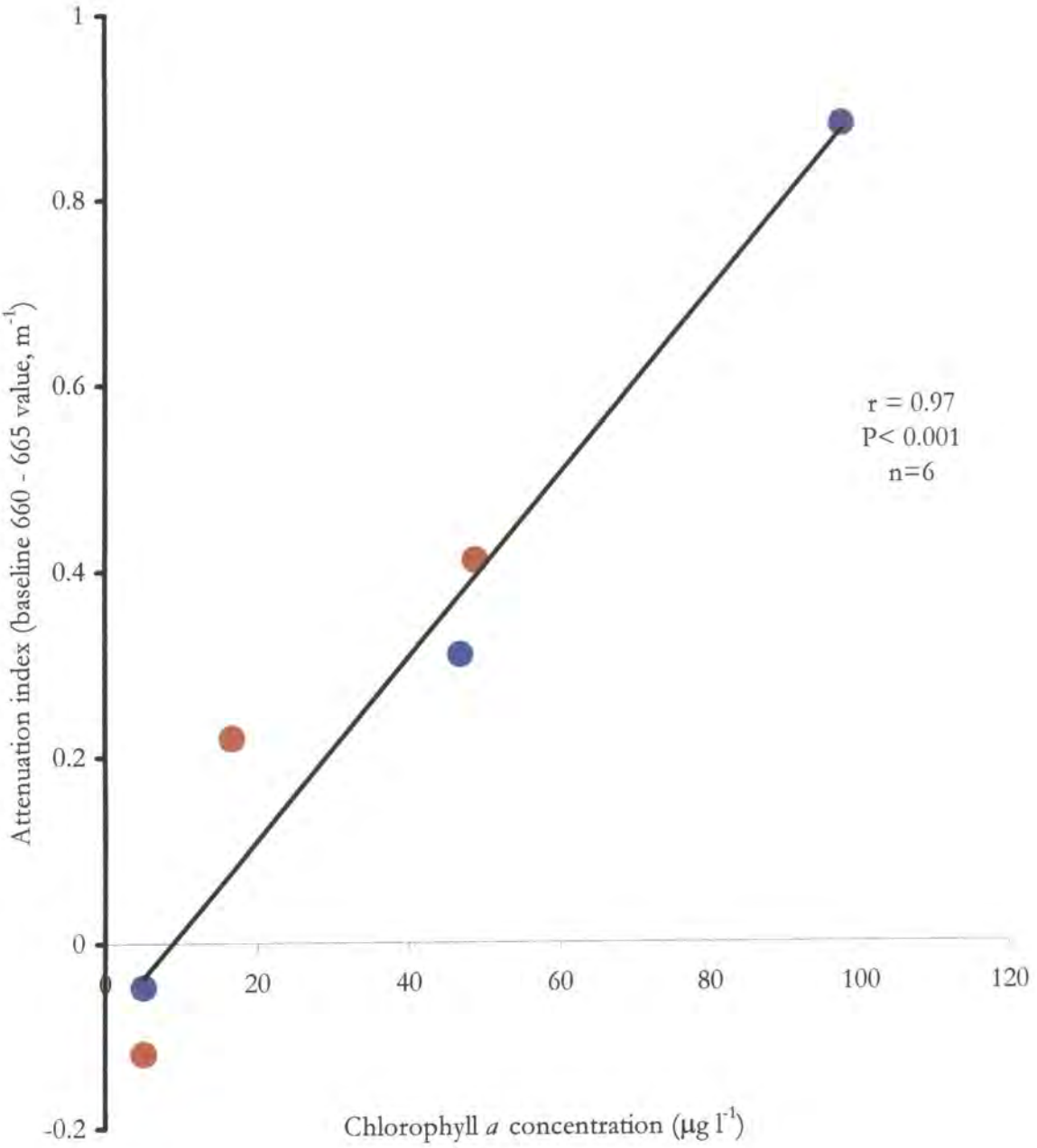

Figure 5.5 Relationship between attenuation coefficient and chlorophyll *a* concentration using spectroradiometric data shown in Fig. 5.4 for the Trent (red) and Ouse (blue). The attenuation index was calculated from the difference in attenuation between the readings at 660 and 675 nm.

A maximum K_d value of 3.24 m^{-1} was measured at 660 nm on 11 February 1997 (Fig. 5.4). On 29 April and 5 June 1997, however, maximal K_d values of 2.49 and 1.88 m^{-1} were measured at 675 nm (Fig 5.4, inset). Attenuation over 300 to 700 nm increased with increasing discharge and there was a positive correlation between K_d and chlorophyll *a* over the 650 to 700 nm band (Fig. 5.5). On 11 February 1997, the maximum K_d value over the full spectrum coincided with the lowest concentration of chlorophyll *a* and the highest discharge over the three dates sampled at 5 $\mu g\ l^{-1}$ and 115 $m^3\ s^{-1}$, respectively. The lowest K_d values over the spectra coincided with the lowest discharge and the highest chlorophyll concentration over the three dates sampled of 26 $m^3\ s^{-1}$ and 49 $\mu g\ l^{-1}$, respectively.

Maximum K_d values during high discharge events suggests that the attenuation of light in the Ouse was controlled by non-phytoplankton sources, assuming that an increase in discharge would result in an increase in non-phytoplankton suspended solids and dissolved, coloured substances. The maximum K_d values at 675 on 29 April 1997 suggests that phytoplankton strongly influenced attenuation of light in the 650 to 700 nm band.

Overall, for the Ouse at Acaster, there was no evidence of phytoplankton density as a controlling factor influencing the attenuation of light. Non-phytoplankton suspended solids appeared to be the primary variables. The magnitude of the variation between K_d values in the blue section of the spectrum (Fig. 5.4) suggests that dissolved substances, particularly humic and fulvic acids, also played an important role in light attenuation in the Ouse.

5.2 The photosynthetic response of phytoplankton to irradiance (P vs I)

5.21 Trent

The photosynthetic response of phytoplankton was investigated for the tidal limits of the Trent and Ouse at Cromwell and Acaster, respectively. River water was incubated in a water bath, in the laboratory, at between six and seven light levels, including incubation in the dark to measure respiration. Net exchange of O_2 was measured using the Winkler technique and the photosynthetic response of the phytoplankton to light was modelled according to Platt *et al.* (1980; Section 3.6). Table 5.1 shows the curve parameters derived from P vs I incubations. The temporal change in these parameters is shown as a time series in Figure 5.6. P Vs I curves are shown in Appendix 2).

The rate of P_{max} (net) followed a similar seasonal pattern in 1996 and 1997 with highest rates observed during spring and early summer, coinciding with chlorophyll *a* maxima (Fig. 5.6, Table 5.1). Spring and summer maxima were followed by a decline in late summer and a decline to minimum rates in winter (Fig. 5.6, Table 5.1).

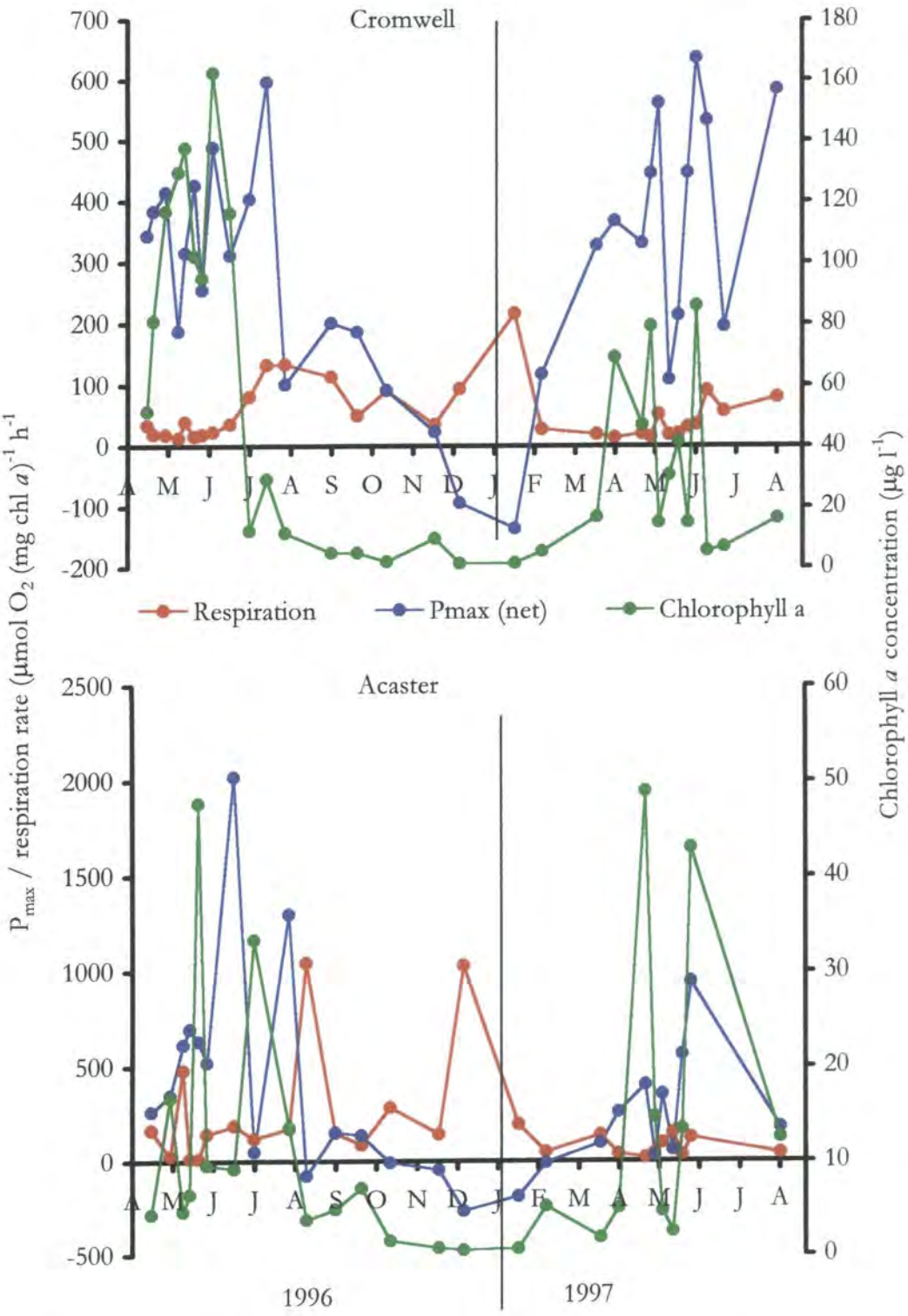

Figure 5.6 Temporal change in P_{max}(net), respiration rate and chlorophyll *a* concentration for the tidal limits of the Trent (top figure) and Ouse (bottom figure). Data are derivec from Tables 5.1 and 5.3 from April 1996 to August 1997.

Table 5.1 Curve parameters calculated from P vs I incubations for the Trent at Cromwell. As a result of slow rates of oxygen exchange relative to the sensitivity limits of the method of measurement, data for 10 December 1996 were not fitted to the model of Platt *et al.* (1980) and so values for P_{max} and R were interpolated manually. See list of abbreviations for column headings.

Date	P_s	P_{max}	R	α	β	I_k	I_b	I_m
16-Apr-96	457	342	34	4.31	0.21	95	2227	328
21-Apr-96	486	383	20	2.66	0.12	159	3987	571
30-Apr-96	721	414	18	3.35	0.62	135	1172	401
10-May-96	381715	188	13	1.36	953.03	157	401	400
15-May-96	423	314	40	3.40	0.15	116	2906	397
22-May-96	818	426	16	2.57	0.63	178	1305	519
28-May-96	430	254	19	1.87	0.29	156	1483	461
05-Jun-96	797	488	23	3.06	0.46	174	1733	530
18-Jun-96	498	311	35	2.04	0.23	187	2183	561
03-Jul-96	546	403	80	5.15	0.14	109	4015	388
16-Jul-96	1253	597	133	3.51	0.70	246	1787	640
30-Jul-96	699	101	134	3.59	2.28	103	307	184
03-Sep-96	589	201	114	3.01	0.76	142	779	314
23-Sep-96	2415	187	49	2.35	7.71	121	313	274
15-Oct-96	113632	91	90	2.05	470.34	133	242	241
21-Nov-96	62771	23	34	0.99	397.58	93	158	158
10-Dec-96	-	-94	71	-	-	-	-	-
21-Jan-97	-40716	-136	217	2.82	-525.80	105	77	78
11-Feb-97	184	118	27	3.96	0.24	44	759	132
25-Mar-97	468	327	19	3.82	0.33	96	1430	311
08-Apr-97	458	368	14	2.86	0.13	138	3645	507
29-Apr-97	440	331	20	3.39	0.20	110	2223	376
06-May-97	632	446	15	3.02	0.28	158	2283	519
12-May-97	187982	561	52	3.13	351.48	212	535	532
20-May-97	265214	109	18	0.74	563.37	198	471	470
27-May-97	279	214	21	2.28	0.09	112	2980	396
03-Jun-97	26570	447	31	1.90	37.96	267	700	683
10-Jun-97	1465	637	35	2.26	0.80	313	1826	869
18-Jun-97	5094	533	91	2.41	6.08	296	837	705
01-Jul-97	373	196	57	1.88	0.23	165	1610	438
11-Aug-97	265215	584	79	3.07	450.99	241	588	586

Spring and late summer maximum rates of P_{max} (net) of 597and 637 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1} were measured on 16 July 1996 and 9 June 1997, respectively (Fig. 5.6, Table 5.1). These rates declined during summer to around 100 to 200 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1} and declined to minimum rates during winter where a minimum of –136 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1} was measured on 21 January 1997 (Fig. 5.6, Table 5.1).

Occasionally, negative rates of P_{max} (net) and P_s were measured (Fig. 5.6, Table 5.1). These negative rates showed that no positive production was achieved on these occasions. This may have been the result of very high respiration rates compared to production rates, even when light was not limiting. High bacterial biomass may have been present, resulting in high rates of respiration. Alternatively, photochemical oxidation may be partly responsible where negative production increases as irradiance increases.

Respiration rate also followed a similar seasonal pattern during 1996 and 1997 (Fig. 5.6, Table 5.1). Low respiration rates were measured during spring, which increased rapidly during summer. This increase coincided with the decline of the chlorophyll *a* maxima (Fig. 5.6, Table 5.1). Rates decreased again during winter although sporadic increases were observed (Fig. 5.6, Table 5.1). During 1996, a minimum respiration rate of 13 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1} was measured during spring on 10 May (Fig. 5.6, Table 5.1). During 1997, apart from a high respiration rate in winter of 217 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1} measured on 21 January, a maximum rate of 134 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1} was measured during spring on 30 July 1997 (Fig. 5.6, Table 5.1). A minimum rate of 14 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1} was measured during early spring on 6 May 1997 (Fig. 5.6, Table 5.1).

Overall, maximal rates of P_{max} (net) were measured during spring and early summer and minimum rates were measured during winter. In contrast, maximum rates of respiration were measured during summer and minimum rates were measured during spring although high rates were also measured during winter.

The initial slope of the P vs I curve (α) did not follow any clear seasonal pattern. A maximal value of α of 5.15 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1} (μmol photon m^{-2} s^{-1})$^{-1}$ was measured on 3 June 1996 and a minimum value of 0.74 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1} (μmol photon m^{-2} s^{-1})$^{-1}$ was measured on 20 May 1997 (Table 5.1). During 1997, the maximum value of α of 3.96 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1} (μmol photon m^{-2} s^{-1})$^{-1}$ was measured in winter on 11 February although values remained high throughout spring (Table 5.1).

The photoinhibition factor (β) also did not follow any clear seasonal pattern. Values ranged from very low (0.09 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1} (μmol photon m^{-2} s^{-1})$^{-1}$) to very high (563 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1} (μmol photon m^{-2} s^{-1})$^{-1}$, Table 5.1). Although values of β are shown in Table 5.1, the weighted photoinhibition factor (I_b) was used as a clearer representation of photoinhibition

(Fig. 5.7, Table 5.1) with a small value of I_b indicative of strong photoinhibition. I_b, I_k and the irradiance at which the rate of photosynthesis was maximum (I_m) followed a similar seasonal pattern to P_{max} (net) with maximal values occurring during spring and summer and minimum values in winter (Fig. 5.7, Table 5.1). A maximal value of I_b of 4015 μmol m^{-2} s^{-1} was observed on 3 July 1996 while maximal values of I_k and I_m of 246 and 641 μmol m^{-2} s^{-1}, respectively occurred on 16 July 1996 (Fig. 5.7, Table 5.1). Values of I_b, I_k and I_m declined to winter minima of 77, 44 and 78 μmol m^{-2} s^{-1}, respectively on 21 January 1997, 11 February 1997 and 21 January 1997, respectively (Fig. 5.8, Table 5.1). During the spring of 1997, values of I_b, I_k and I_m increased. A maximal 1997 value of I_b of 3645 μmol m^{-2} s^{-1} occurred on 8 April 1997 (Fig. 5.7, Table 5.1). Maximal values of I_k and I_m of 313 and 868 μmol m^{-2} s^{-1}, respectively, were recorded on 10 June 1997 (Fig. 5.7, Table 5.1).

The overall seasonal pattern of I_b suggests that photoinhibition was weakest during spring and summer and strongest during winter. The pattern of I_k suggests that the phytoplankton utilised the light more efficiently during winter and the onset of light saturation occurred at higher irradiances during spring and summer where the rate of photosynthesis was at a maximum.

The pattern of response of some P vs I parameters to environmental variables appear to differ depending on the species composition of the phytoplankton. To test whether or not any differences were statistically significant linear regressions were calculated for the photosynthetic parameters and environmental variables using all the data and separately for times when the phytoplankton population was dominated by either centric diatoms or green algae. A variance ratio-test (F-test) was performed to determine whether the two separate regressions gave a significantly better fit than a single fit to all the data (Mead & Curnow, 1983).

P_{max} (net), respiration rate, I_k and I_m showed a significant relationship with temperature. P_{max} (net) increased with increasing temperature for the whole of the phytoplankton population ($r=0.61$, $P<0.001$; Table 5.2). There was a significant difference between the relationship between P_{max} (net) and temperature for the whole phytoplankton population and between P_{max} (net) and temperature for the times when the population was centric or greens dominated (F-test, $P=0.02$, $f=4.6$). A stronger relationship was observed between P_{max} (net) and temperature when data were categorised into occasions when either centric diatoms ($r=0.42$, $P<0.1$) or greens ($r=0.72$, $P<0.01$) dominated the phytoplankton population (Table 5.2).

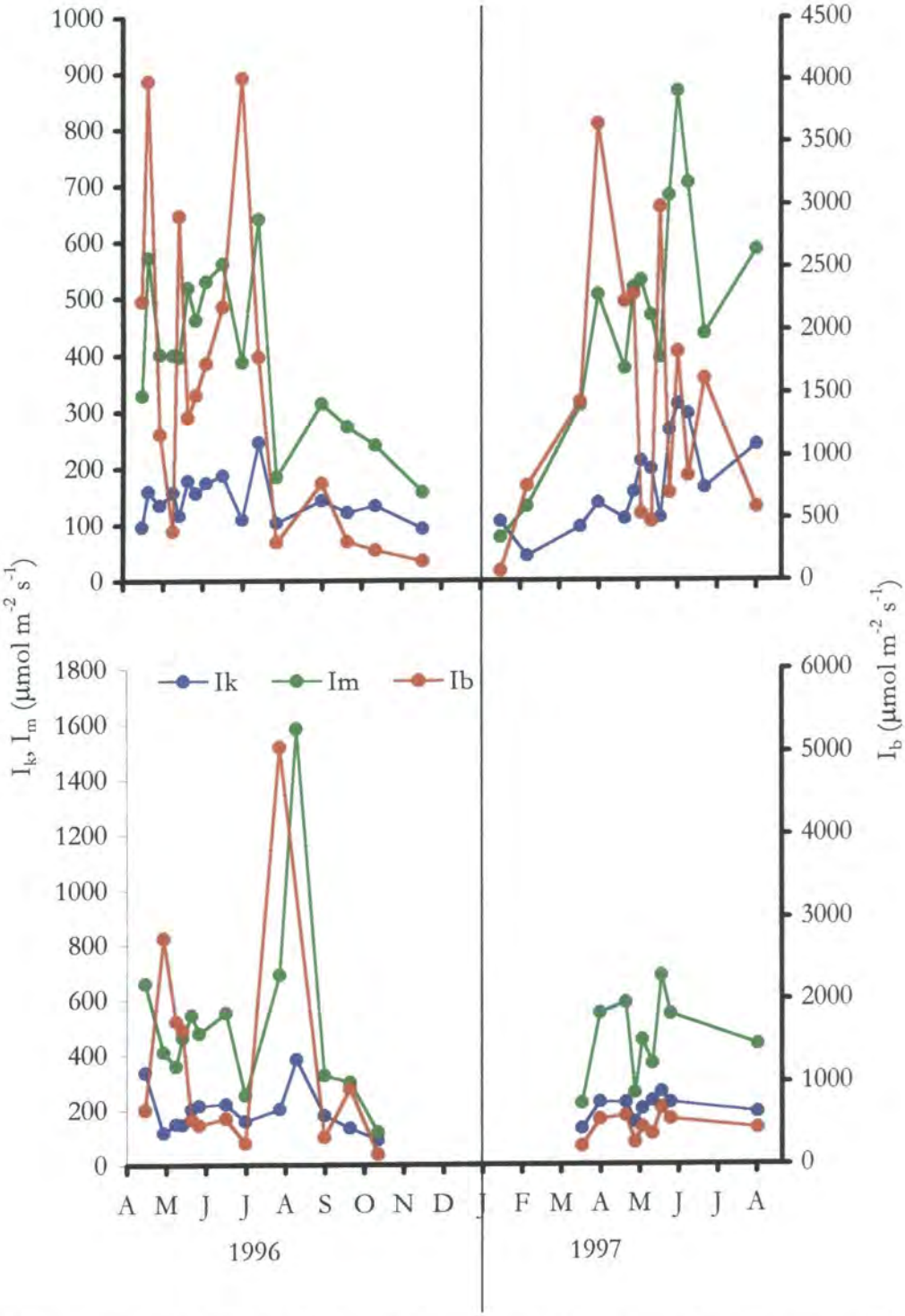

Figure 5.7 Temporal change in I_k, I_m and I_b (see list of abbreviations for descriptors) for the tidal limits of the Trent (top figure) and Ouse (bottom figure). Data are derived from Tables 5.1 and 5.3. Data were not available for 10 December 1996 for the Trent or between 21 November 1996 and 11 February 1997 for the Ouse.

Table 5.2 Coefficients for the correlation between P vs I parameters and environmental variables for the Trent at Cromwell. See list of abbreviations for column headings. Data are shown for the whole population (A), and when populations were dominated by centric diatoms (B) and green algae (C). Shaded sections highlight significant correlations (not significant, ns; P<0.05, *; P<0.01, **; P<0.001, ***).

A		P_{max}(net)	R	α	β	I_k	I_b	I_m
Temperature	r	0.47	0.47	0.13	-0.16	0.56	0.07	0.63
	P	**	**	ns	ns	**	ns	***
	n	29	29	29	29	29	29	29
K_d	r	0.04	-0.18	-0.34	0.00	0.22	-0.09	0.19
	P	ns	ns	ns	ns	ns	ns	ns
	n	29	29	29	29	29	29	29
Irradiance	r	0.47	0.37	0.17	-0.16	0.51	0.14	0.56
	P	**	*	ns	ns	**	ns	**
	n	29	29	29	29	29	29	29

B		P_{max}(net)	R	α	β	I_k	I_b	I_m
Temperature	r	0.52	0.48	-0.35	-0.30	0.72	0.02	0.83
	P	*	*	ns	ns	***	ns	***
	n	18	18	18	18	18	18	18
K_d	r	0.24	-0.04	-0.34	-0.06	0.57	-0.29	0.47
	P	ns	ns	ns	ns	*	ns	*
	n	18	18	18	18	18	18	18
Irradiance	r	0:17	0.33	-0.51	-0.03	0.46	-0.26	0.47
	P	ns	ns	*	ns	ns	ns	*
	n	18	18	18	18	18	18	18

C		P_{max}(net)	R	α	β	I_k	I_b	I_m
Temperature	r	0.54	0.59	0.40	-0.02	0.53	0.15	0.58
	P	ns	ns	ns	ns	ns	ns	ns
	n	11	11	11	11	11	11	11
K_d	r	-0.28	-0.17	-0.37	0.16	-0.24	-0.05	-0.19
	P	ns	ns	ns	ns	ns	ns	ns
	n	11	11	11	11	11	11	11
Irradiance	r	0.66	0.58	0.50	-0.25	0.55	0.41	0.65
	P	*	ns	ns	ns	ns	ns	*
	n	11	11	11	11	11	11	11

The relationship between respiration rate, I_k and I_m and temperature showed a significantly weaker relationship when expressed for the whole population than when expressed as occasions when the population was dominated by centrics or greens. A stronger relationship was observed when data were categorised into centric and greens dominance between respiration rate and

temperature (F-test; P=0.003, P=2.9), I_k and temperature (F-test; P=0.01, f=5.2) and I_m and temperature (F-test; P=0.03, P=7.5).

A significant, positive relationship existed between respiration rate and temperature for the centric diatom dominated population (r=0.87, P<0.001; Table 5.2) and during greens dominance (r=0.71, P<0.02; Table 5.2). Although the relationship was stronger between respiration rate and temperature during centric diatom dominance, higher rates were evident when greens were dominant (Fig. 5.6). This suggests that respiration by greens was more responsive than centric diatoms to temperature.

A significant, positive relationship was observed between I_k and temperature and I_m and temperature. This was a direct consequence of increasing P_{max}(net) with temperature as P_{max}(net) is used to calculate both I_k and I_m.

Overall, rates of photosynthesis and respiration increased with increasing temperature. Populations dominated by centric diatoms or greens showed similar rates of P_{max} (net) but higher respiration rates with increasing temperature were observed for greens dominated populations. There was no significant relationship between the α, β, I_b and temperature during the period of study.

A significant, positive relationship was observed between α and K_d, and between I_k, I_m, I_b and irradiance. The value of α increased with an increase in K_d (r=0.37, P<0.05; Table 5.2) for the phytoplankton population as a whole. This may indicate that cells may be adapting to the light climate. As the K_d value increased, indicating a decrease in light penetration, the cells may have utilised light more efficiently, as indicated by an increase in α.

P_{max}(net) increased with increasing average daily irradiance (r=0.63, P<0.001; Table 5.2) for the population as a whole. Even so, a stronger relationship existed between P_{max}(net) and irradiance when data were categorised into events dominated by either centric diatoms or green algae (F-test; P=0.02, f=4.7). There was no significant relationship between and P_{max}(net) and irradiance for centric dominated populations. For populations dominated by green algae, however, P_{max}(net) increased significantly with increasing irradiance (r=0.79, P<0.05; Table 5.2). This suggests that irradiance had a marked effect upon photosynthesis of green algae but other factors were more important in regulating photosynthesis of centric diatoms.

As with the relationship between I_k and I_m and temperature, the positive relationship observed between I_b, I_m and irradiance for populations dominated by green algae was a direct consequence of an increase in P_{max}(net) with irradiance.

A positive relation existed between I_b and irradiance for populations dominated by green algae (r=0.58, P<0.05; Table 5.2) but not for populations dominated by centric diatoms. As a high value of I_b is indicative of weak photoinhibition, this relationship suggests that green algae exposed

to a high light climate were less susceptible to photoinhibition than those exposed to a low light climate

Overall, the irradiance at which maximal P_{max}(net) was achieved increased with increasing irradiance. Green algal dominated populations appeared to be more responsive to the increase in irradiance than centric dominated populations.

5.22 Ouse

Table 5.3 shows the curve parameters derived from data obtained from P vs I incubations (Section 3.6). P vs I curves are shown in Appendix 2. The temporal change in the P vs I parameters is shown in Figure 5.6. The rate of P_{max} (net) followed a similar seasonal pattern in 1996 and 1997. Maximum rates of P_{max} (net) were observed during spring and early summer although these maxima did not coincide with chlorophyll *a* maxima (Fig. 5.6, Table 5.3). Spring and summer maxima were followed by late summer decline and winter minima (Fig. 5.6, Table 5.3). Spring/late summer maximum rates of P_{max} (net) of 2019 and 945 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1} were measured on 16 July 1996 and 2 June 1997, (Fig. 5.6, Table 5.3). These rates were perhaps unrealistically high and outside the range given by Kirk (1994). Rates declined during late summer to around 150 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1} and declined to minimum rates during winter where a minimum of –268 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1} was measured on 21 January 1997 (Fig. 5.6, Table 5.3).

Respiration rates did not follow any clear seasonal pattern during 1996 and 1997 although minimum values were recorded during early spring. Respiration rate maxima of 1043 and 1027 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1} were measured on 11 August 1996 and 9 December 1997, respectively (Fig. 5.6, Table 5.3). As these rates appear to be unrealistically high, it is possible that bacterial respiration and/or photochemical oxidation were responsible for this high respiration rate when chlorophyll *a* concentration and temperature were low. Respiration minima of 9.8 and 17.5 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1} were recorded during early spring on 22 May 1996 and 29 March 1997, respectively (Fig. 5.6, Table 5.3).

Overall, highest rates of P_{max}(net) were measured during spring and minimum rates were measured during winter. In contrast, maximum rates of respiration were measured during spring although there was no clear seasonal pattern during the rest of the year.

The initial slope of the P vs I curve (α) for the Ouse at Acaster did not follow any clear seasonal pattern. A maximal value of α of 10.9 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1} (μmol photon m^{-2} s^{-1})$^{-1}$ was measured on 18 June 1996. A minimum value of 0.2 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1} (μmol photon m^{-2} s^{-1})$^{-1}$ was measured on 30 April 1996 (Table 5.3). During 1997, the maximum value of α of 5.3 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1} (μmol photon m^{-2} s^{-1})$^{-1}$ was measured on 3 June (Table 5.3).

Table 5.3 Curve parameters calculated from P vs I incubations for the Ouse at Acaster. As a result of slow rates of oxygen exchange relative to the sensitivity limits of the method of measurement, data from 21 November 1996 to 11 February 1997 were not fitted to the model of Platt *et al.* (1980) and so values for P_{max} and R were interpolated manually. See list of abbreviations for column headings.

Date	P_s	P_{max}	R	α	β	I_k	I_b	I_m
16-Apr-96	69355	260	163	1.74	104.4	336	664	659
30-Apr-96	455	348	26	3.41	0.2	117	2745	410
10-May-96	1451	616	479	10.60	0.8	148	1740	358
15-May-96	1062	696	10	4.92	0.7	146	1634	464
22-May-96	201386	632	10	3.21	368.4	203	547	544
28-May-96	256452	521	143	3.77	534.1	214	480	479
18-Jun-96	149418	2019	187	10.86	265.2	220	563	552
03-Jul-96	14915	48	118	1.79	58.4	159	256	252
30-Jul-96	1758	1298	172	8.12	0.3	202	5051	691
12-Aug-96	965	-80	1043	5.22	0.0	385		1584
03-Sep-96	14197	150	148	2.49	42.4	179	335	325
23-Sep-96	364	138	87	2.35	0.4	133	922	301
15-Oct-96	11403	-10	282	6.21	92.8	89	123	119
21-Nov-96	-	-48	141	-	-	-	-	-
10-Dec-96	-	-268	1027	-	-	-	-	-
21-Jan-97	-	-190	194	-	-	-	-	-
11-Feb-97	-	-11	48	-	-	-	-	-
25-Mar-97	780495	95	140	2.86	3495.2	131	223	223
08-Apr-97	773196	259	35	1.45	1404.5	227	550	550
29-Apr-97	773197	402	18	1.94	1314.6	225	588	588
06-May-97	773190	28	42	0.72	2955.1	154	262	262
12-May-97	773191	353	96	2.70	1710.5	202	452	452
20-May-97	773191	58	152	1.55	2109.8	232	366	366
27-May-97	773193	563	31	2.36	1127.0	265	686	685
03-Jun-97	773192	945	124	5.31	1411.8	224	548	547
11-Aug-97	773190	178	40	1.35	1770.2	190	437	437

The photoinhibition factor (β) did not follow any clear seasonal pattern. Values ranged from very low (0.2 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1} (μmol photon m^{-2} s^{-1})$^{-1}$) to very high (534 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1} (μmol photon m^{-2} s^{-1})$^{-1}$, Table 5.3). Even though the values of β are shown, the weighted photoinhibition factor (I_b) was used as clearer representation of photoinhibition (Fig. 5.8, Table 5.3).

I_b, I_k and I_m all followed a similar seasonal pattern to P_{max} (net) with maximal values occurring during spring and summer and minimum values in winter (Fig. 5.7, Table 5.3). A maximal value of I_b of 5051 μmol m^{-2} s^{-1} was observed on 30 July 1996 while maximal values of I_k and I_m of 385 and 1584 μmol m^{-2} s^{-1}, respectively occurred on 12 August 1996 (Fig. 5.7, Table 5.3). Although data were not available from 21 November 1996 to 11 February 1997, values of I_b, I_k and I_m declined to

early winter minima of 123, 89 and 119 μmol m^{-2} s^{-1}, respectively 10 October 1996 (Fig. 5.7, Table 5.3). During the spring of 1997, values of I_b, I_k and I_m increased. A maximal 1997 value of I_b of 685 μmol m^{-2} s^{-1}, recorded on 27 May 1997 (Fig. 5.7, Table 5.3) was over 7 times that of the 1996 maximum value. Maximal values of I_k and I_m of 265 and 686 μmol m^{-2} s^{-1}, respectively were recorded on 27 May 1997 (Fig. 5.7, Table 5.3).

The overall seasonal pattern of I_b suggests that photoinhibition was weakest during spring and summer and strongest during winter. The pattern of I_k suggests that the phytoplankton utilised the light more efficiently during winter and light saturation occurred at higher irradiances during spring and summer where the rate of photosynthesis was at a maximum (I_m).

A relationship between P_{max} (net) and temperature was the only significant relationship observed between the P vs I parameters and temperature (Table 5.4). The relationship was stronger for times when centric diatoms dominated ($r=0.78$, $P<0.01$) than when greens dominated ($r=0.36$, ns) or for the population as a whole ($r=0.57$, $P<0.01$; Table 5.4). This suggests that centric diatoms responded to the increase in temperature with an increase in P_{max} (net) to a greater extent than the greens. However statistical analysis (F-test) suggested that there was no significant difference between a relationship between P_{max} (net) and temperature for the whole of the data and when data were split into occasions when either centric diatoms or greens dominated the population (F-test, $P=0.12$, $f=2.3$).

Only two significant relationships were observed between the P vs I parameters and irradiance for the Ouse at Acaster during the study period. The value of the photoinhibition factor (β) increased with an increase in the attenuation coefficient (K_d) for the whole phytoplankton population ($r=0.36$, $P<0.1$; Table 5.4). This was largely a result of the relationship when populations were dominated by centric diatoms ($r=0.66$, $P<0.05$; Table 5.4). This suggests that, especially for centric diatoms, photoinhibition increased for cells acclimatised to low light conditions.

For the population as a whole, there was a positive relationship between P_{max} (net) and irradiance ($r=0.67$, $P<0.01$, Table 5.4). This relationship suggests that irradiance was important in the regulation of phytoplankton photosynthesis.

Table 5.4 Coefficients for the correlation between P vs I parameters and environmental variables for the Ouse at Acaster. See list of abbreviations for column headings. Data are shown for the whole population (A), and when populations were dominated by centric diatoms (B) and green algae (C). Shaded sections highlight significant correlations (not significant, ns; P<0.05, *; P<0.01, **; P<0.001, ***).

A		P_{max}(net)	R	α	β	I_k	I_b	I_m
Temperature	r	0.62	-0.08	0.27	-0.25	0.35	0.24	0.36
	P	***	ns	ns	ns	ns	ns	ns
	n	24	24	21	21	21	21	21
K_d	r	-0.23	-0.14	-0.28	0.53	-0.29	-0.29	-0.30
	P	ns	ns	ns	*	ns	ns	ns
	n	24	24	21	21	21	21	21
Irradiance	r	0.67	-0.09	0.34	-0.24	0.44	0.29	0.44
	P	***	ns	ns	ns	*	ns	*
	n	24	24	21	21	21	21	21

B		P_{max}(net)	R	α	β	I_k	I_b	I_m
Temperature	r	0.71	0.77	0.69	-0.33	0.04	-0.39	0.04
	P	*	*	*	ns	ns	ns	ns
	n	9	9	9	9	9	9	9
K_d	r	-0.02	0.50	-0.07	0.64	0.01	-0.61	0.04
	P	ns	ns	ns	ns	ns	ns	ns
	n	9	9	9	9	9	9	9
Irradiance	r	0.53	0.57	0.57	-0.61	-0.17	-0.24	-0.20
	P	ns	ns	ns	ns	ns	ns	ns
	n	9	9	9	9	9	9	9

C		P_{max}(net)	R	α	β	I_k	I_b	I_m
Temperature	r	0.65	-0.11	0.08	-0.23	0.56	0.42	0.47
	P	**	ns	ns	ns	ns	ns	ns
	n	15	15	12	12	12	12	12
K_d	r	-0.23	-0.41	-0.38	0.51	-0.25	-0.28	-0.30
	P	ns	ns	ns	ns	ns	ns	ns
	n	15	15	12	12	12	12	12
Irradiance	r	0.74	0.02	0.25	-0.09	0.66	0.49	0.60
	P	***	ns	ns	ns	*	ns	*
	n	15	15	12	12	12	12	12

5.3 Respiration rates of algae in culture

Data collected from the field highlighted the correlation between phytoplankton respiration rates and temperature, particularly of green algae in the Trent (Section 5.2). To compare the effect of temperature on respiration rates of different groups of phytoplankton, two species of centric

diatom and one green alga were grown at four different temperatures and their respiration rates measured (Section 3.73).

Figure 5.8 shows the respiration rate of *Cyclotella meneghiniana, Cyclostephanos invisitatus* and *Scenedesmus intermedius* when incubated at 5, 10, 15 and 20°C. All three species exhibited an increase in respiration rate with increasing temperature (Fig. 5.8). The linear relationship between respiration rate and temperature was strongest for *C. invisitatus* ($r=0.97$, $P<0.02$), then *C. meneghiniana* ($r=0.92$, $P<0.1$) and weakest for *S. intermedius* ($r=0.82$, ns). Respiration rates of centric diatoms were higher than those for the greens from 5 to 15°C (Fig. 5.8). Although no respiration rate was measured for *C. meneghiniana* at 5°C, the respiration rate of *C. invisitatus* of 32 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1} at 5°C was over twice that of *S. intermedius* of 15 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1} at the same temperature (Fig. 5.8).

Respiration rates of the centric diatoms increased greater in proportion to the greens over 10 and 15°C. Rates of 54 and 47 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1} at 10°C and 67 and 101 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1} at 15°C for *C. meneghiniana* and *C. invisitatus*, respectively were between three and four times those for *S. intermedius* of 18 and 29 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1} at 10 and 15°C, respectively (Fig. 5.8). Respiration rates for *S. intermedius* increased rapidly from 15 to 20°C with over a five fold increase from 29 to 161 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1}. The increase in respiration rate from 15 to 20°C was not as high for the centric diatoms with little over a two fold increase from 67 to 150 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1} for *C. meneghiniana* and a small increase from 101 to 117 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1} for *C. invisitatus*. At 20°C, the respiration rate of *S. intermedius* was a third higher than that of *C. intermedius* at the same temperature (Fig. 5.10).

The data suggest that green algae respire at a lower rate than centric diatoms at lower temperatures but respiration rate of the green algae increases at a much faster rate than for centric diatoms at temperatures above 15°C. This results in higher respiration rates of green algae and therefore a higher respiratory loss of carbon in comparison to those of centric diatoms at higher temperatures.

The higher rates of respiration exhibited by species in culture, with apparently low bacterial biomass, when compared to average rates shown in the Trent is discussed fully in Section 8.34.

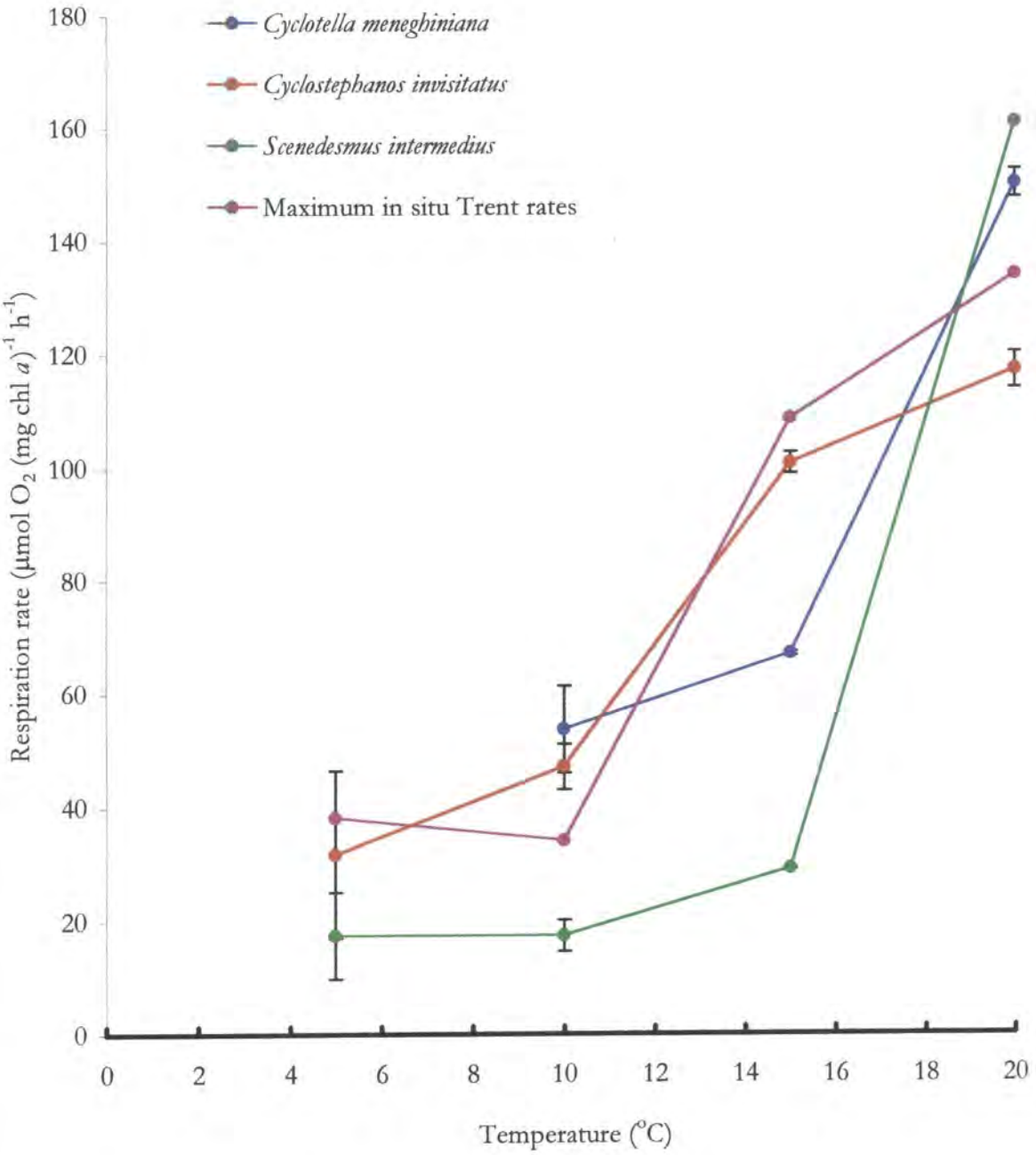

Figure 5.8 Respiration rates of three phytoplankton species, two centric diatoms and one Chlorophyta, in culture; *Cyclotella meneghiniana, Cyclostephanos invisitatus* and *Scenedesmus intermedius*. Rates were measured in triplicate at four temperatures; 5, 10, 15 and 20°C Horizontal bars show standard deviation. Problems with growing *Cyclotella meneghinia* at 5°C resulted in no respiration rate being measured at this temperature. The maximum *in situ* respiration rates for the Trent are also shown.

5.4 Measuring column productivity using the photosynthesis-irradiance-depth-time model (PIZT)

5.41 Trent

Average daily column production was estimated for the tidal limit of the Trent at Cromwell to estimate phytoplankton productivity and trend of river primary production in order to identify and quantify the processes controlling carbon production and flux within the river. Average daily column productivity in the Trent followed a similar pattern in both 1996 and 1997 (Fig. 5.9).

Maximum production rates were observed when centric diatoms dominated the population and minimum rates observed when green algae dominated (Fig. 5.9). Rates of production reached spring maxima of 1081 μmol O_2 (mg chl *a*)$^{-1}$ d^{-1} on 5 June 1996 (Fig. 5.9). During 1997, a maximal rate of 1114 μmol O_2 (mg chl *a*)$^{-1}$ d^{-1} was observed on 8 April 1997 (Fig. 5.9). Maximal rates of production coincided with temperatures of between 9 and 14 °C, high spring chlorophyll *a* concentrations of between 69 and 100 μg l^{-1} and low respiration rates between 11 and 16 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1} (Fig. 5.9). During late summer, as temperature and the rate of respiration increased, the rate of production declined to annual summer minima of –1954 and –709 μmol O_2 (mg chl *a*)$^{-1}$ d^{-1} on 30 July 1996 and 1 July 1997, respectively (Fig. 5.9). This decline in production corresponded with the rapid decline in chlorophyll *a* concentration and the switch from a centric diatom population to a green algal dominated one (Fig. 5.9). During winter, rates of production remained negative and a minimum of –5026 μmol O_2 (mg chl *a*)$^{-1}$ d^{-1} was observed on 21 January 1997 which corresponded with a high respiration rate of 217 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1}. However, during winter, temperature was low at around 4.5 °C and chlorophyll *a* concentration was around 1.5 μg l^{-1} (Fig 5.9). The low temperature and low chlorophyll *a* indicate that high respiration rates in winter may have been a result of high bacterial activity and not phytoplankton. Results of experiments upon respiration rates of phytoplankton in culture (Section 5.3) show that rates are much lower at between 17 and 32 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1} at 5°C in culture than in the Trent on 21 January 1997. The data for 21 January 1997 may be erroneous as respiration rates on other dates during winter at temperatures of between 4.3 and 5.5 °C are only between 24 and 34 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1}. As a result data for 21 January 1997 were excluded from further analysis. Overall, the pattern in average daily column algal production in the Trent was an increase in production to maximal rates during spring while respiration rates were relatively low. This coincided with an increase in chlorophyll *a* concentration and a slight increase in temperature.

As temperature and respiration rate increased during summer, production decreased and reached minima during the summer. Production remained low during winter even though temperature and, despite one occasion, respiration rates were relatively low.

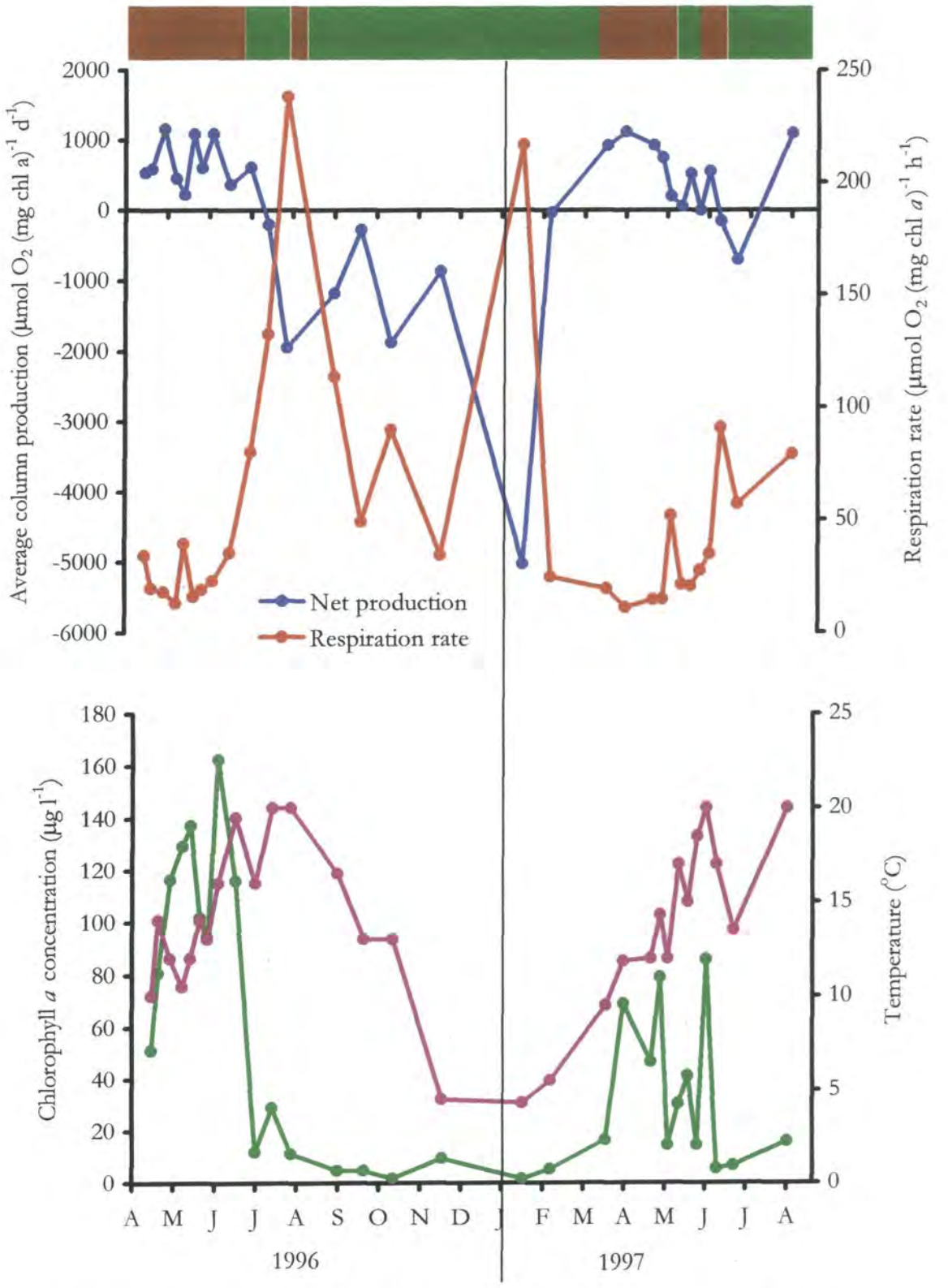

Figure 5.9 Temporal change in average daily column production and hourly respiration rate (top figure) and chlorophyll *a* concentration and temperature for the Trent at Cromwell. Times when centric diatoms (brown) and green algae (green) were dominant are shown on the bar at the top of the chart.

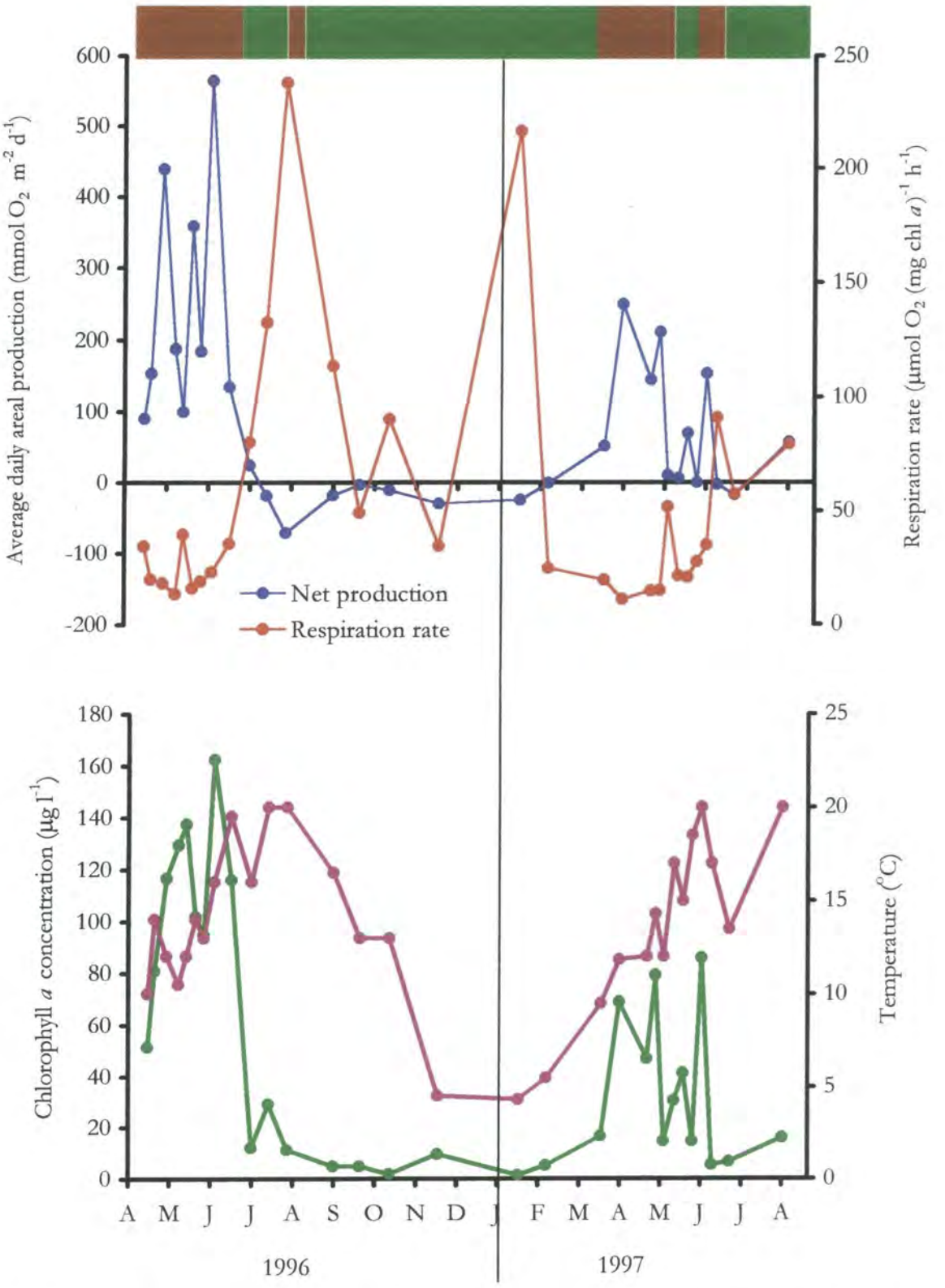

Figure 5.10 Temporal change in average daily areal production and hourly respiration rate (top figure) and chlorophyll *a* concentration and temperature for the Trent at Cromwell. Times when centric diatoms (brown) and green algae (green) were dominant are shown on the bar at the top of the chart.

River productivity, measured as average daily areal production followed a similar seasonal pattern to algal production. Spring maxima attained maximal rates of 564 and 249 μmol O_2 m^{-2} d^{-1} on 5 June 1996 and 8 April 1997, respectively (Fig. 5.10). During summer, as temperature and respiration rates increased, rates of production decreased to annual summer minima of –71 and –17 μmol O_2 m^{-2} d^{-1} on 30 July 1996 and 1 July 1997, respectively (Fig. 5.10). As with algal productivity, rates of areal production remained low throughout winter. Winter rates ranged from between -0.7 and –30 μmol O_2 m^{-2} d^{-1} (Fig. 5.10).

To identify the variables controlling average daily column production, the data were analysed with respect to identifying any significant relationships between variables and column production. The primary factors linked to average daily column production were chlorophyll *a* concentration, respiration rate, I_k, I_b, I_m and P_{max}(net) as significant relationships were observed between production and these variables (Table 5.5). An F test showed that there was no difference between the relationship between production and respiration when expressed for the population as a whole or when expressed as populations dominated by centrics or green algae. However, significant differences were shown for the relationships between productivity and chlorophyll *a* concentration (F test; F=4.0, P=0.03), I_k (F test; F=6.1, P=0.006), I_b (F test; F=3.9, P=0.03), I_m (F test; F=5.5, P=0.009) and P_{max}(net) (F test; F=6.45, P=0.005). Even so, for all these variable, the most significant relationship existed for the population as a whole. There was a positive, significant relationship between production and chlorophyll *a* concentration (r=0.6, P<0.01; Table 5.5) for the phytoplankton population as a whole. This indicates that high production resulted in the creation of new phytoplankton biomass.

A significant, negative relationship existed between productivity and respiration rate for the population as a whole (r=-0.78, P<0.01; Table 5.5) as well as for populations dominated by centric diatoms (r=-0.71, P<0.01; Table 5.5) and by green algae (r=-0.77, P<0.01; Table 5.5). As respiration rates increased, as a result of increasing temperature, production rates declined. High respiration rates in summer resulted in minimum production rates (Fig 5.10). As temperature influences the rate of respiration, temperature would have influenced average daily column production indirectly even though no significant relationship was observed between production and temperature (Table 5.5). This was probably a result of an increase in both the rates of P_{max}(net) and respiration with increasing temperature (Table 5.2).

A significant, positive relationship existed between production and I_k (r=0.42, P<0.05; Table 5.5), I_b (r=0.49, P<0.01; Table 5.5) and between production and I_m (r=0.39, P<0.05; Table 5.5) for the population as a whole. For populations dominated by green algae, significant relationships were observed between production and I_k (r=0.69, P<0.05; Table 5.5) and production and I_m

(r=0.6, P<0.05; Table 5.5). No such relationship was evident for populations dominated by centrics (Table 5.5).

Table 5.5 Coefficients of correlation between average daily column production and environmental variables for the Trent at Cromwell. See list of abbreviations for column headings. Data are shown for the whole population (A) and when dominated by centric diatoms (B) and green algae (C). Shaded sections highlight significant correlations (not significant, ns; P<0.05, *; P<0.01, **; P<0.001, ***).

A	Temp.	Qs	K_d	Chl *a*	P_s	α	R	β	I_k	I_b	I_m	P_{max}(net)
r	-0.14	0.01	-0.06	0.60	-0.01	-0.03	-0.78	-0.13	0.42	0.49	0.39	0.51
P	ns	ns	ns	**	ns	ns	**	ns	*	**	*	**
n	30	30	30	30	30	30	30	30	30	30	30	30

B	Temp.	Qs	K_d	Chl *a*	P_s	α	R	β	I_k	I_b	I_m	P_{max}(net)
r	-0.44	-0.35	-0.41	0.42	-0.21	0.10	-0.71	-0.17	-0.30	0.16	-0.35	-0.21
P	ns	ns	ns	ns	ns	ns	**	ns	ns	ns	ns	ns
n	18	18	18	18	18	18	18	18	18	18	18	14

C	Temp.	Qs	K_d	Chl *a*	P_s	α	R	β	I_k	I_b	I_m	P_{max}(net)
r	0.41	0.43	-0.04	0.45	0.44	-0.07	-0.77	0.62	0.69	0.42	0.60	0.70
P	ns	ns	ns	ns	ns	ns	**	*	*	ns	*	**
n	12	12	12	12	12	12	12	12	12	12	12	12

As the parameters I_k, I_b and I_m are all indicators of phytoplankton response to irradiance, relationships evident only for populations dominated by green algae suggest that irradiance was an important factor in controlling production, especially for green algal dominated populations. Alternatively the data suggest that these parameters were more variable for greens than for centrics. As I_k and I_m increased, production increased, suggesting that cells were adapting and were able to utilise more light when exposed to higher irradiance. However, as both I_k and I_m are linked to P_{max} (net), the increase in the values with temperature may have been because the rate of P_{max} (net) increased with temperature.

A high value of I_b indicates low photoinhibition so an increase in production as I_b increased indicated that productivity increased as the burden of photoinhibition decreased. Average daily irradiance did not appear to directly affect production (Table 5.5). However, it influenced production indirectly as positive, significant relationships were observed between I_k, I_m and irradiance (Table 5.2)

The relationship between production and P_{max} (net) was also positive and significant for the whole population ($r=0.51$, $P<0.01$; Table 5.5) and when dominated by green algae ($r=0.7$, $P<0.01$; Table 5.5). The increase in average daily column production with increasing rates of P_{max} (net) are to be expected as long as the respiratory burden does not offset production. Irradiance also influenced production indirectly by influencing the rate of P_{max} (net). Significant, positive relationships were observed between P_{max} (net) and irradiance (Table 5.2).

No significant relationship was observed between average daily column production and temperature, irradiance, K_d, P_s, α or β (Table 5.5). However, as mentioned previously, temperature and irradiance may have indirectly affected production by influencing the P vs I characteristics of the phytoplankton.

The important variables controlling average daily column production are chlorophyll *a* concentration, respiration rate, and P_{max} (net). Production increased with increasing chlorophyll *a* concentration and with increased rates of P_{max} (net). Production increased with decreasing rates of respiration. It was considered that temperature and irradiance controlled production indirectly by influencing rates of respiration and P_{max} (net) as well as I_k, and I_m.

Factors linked to river production, measured as areal production, were less numerous than for algal production. Positive correlations existed only between areal production and chlorophyll *a*, respiration rate and the rate of P_{max}(net). F tests suggested that data were not significantly different if expressed for the whole population or when populations were dominated by either centrics or greens. A positive correlation existed between areal productivity and chlorophyll *a* for the whole population ($r=0.8$, $P<0.001$; Table 5.6) and when dominated by centrics ($r=0.69$, $P<0.01$; Table 5.6). No relationship was observed when populations were dominated by greens. These data suggest that algal biomass and production strongly influenced overall river productivity. A negative relationship existed between areal production and respiration rate for the whole population ($r=-0.52$, $P<0.01$; Table 5.6), and when dominated by centrics ($r=-0.48$, $P<0.05$; Table 5.6) and by greens ($r=-0.62$, $P<0.05$; Table 5.6). This was a similar relationship observed for algal (column) productivity.

A positive correlation existed between areal production and P_{max}(net) only when green algae dominated the population ($r=0.59$, $P<0,001$; Table 5.6). This suggests that P_{max}(net) was only important in controlling river production when green algae dominated. However, other factors such as respiration rate may have masked the importance of P_{max}(net) for the whole population and when centrics dominated.

Table 5.6 Coefficients of correlation between average daily areal production and environmental variables for the Trent at Cromwell. See list of abbreviations for column headings. Data are shown for the whole population (A) and when dominated by centric diatoms (B) and green algae (C). Shaded sections highlight significant correlations (not significant, ns; P<0.05, *; P<0.01, **; P<0.001, ***).

A	Temp.	Qs	K_d	Chl *a*	P_s	α	R	β	I_k	I_b	I_m	P_{max}(net)
r	-0.07	0.10	-0.04	0.80	-0.12	-0.03	-0.52	-0.14	0.27	0.27	0.24	0.33
P	ns	ns	ns	***	ns	ns	**	ns	ns	ns	ns	ns
n	30	30	30	30	30	30	30	30	30	30	30	26

B	Temp.	Qs	K_d	Chl *a*	P_s	α	R	β	I_k	I_b	I_m	P_{max}(net)
r	-0.12	0.08	-0.19	0.69	-0.11	-0.03	-0.48	-0.08	-0.03	0.00	-0.09	0.01
P	ns	ns	ns	**	ns	ns	*	ns	ns	ns	ns	ns
n	18	18	18	18	18	18	18	18	18	18	18	14

C	Temp.	Qs	K_d	Chl *a*	P_s	α	R	β	I_k	I_b	I_m	P_{max}(net)
r	0.09	0.07	-0.24	0.25	0.50	-0.23	-0.62	0.32	0.54	0.36	0.54	0.59
P	ns	ns	ns	ns	ns	ns	*	ns	ns	ns	ns	*
n	12	12	12	12	12	12	12	12	12	12	12	12

These relationships suggest that phytoplankton production was responsible for influencing river productivity. As algal biomass increased, indicated by an increase in chlorophyll *a*, river productivity increased. As algal respiration rates increased, river productivity decreased. These are similar relationships observed for column production (Table 5.5). Therefore, factors which influenced algal production such as chlorophyll *a*, respiration and P_{max}(net), as well as those which indirectly influenced algal production such as temperature and light, by their control over phytoplankton, also influenced river production.

5.42 Ouse

Average daily column production for the Ouse was sporadic (Fig. 5.13) and did not follow any clear seasonal pattern (Fig. 5.11). However, spring maxima were observed. Rates of 2721 and 593 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1} were measured on 15 May 1996 and 27 May 1997, respectively (Fig. 5.11). However, the high rate of 2721 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1} may be considered as unachievable as the chlorophyll *a* concentration on this data was only 6 μg l^{-1}. The reason for the unrealistically high and low rates for the Ouse in unclear. They do however emphasise that these rates must be considered with caution.

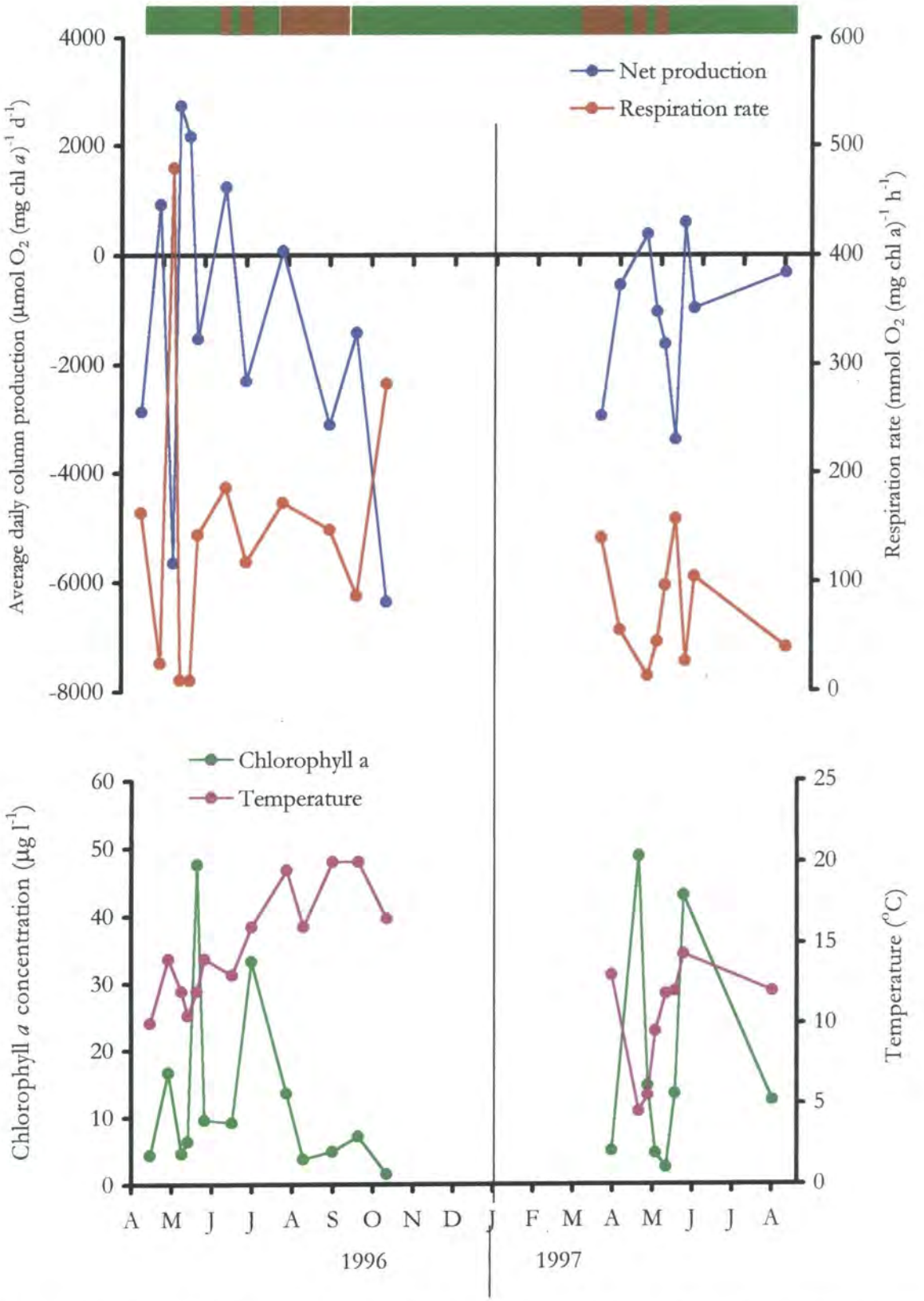

Figure 5.11 Temporal change in average daily column production and hourly respiration rate top figure) and chlorophyll *a* concentration and temperature for the Ouse at Acaster. Times when centric diatoms (brown) and green algae (green) were dominant are shown on the bar at the top of the chart.

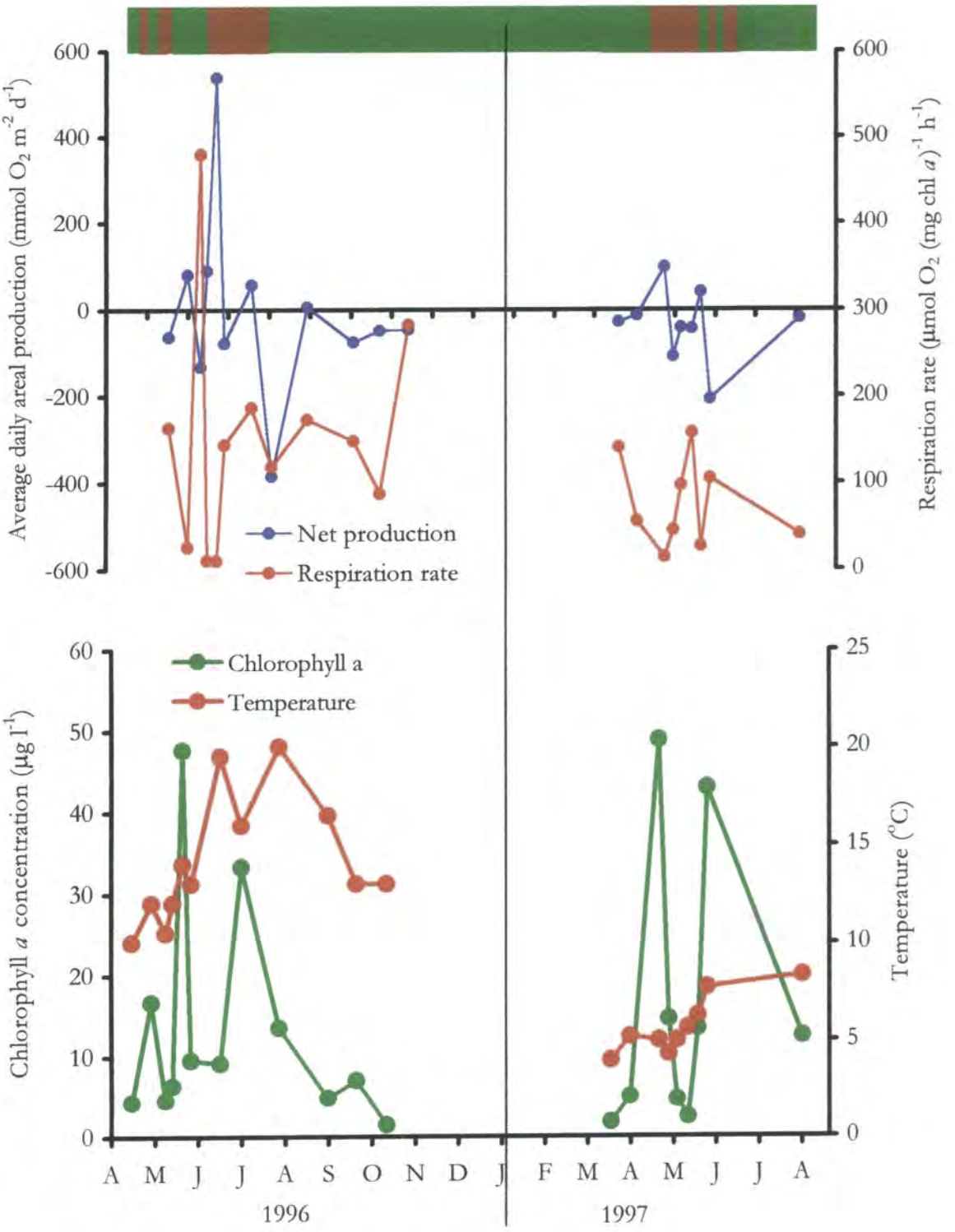

Figure 5.12 Temporal change in average daily areal production and hourly respiration rate (top figure) and chlorophyll *a* concentration and temperature for the Ouse at Acaster. Times when centric diatoms (brown) and green algae (green) were dominant are shown on the coloured bar at the top of the chart.

There was no clear seasonal pattern for minimum rates of column production. Minima of –1528 and –6366 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1} were measured on 10 May 1996 and 15 October 1997, respectively (Fig. 5.11). An unrealistically low rate of –22723 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1} was measured on 12 August 1996. Consequently, data collected on this date were omitted from further analysis.

Areal production rates showed more of a seasonal pattern than for rates of column production. Maximal rates were observed in spring. Rates then declined during summer as temperature and respiration rates increased (Fig. 5.12). Rates were not calculated during winter from November to February as the P vs I data could not be fitted to a P vs I model.

Maximal rates of 536 and 98 μmol O_2 m^{-2} d^{-1} were observed in spring on 22 May 1996 and 29 April 1997, respectively. Rates then declined to seasonal annual minima of –427 and –108 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1} on 12 August 1996 and 20 May 1997, respectively.

Significant relationships were observed between column production and irradiance, K_d, respiration rate, I_k and I_b (Table 5.7). A positive relationship existed between column production and average daily surface irradiance for the population as a whole (r=0.47, P<0.001; Table 5.7). This was expected as irradiance was seen to influence the rate of P_{max}(net) (Table 5.4).

Table 5.7 Coefficients of correlation between average daily column production and environmental variables for the Ouse at Acaster. See list of abbreviations for column headings. Data are shown for the whole population (A) and when dominated by centric diatoms (B) and green algae (C). Shaded sections highlight significant correlations (not significant, ns; P<0.05, *; P<0.01, **; P<0.001, ***).

A	Temp.	Qs	K_d	Chl *a*	P_s	α	R	β	I_k	I_b	I_m	P_{max}(net)
r	0.28	0.47	-0.15	0.43	0.10	-0.09	-0.77	-0.05	0.70	0.26	0.57	0.47
P	ns	*	ns	ns	ns	ns	***	ns	***	**	ns	ns
n	21	21	21	21	21	21	21	21	21	21	21	21
B	Temp.	Qs	K_d	Chl *a*	P_s	α	R	β	I_k	I_b	I_m	P_{max}(net)
r	-0.02	0.09	-0.70	0.06	-0.34	0.44	-0.43	-0.42	0.56	0.45	0.54	0.48
P	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	ns	ns
n	9	9	9	9	9	9	9	9	9	9	9	9
C	Temp.	Qs	K_d	Chl *a*	P_s	α	R	β	I_k	I_b	I_m	P_{max}(net)
r	0.53	0.57	0.16	0.53	0.35	-0.40	-0.78	0.21	0.62	0.32	0.56	0.39
P	ns	ns	ns	ns	ns	ns	**	ns	*	ns	ns	ns
n	12	12	12	12	12	12	12	12	12	12	12	12

A negative correlation was observed between column production and K_d when the population was dominated by centric diatoms ($r=-0.7$, $P<0.001$; Table 5.7). No relationship was observed when greens dominated. This suggests that water clarity was important in controlling production of centrics.

A negative relationship was observed between column production and respiration rate for the whole population ($r=-0.77$, $P<0.001$; Table 5.7) and when green algae dominated ($r=-0.78$, $P<0.01$; Table 5.7). This suggests that respiration is an important factor controlling column production in the Ouse.

A positive relationship was observed between column production and I_k for the whole population ($r=0.7$, $P<0.001$; Table 5.7) and when green algae dominated ($r=0.62$, $P<0.05$; Table 5.7) and could be a result of the increase in the rate of P_{max}(net) with increasing temperature. However, for the Ouse there was no relationship between column production and P_{max}(net) and so the relationship with I_k was possibly real. If this was the case then the data suggest that the onset of light saturation influenced column production. If so, factors influencing I_k, such as temperature also indirectly influenced column production.

A positive relationship was observed between column production and I_b ($r=0.26$, $P<0.01$; Table 5.7). This suggests that photoinhibition had a direct effect upon column production. However, the turbid nature of the Ouse allows the assumption to be made that photoinhibition was of little importance here. Overall, the most important factors influencing column production in the Ouse were irradiance and respiration.

Areal production was linked only to chlorophyll *a* concentration and I_K (Table 5.8). Surprisingly, a negative correlation was observed between areal production and chlorophyll *a* when green algae dominated ($r=-0.67$, $P<0.05$; Table 5.8). This was not expected although it suggests that an increase in algal biomass resulted in a decrease in river productivity. This may be the result of an increase in the algal respiratory burden.

A positive relationship was observed between areal production and I_k for the whole population ($r=0.44$, $P<0.05$; Table 5.8) and when dominated by centrics ($r=0.69$, $P<0.05$; Table 5.8). This was also observed for column production and suggests that the onset of light saturation was important in controlling both river and algal productivity in the Ouse.

Overall, the important factors controlling riverine production in the Ouse were chlorophyll *a* concentration and I_k, possibly indicating the importance of increased algal biomass and respiration, and the onset of light saturation.

Table 5.8 Coefficients of correlation between average daily areal production and environmental variables for the Ouse at Acaster. See list of abbreviations for column headings. Data are shown for the whole population (A) and when dominated by centric diatoms (B) and green algae (C). Shaded sections highlight significant correlations (not significant, ns; P<0.05, *; P<0.01, **; P<0.001, ***).

A	Temp.	Qs	K_d	Chl *a*	P_s	α	R	β	I_k	I_b	I_m	P_{max}(net)
r	-0.06	0.00	-0.28	0.25	-0.02	0.05	-0.37	-0.06	0.44	0.12	0.30	0.23
P	ns	ns	ns	ns	ns	ns	ns	ns	*	ns	ns	ns
n	21	21	21	21	21	21	21	21	21	21	21	21

B	Temp.	Qs	K_d	Chl *a*	P_s	α	R	β	I_k	I_b	I_m	P_{max}(net)
r	-0.16	-0.12	-0.50	0.32	0.00	0.15	-0.49	-0.04	0.69	0.16	0.64	0.27
P	ns	ns	ns	ns	ns	ns	ns	ns	*	ns	ns	ns
n	9	9	9	9	9	9	9	9	9	9	9	9

C	Temp.	Qs	K_d	Chl *a*	P_s	α	R	β	I_k	I_b	I_m	P_{max}(net)
r	0.09	-0.20	-0.29	-0.67	-0.18	-0.14	-0.17	0.04	-0.32	0.27	-0.20	-0.24
P	ns	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	ns
n	12	12	12	12	12	12	12	12	12	12	12	12

5.5 Modelling of column productivity with changing environmental variables

5.51 Trent

5.511 Depth

The PIZT model was used to predict the seasonal trend in average daily column production in response to a change in river depth, K_d and respiration rate and when taking into account photoinhibition. This was used to test the sensitivity of predicted production in response to changes in these selected environmental variables.

To estimate the change in production as a result of a change in river depth, the depths of the river at Cromwell and depths of 2 m and 5 m, approximately 1.5 m shallower and deeper than at Cromwell, respectively were placed into the PIZT model. Figure 5.13a shows the estimated production at the shallower and deeper depths in relation to the modelled production at Cromwell. A maximal seven-fold difference existed between production at Cromwell and when modelled at 2 m. However, the overall average difference throughout the sampling period was a two-fold increase. The difference between production at Cromwell and when modelled at 5 m was similar to that when modelled at 2m although with a maximal seven-fold decrease and an overall two-fold average decrease during the sampling period.

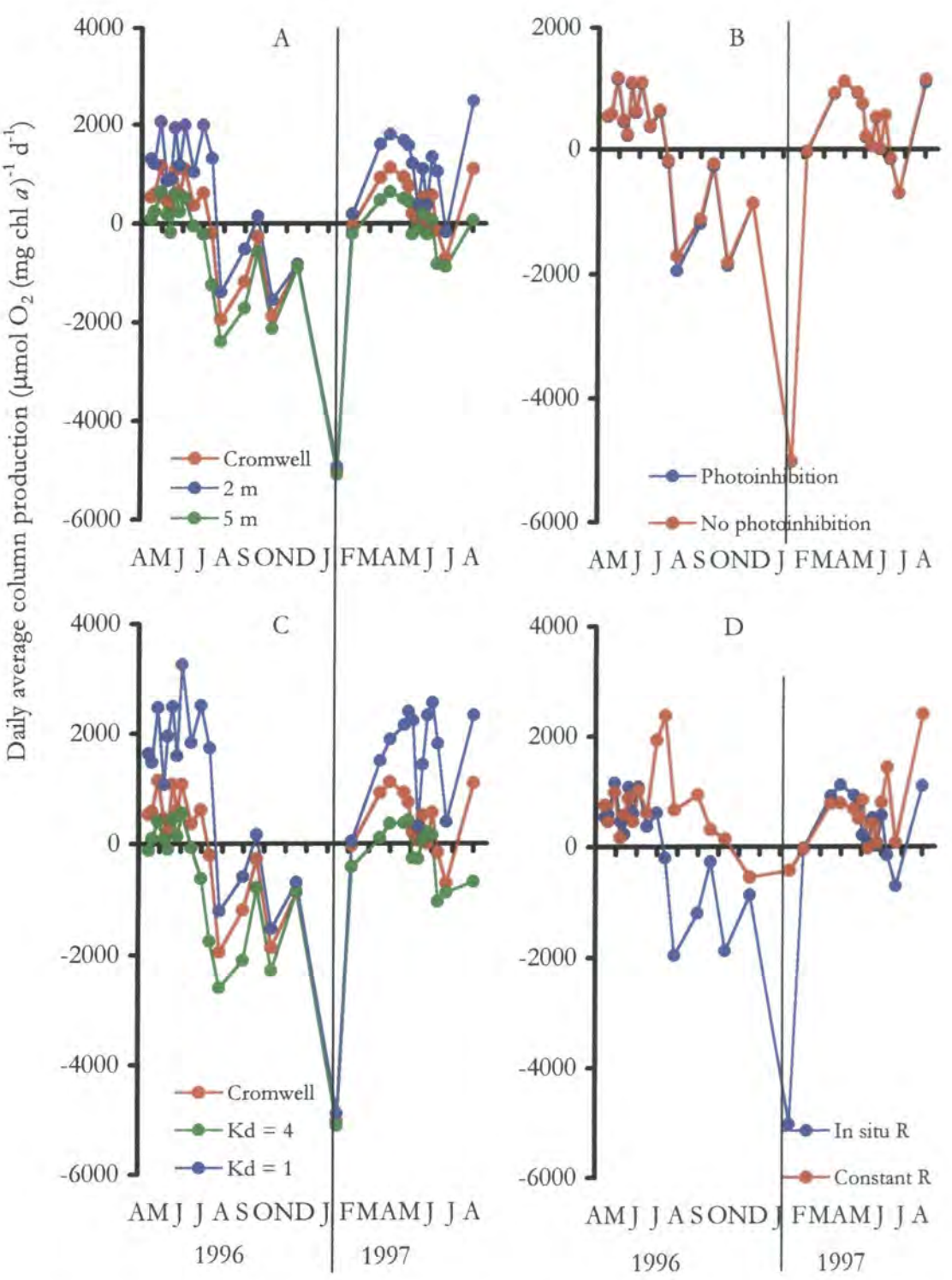

Figure 5.13 Daily average column production calculated using the PIZT model (Section 3.10) with a change in environmental variables for the Trent at Cromwell. Production was modelled at three different depths (A), with and without photoinhibition (B), for three different K_d values (C) and with *in situ* respiration rates and with a constant respiration rate (D).

Differences were least during winter and early spring and greatest during late summer (Fig 5.13a). This indicates that depth was an important factor in primary production especially during summer and less important during winter and spring.

5.512 Photoinhibition

The PIZT model was modified so that the effect of photoinhibition on production could be omitted. The production rates for Cromwell were re-estimated as if photoinhibition had no effect upon average daily column production and were compared to rates estimated for Cromwell when photoinhibition occurred. Estimates of production when photoinhibition was not included in the model had little effect upon column productivity. Figure 5.13b shows that the seasonal pattern is the same as when photoinhibition is included and the rates of production are very similar. Apart from an exceptionally high difference on 3 June 1997, differences between the two modelling approaches ranged from 0.003 to 15.1 % and averaged only 4.2 %. Differences were greatest during early summer of 1997 (Fig. 5.13b). Even so there was no clear pattern and differences rarely exceeded 7 %. Figure 5.14 highlights the fact that photoinhibition had only a small effect upon column productivity. Even when photoinhibition did have a marked affect upon production it was only in the upper part of the water column (Fig. 5.14) and was not a factor which greatly affected total column productivity.

Although changes in irradiance were not modelled, Figure 5.15 shows an example of how average daily column production changed in response to the day to day changes in average daily irradiance, assuming a constant P vs I response throughout. There was a positive correlation between daily column production and irradiance ($r=0.98$, $P<0.001$; Fig. 5.15, inset). Highest rates of production were evident when average daily irradiance was highest. However, this does not take into account changes in temperature, K_d value and rates of respiration and is just an example of day to day changes in production whilst this project was concerned with seasonal trends in production especially during the times when large phytoplankton populations developed and collapsed.

5.513 Attenuation coefficient

The PIZT model was also used to estimate production when K_d values were fixed at a lower value of 1 m^{-1} and a higher value of 4 m^{-1}. Figure 5.13c shows the variation in rates of production when modelled at a fixed K_d value and are compared to modelled production for Cromwell under K_d values measured *in situ*. The difference between production for Cromwell and when modelled for a K_d of 1 m^{-1} was quite large with a maximum 40-fold increase and an average four-fold increase throughout the sampling period. Differences were greatest during spring and early summer and least during winter.

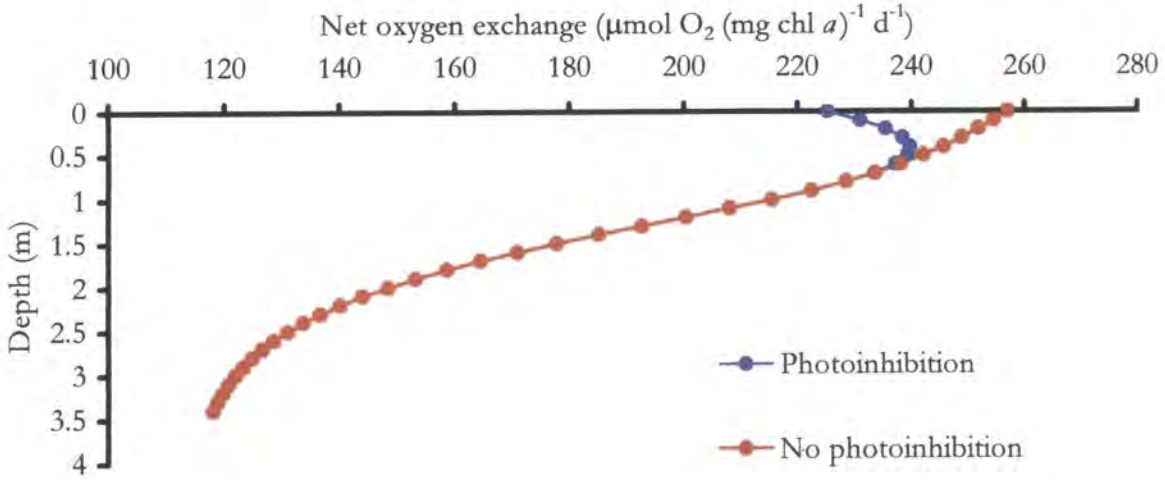

Figure 5.14 Example of effect of photoinhibition upon primary production in the upper water column for the Trent at Cromwell on 3 September 1996. The corresponding response when photoinhibition is excluded, using the PIZT model is shown for comparison.

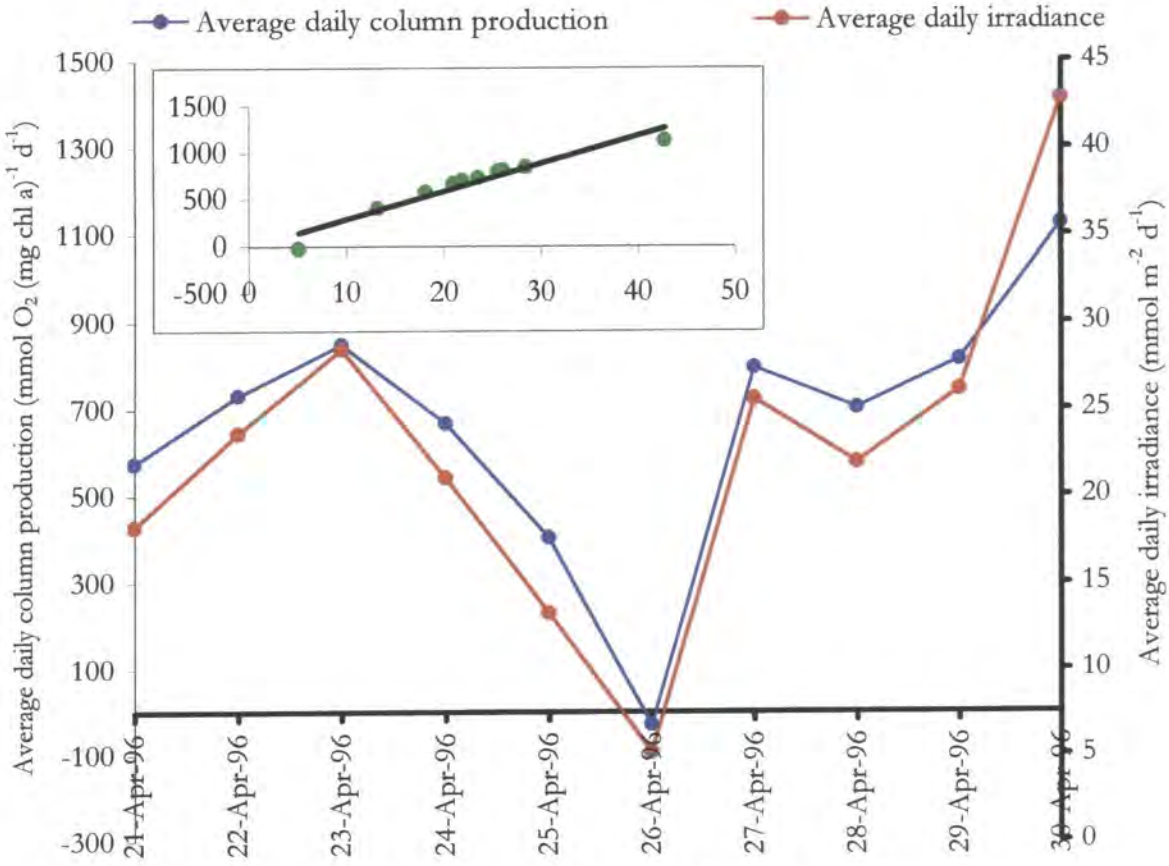

Figure 5.15 Daily change in column production and irradiance for the Trent at Cromwell assuming constant P vs I characteristics. The incept shows the relationship between average daily column production (y-axis, same units as main chart) and average daily irradiance (mol m^{-2} d^{-1}); r=0.96, P<0.001, n=10.

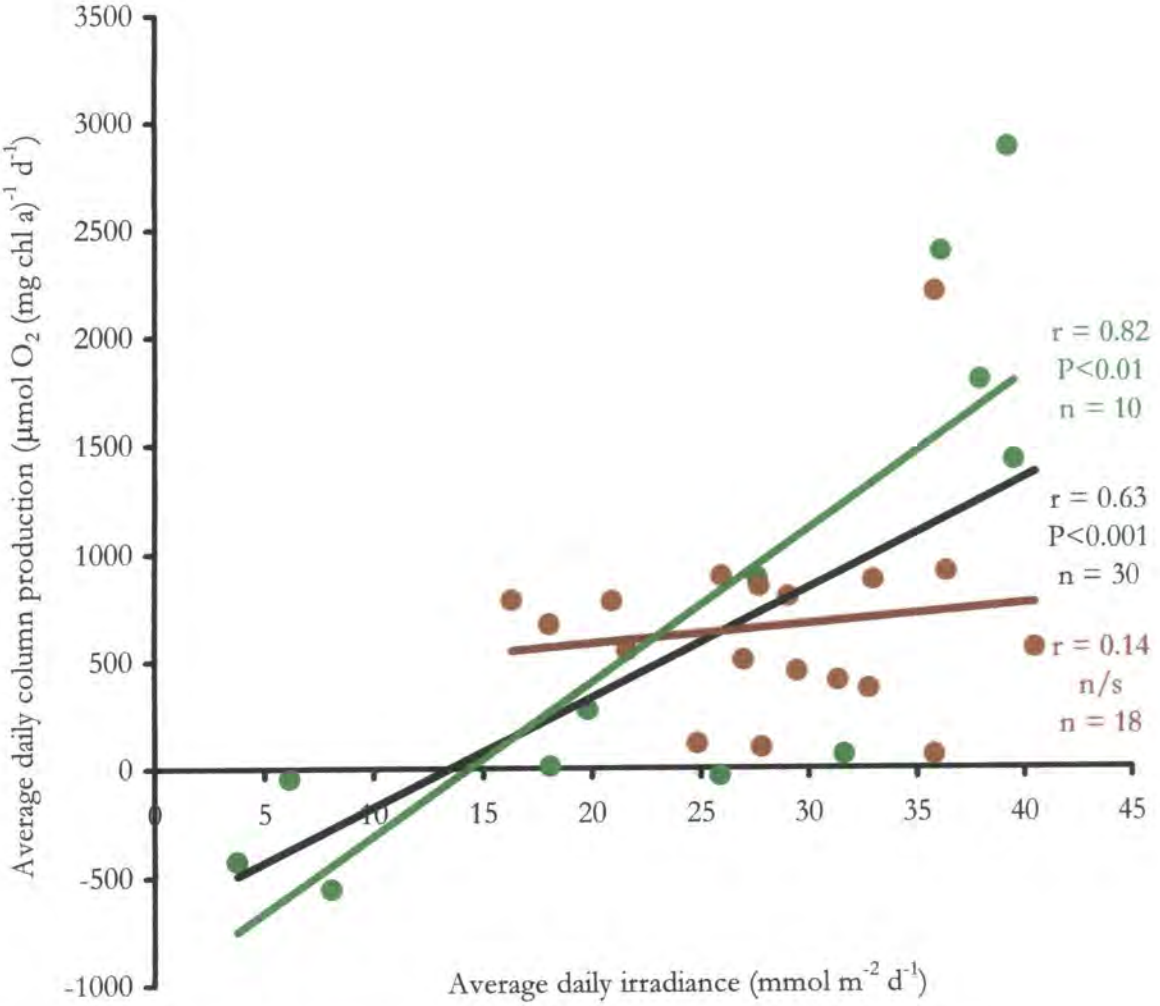

Figure 5.16 Relationship between average daily column production and average daily irradiance when respiration rate is fixed at average spring rate for the Trent at Cromwell. Trend lines show relationship for the whole population (black line), and times when populations were dominated by centric diatoms (brown line) and green algae (green line).

When production was modelled using a K_d of 4 m^{-1}, the water column was heterotrophic for much of the year (Fig. 5.13c). The maximal and average differences when compared to *in situ* production at Cromwell under natural conditions were very similar to those when modelled with a K_d of 1 m^{-1} but with a decrease rather than an increase in production.

Overall, a change in the K_d value resulted in differences being most marked during the spring and early summer where irradiance was high and respiration rate was increasing with an increase in temperature. During this period, an increase in the K_d value resulted in a decrease in the amount of light penetrating through the water column. When this was coupled with a high respiration rate, the respiratory burden in the water column increased. Differences were less marked during winter as winter production was controlled primarily by low irradiance.

5.514 Respiration rate

The modelling of column productivity with a fixed respiration rate showed a marked difference in average daily column production when compared to the results obtained using data collected *in situ* from Cromwell. A fixed respiration rate of –25 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1} was used in the PIZT model as this was the average spring respiration rate observed for Cromwell during 1996 and 1997. Using this low, spring rate of respiration, positive column production was possible throughout the summer and the switch to a heterotrophic system occurred on 21 November 1996 and lasted until 11 February 1997 (Fig. 5.13d). This is a period of three months compared to nearly seven months when compared to column production for Cromwell with *in situ* respiration rates. Figure 5.16 shows that when modelled with a fixed, low respiration rate, a strong relationship exists between irradiance and average daily column production.

High rates of production could be attained during summer if irradiance was high and the respiratory loss was low. However, using *in situ* respiration rates, production became negative during summer and a maximum rate of 1095 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1} was observed in spring; on 22 May 1996 (Fig 5.13d). Using *in situ* rates of respiration, production declined during summer (Fig 5.13) as respiration rates increased (Fig. 5.9). Increased rates of respiration were attributed to increased water temperature (Table 5.3).

A maximal 10-fold difference existed between production using *in situ* and fixed rates of respiration with an average one and a half-fold difference over the sampling period. Differences were least during spring when *in situ* rates of respiration were similar to fixed rates. Differences were most marked in summer. Large differences were also observed during winter. This may be a result of a bacterial activity and is discussed in Section 8.34.

Overall, increasing rates of respiration with increasing temperature and an increase in the attenuation coefficient may be the most important factor resulting in the fall in rates of average daily column production and the switch from an autotrophic to a heterotrophic system during

summer. River depth and K_d value may also be important in regulating rates of production during spring and summer by increasing the respiratory burden of the phytoplankton. The decrease in daily irradiance is thought to be important in regulating production during winter as respiration rate, depth and K_d value are less important during this period.

5.52 Ouse

5.521 Depth

The PIZT model was used to calculate the column production at Acaster using *in situ* depths and depths of 4 m and 7 m; roughly 1.5 m shallower and deeper than the average depth at Acaster respectively. The data obtained from the three modelling procedures followed a similar seasonal pattern (Fig. 5.17a). Although there was no clear seasonal pattern marked differences were evident. When modelled at a depth of 4 m, a maximal 35-fold increase and average two-fold increase existed when compared to column production measured for *in situ* depths. When modelled at 7 m a maximal 13-fold decrease and average 0.9-fold decrease was observed. Differences were most marked during spring and summer. Depth was an important factor influencing column production, especially during spring and summer.

5.522 Photoinhibition

Photoinhibition had little effect upon column production at Acaster. Figure 5.17b shows how close the seasonal pattern of production when no photoinhibition is evident follows the pattern when photoinhibition is possible. Differences ranged between 0 and 27 % and averaged only 1.4 %. This suggests that photoinhibition unimportant in the turbid, humic coloured Ouse.

5.523 Attenuation coefficient

In addition to column production measurements using *in situ* values of K_d, estimates were made using K_d values of 1 and 4 m^{-1}. These were approximately an increase or decrease of 1.5 m^{-1} from the average *in situ* value, respectively.

Again, no clear seasonal pattern existed (Fig. 5.17c). When modelled with a K_d of 1 m^{-1}, differences when modelled using *in situ* K_d values attained a maximal 30-fold increase and an average 1.7-fold increase. When modelled using a K_d value of 4 m^{-1}, differences attained a maximal 41-fold decrease and an average 2.7-fold decrease. Differences were greatest in spring and summer and least in winter. This suggests that the attenuation of light was important in controlling production in spring and summer but not in winter when other processes may have been more important.

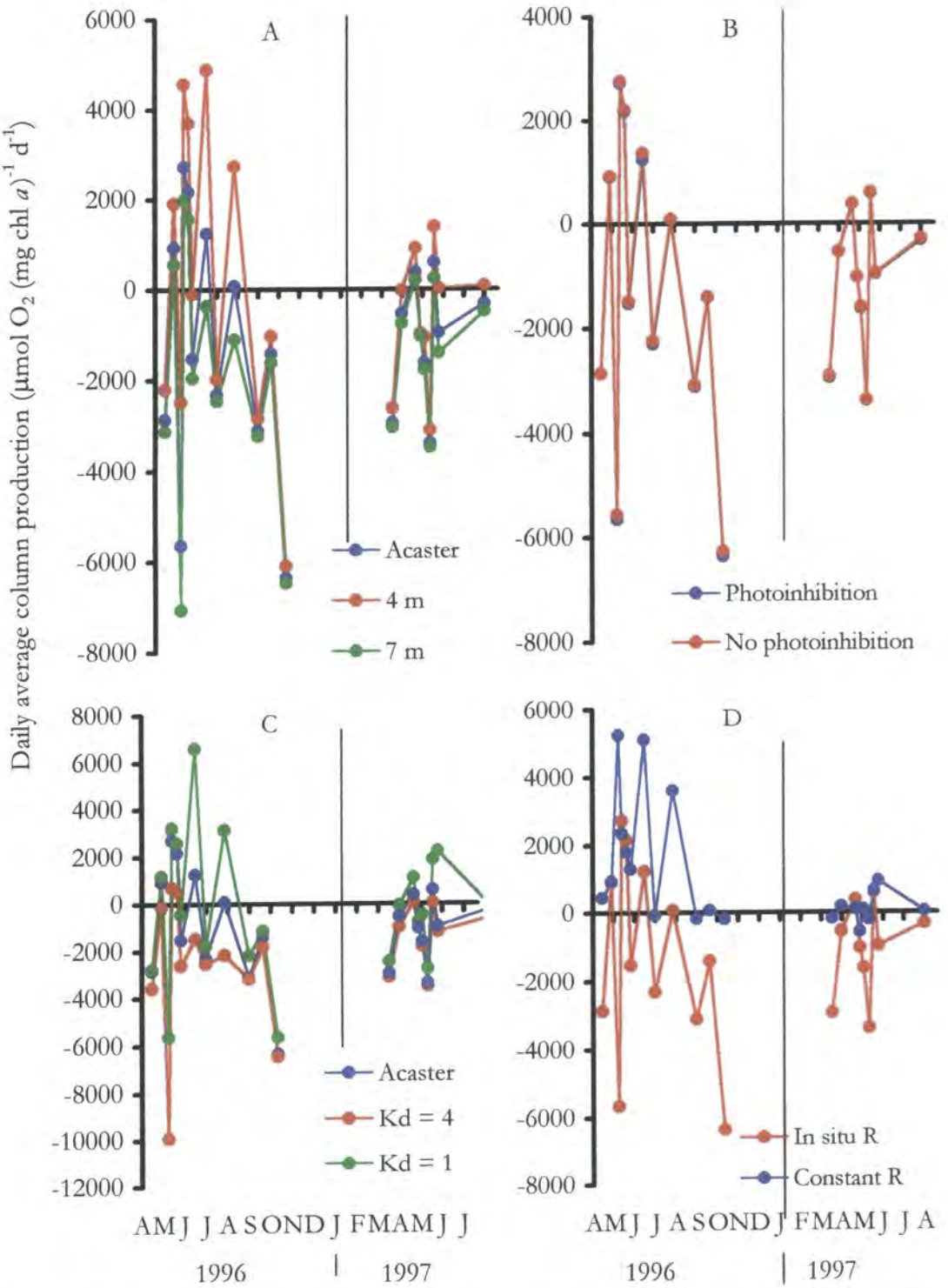

Figure 5.17 Daily average column production calculated using the PIZT model (Section 3.10) with a change in environmental variables for the Ouse at Acaster. Production was modelled with changing depth (A), with and without photoinhibition (B), for three different Kd values (C) and with *in situ* respiration rates and with a constant respiration rate (Chart D).

5.524 Respiration rate

Figure 5.17d shows the seasonal pattern of column production using *in situ* respiration rates and when modelled using a fixed spring average rate of 25 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1}. The overall effect was a shift in the production rate to an overall increase, especially during 1996. Differences a maximal 48-fold increase and an average 3-fold increase over the sampled period indicating that respiration rate had an important effect upon column production in the Ouse.

Depth, attenuation coefficient and respiration rate were all important in controlling column production. The importance of these factors was most marked during spring and summer when conditions were favourable for phytoplankton production. During this period, any change in depth, K_d or respiration rate would have a dramatic effect upon overall column production.

5.6 Discussion

The collated data concerning phytoplankton and river productivity shows patterns similar to those shown for phytoplankton abundance and biomass in Chapter 4. Maximum rates of P_{max} and respiration were higher for the Ouse than for the Trent. However, a clearer seasonal pattern and correlation with temperature were evident for the Trent compared with the Ouse. Values of the P vs I parameters I_k, I_b and I_m were similar for the Trent and Ouse and showed a general seasonal patttern of maximal values in spring and lower values in summer and winter.

Phytoplankton and river production showed a similar seasonal pattern to the P vs I parameters P_{max} and respiration and these two P vs I parameters were thought to strongly infuence production. The clear seasonal pattern for production shown for the Trent was not evident for the Ouse. However, apart from one or two unrealistically high values, maximum rates of phytoplankton and river production were similar in both rivers.

Rates of both phytoplankton and river productivity were at a maximum during spring for both the Trent and Ouse. This was when rates of production were at a minimium as temperature was relatively low and underwater light climate started to improve. These conditions resulted in net productivity in the Trent through most of spring. For the Ouse, net production did occur during spring and early summer. However, net production was sporadic.

During summer rates of production decreased in the Trent and Ouse. This pattern was striking in the Trent in 1996 as temperature dependent increase in respiration rate and the poor underwater light climate resulted in negative production in the Trent during summer. Negative production also occurred during summer for the Ouse, but again, the pattern was less clear than in the Trent. Use of the PIZT model led to the conclusion that respiration was the primary factor influencing phytoplankton and river production in the Trent. This was also observed for the Ouse although it was hypothesised that other, unknown factors are also important in controlling production here. River depth and attenuation coefficient also had marked influence upon

production, especially in spring and summer. The importance of these variables was probably their influence upon respiration rates when coupled with temperature. High light attenuation in the Trent and Ouse was often observed, especially during flood events and when dissolved humic substances entered the system. Attenuation was typically higher in the Ouse than the Trent, especially during flood events. Phytoplankton biomass was found to influence light attenuation in the Trent while in the Ouse non-algal solids were considered more important. As a result of the turbid nature of the Trent and Ouse photoinhibition was not considered as important in influencing production in these rivers. Increased river depth, low temperature and poor underwater light climate, coupled with decreasing insolation were thought responsible for minimum rates of production being observed for both rivers during winter.

When coupled with data from Chapter 4 it is evident that maximum production was attained when centric diatoms dominated the phytoplankton and minimum rates were observed when green algae dominated. Regression analysis suggested that respiration rates of green algae were higher than those of cenric diatoms when temperatures exceeded 15°C. It was therefore hypothesised that the switch from a centric diatom dominated population to a green algal dominated one was partly responsible for the switch from an autotrophic to a heterotrophic system. This switch was clearly seen for the Trent. However, no explanation was offered to suggest why the switch from a centric to a green dominated phytoplankton occurred in the first place.

Once the production rates of Trent and Ouse phytoplankton had been estimated, the next stage in the investigation was to estimate growth rates of *in situ* populations and dominant phytoplankton species. The production data was to verify as to whether or not estimated growth rates were viable. Also, once both production and growth rates were estimated, a more comprehensive picture could be attained with regard to phytoplankton development and the factors controlling this development. The next stage of work also considers grazing as a loss process.

5.7 Summary

1. Attenuation was influenced by discharge in both rivers and by chlorophyll *a* concentration in the Trent. Maximum K_d values of 9 and 11.6 m^{-1} were observed for the Trent and Ouse, respectively. These occurred during flood events.
2. Attenuation of light at the red end of the spectrum was influenced by chlorophyll *a* concentration for both the Trent and Ouse. A positive correlation existed between attenuation at 675 nm and chlorophyll *a* concentration.

3. Chlorophyll *a* concentration and discharge were the most important factors influencing light attenuation in the Trent and Ouse. Humic and fulvic acids were also considered as important for the Ouse.
4. Rates of P_{max} (net) were maximal in spring and summer (637 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1}) and minimal in winter (-136 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1}) for the Trent. No clear seasonal pattern was observed for the Ouse. Although, apart from a potentially erronious maximum rate of 2019 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1} , a maximum of 945 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1} was observed in spring and a minimum of –268 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1} in winter. Rates of P_{max}(net) showed a positive correlation with temperature and average daily irradiance.
5. Rates of respiration were low during spring, falling to minima of 13 and 10 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1} and increased during summer to seasonal maxima of 134 and 1043 μmol O_2 (mg chl *a*)$^{-1}$ h^{-1} for the Trent and Ouse, respectively. A clearer seasonal pattern was observed for the Trent than the Ouse. However, for both rivers, a positive correlation was observed between respiration rate and temperature.
6. Respiration rates of algae grown in culture showed a similar response to temperature to the response *in situ*. Rates increased with increasing temperature and were similar to *in situ* rates. Rates were similar between centric diatoms and a green algal species. However, rates of respiration at 20°C were higher than for the centric diatoms.
7. For the Trent, column and areal production followed a similar seasonal pattern. Maximal rates of column production of 1114 and 2721 μmol O_2 (mg chl *a*)$^{-1}$ d^{-1} and rates of areal production of 546 and 536 μmol O_2 m^{-2} d^{-1} were observed during spring and early summer for the Trent and Ouse, respectively, when temperatures and respiration rates were relatively low. During summer, as temperature and respiration rate increased, rates of production declined and negative rates were observed. Rates remained low through the winter although this was the result of low light and temperature.
8. The most important factors influencing column and areal production were chlorophyll a concentration and respiration. Irradiance and temperature were considered as indirectly influencing production as a result of their influence upon rates of respiration and P_{max} (net).
9. When production was modelled using different values for depth, K_d and respiration, maximal differences were observed during spring and summer but not for winter. Therefore, it was considered that a change in these variables could have marked effects upon production, especially during spring and summer.
10. As a result of the turbidity of the Trent and Ouse photoinhibition was not important in controlling production in these turbid rivers.

6 GROWTH AND LOSS

6.1 Downstream growth and loss of phytoplankton populations

Rates of *in situ* growth and loss were estimated to comply with objectives 2 and 3 of the overall aims of the project (Section 1.11) to assess the seasonal growth and loss of phytoplankton populations. *In situ* rates of growth were calculated for the Trent as change in chlorophyll *a* with distance downstream (Section 3.71). *In situ* rates of growth and loss were also estimated from grazing and production studies (Sections 3.74 & 5.4, respectively). These rates were compared with growth rates of 'dominant' phytoplankton species in culture (Section 3.73).

Loss rates were estimated from grazing rate studies conducted in the laboratory (Section 3.74). Growth and loss estimates concentrated on the Trent as a greater number of sites over a large spatial range were sampled. Estimations for the Ouse were restricted to grazing rate estimations during 1996.

At the time of the annual maximum, chlorophyll *a* concentration increased markedly downstream (Figs 6.1, 6.2, 6.3). During 1995, the first year of sampling, measurements were made on changes with chlorophyll *a* concentration with distance downstream at seven sites over a 63 km length of the Trent; from Cavendish Bridge to Cromwell (Fig. 6.1). Between April and July 1995, there was a downstream increase in the average chlorophyll *a* concentration of 51 % (45 to 68 $\mu g\ l^{-1}$, Fig. 6.1). During the first year of sampling, this large increase in chlorophyll *a* with distance downstream was greatest on 10 May 1995 with an increase of 66 % (49.9 to 146.7 $\mu g\ l^{-1}$). In contrast, between August and October there was a downstream decrease of 42 % (19 to 11 $\mu g\ l^{-1}$, Fig. 6.1).

The second year of sampling included one survey (9 May 1996) starting further upstream, with ten sites (Fig. 6.2) over a 103 km length of river (Section 3.71). In this case the chlorophyll *a* concentration increased by 293 % (27 to 106 $\mu g\ l^{-1}$, Fig. 6.2). This showed an exponential rate of increase in chlorophyll *a* concentration with distance of 0.0115 km^{-1} (growth rate of 0.19 d^{-1}, Fig. 6.2).

Seasonal monitoring of the tributaries during 1995 showed relatively low phytoplankton chlorophyll *a* concentrations in the Derwent and Devon, but concentrations in the Soar were similar in magnitude to the Trent at Cromwell (Fig. 6.1). On the whole, tributaries did not provide a major input of phytoplankton chlorophyll *a* to the main river, suggesting that increase in phytoplankton chlorophyll *a* downstream was a result of *in situ* growth.

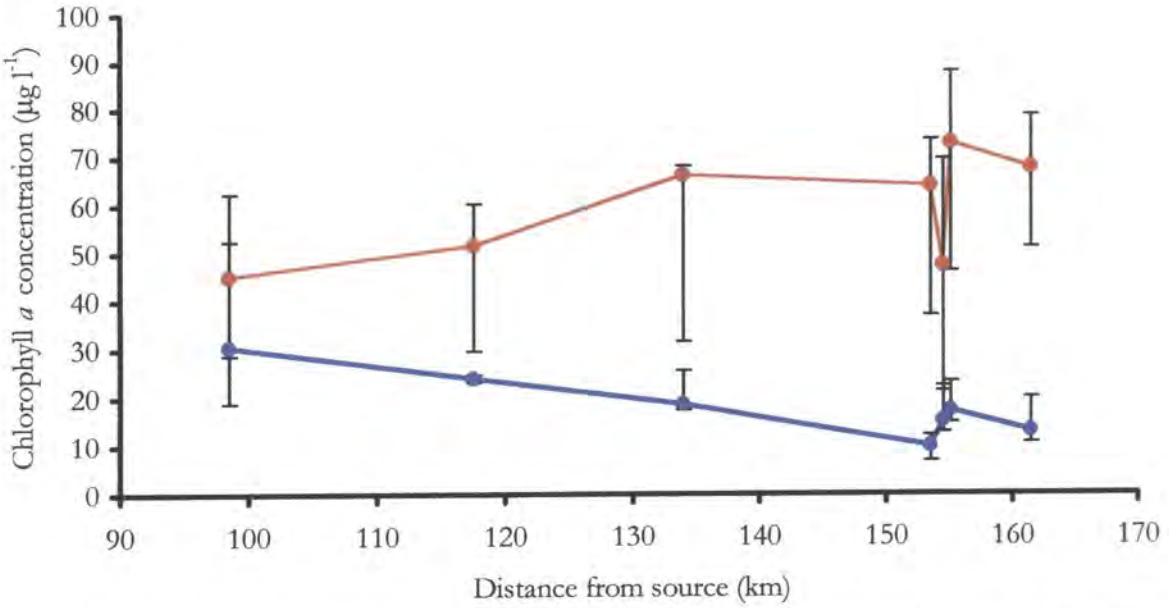

Figure 6.1 Spatial variation in mean chlorophyll *a* concentration for seven sites on the Trent during April - June (red circles) and July - October (blue circles) 1995. The sites are in order of increasing distance downstream (Cavendish Bridge, Wilford, Gunthorpe, Kelham, Newark, South Muskham and Cromwell). Bars show maximum and minimum chlorophyll *a* concentration measured.

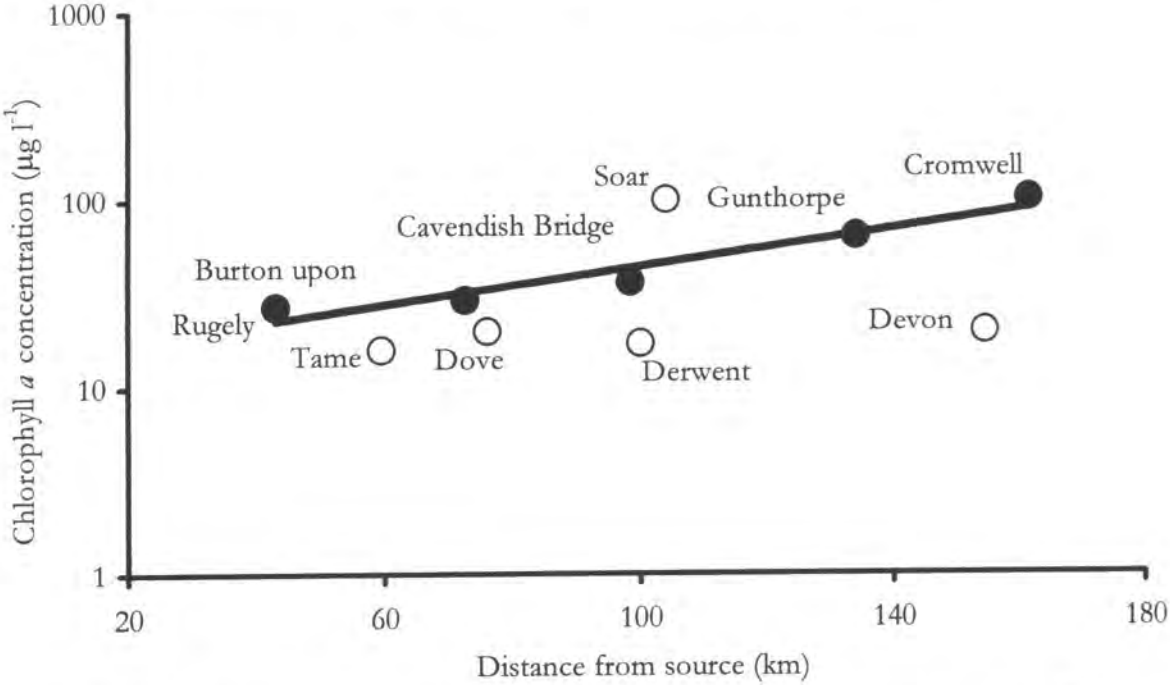

Figure 6.2 Downstream increase in chlorophyll *a* concentration at five sites on the Trent (closed circles) and contribution by five tributaries (open circles) during the biomass maximum, 9 May 1996. The line represents the linear regression of the logarithm of chlorophyll a concentration against distance downstream ($r=0.98$, $P<0.001$). The constant slope is consistant with exponential growth.

The study conducted on 9 May 1996 confirmed the low contribution of the tributaries. Chlorophyll *a* concentrations in the Tame, Dove, Derwent and Devon were relatively low (between 16 and 20 $\mu g\ l^{-1}$) in comparison to the main river (between 27 and 106 $\mu g\ l^{-1}$) as shown in Figure 6.2. However, concentrations in the Soar (108 $\mu g\ l^{-1}$) exceeded the interpolated concentration of chlorophyll *a* at the confluence with the Trent (Fig. 6.2).

The three sites furthest downstream on the Trent sampled on 9 May 1996; Cavendish Bridge, Gunthorpe and Cromwell (Fig. 6.2), were also sampled in unison throughout 1995, 1996 and 1997. The exponent of change in chlorophyll *a* concentration with distance, and resulting rate of growth or loss, (Section 3.71) were calculated for these three sites from April 1995 to June 1997 (Fig. 6.3). A similar pattern of downstream growth in spring existed for all three years and downstream decrease in phytoplankton chlorophyll *a* in summer and autumn was shown for 1995 and 1996. Sampling did not continue into late summer and autumn 1997 so the growth rates during this period are not known. In spring, the concentration of chlorophyll *a* increased on passing downstream at rates of 0.020, 0.028 and 0.04 km^{-1} in 1995, 1996 and 1997 respectively (Fig. 6.3). This corresponded with growth rates of 0.48, 0.59 and 0.70 d^{-1} respectively (Fig. 6.3). In late summer and autumn, however, the concentration decreased downstream at rates of 0.030 and 0.029 km^{-1} in 1995 and 1996, corresponding with growth rates of -0.46 and -0.76 d^{-1}, respectively (Fig. 6.3).

Temperature was the main environmental variable influencing the pattern of downstream growth and loss. Figure 6.4 shows the relationship between rates of growth and loss of phytoplankton chlorophyll *a* and temperature for the Trent. The population was categorised into the times when either centric diatoms or Chlorophyta dominated (i.e. comprised the greater proportion of the population).

The downstream increase in phytoplankton chlorophyll *a* when the population was dominated by centric diatoms showed a significant positive relationship with temperature ($r^2=0.57$, $P<0.01$, $n=21$; Fig 6.4). Although no positive relationship existed between downstream growth or loss and temperature when the population was Chlorophyta dominated ($r^2=0.003$, $n=14$; Fig 6.4), most data points showed a downstream loss of phytoplankton chlorophyll *a* (Fig. 6.4). This suggests that downstream growth occurred when the population was dominated by centric diatoms, during spring, and downstream loss occurred when dominated by Chlorophyta, during summer.

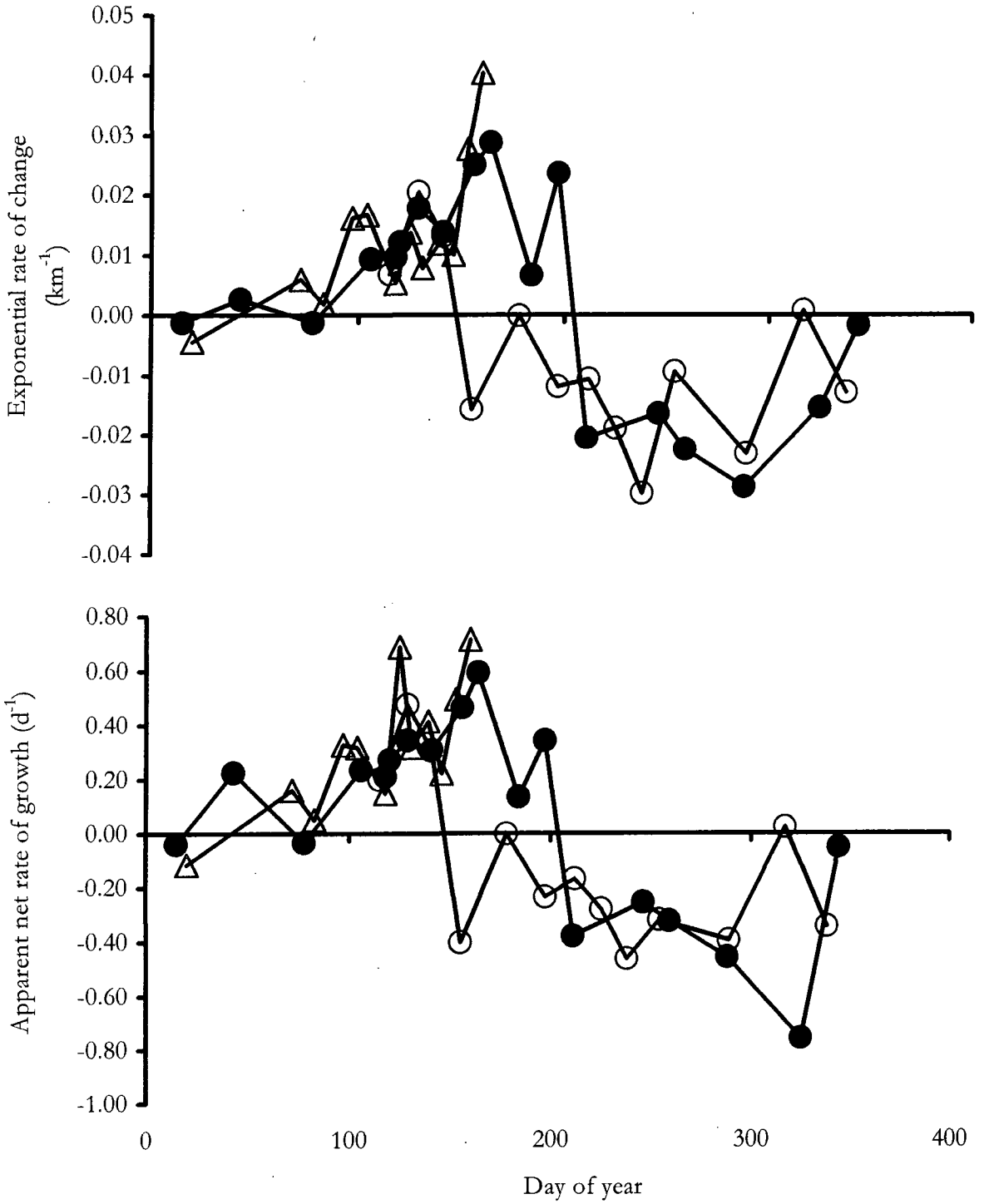

Figure 6.3 Seasonal pattern of exponential rate of change of chlorophyll *a* concentration with distance downstream (top figure) and calculated apparent net rate of growth (bottom figure) in 1995 (open circles), 1996 (closed circles) and 1997 (open triangles) based on measurements for the Trent at Cavendish Bridge, Gunthorpe and Cromwell.

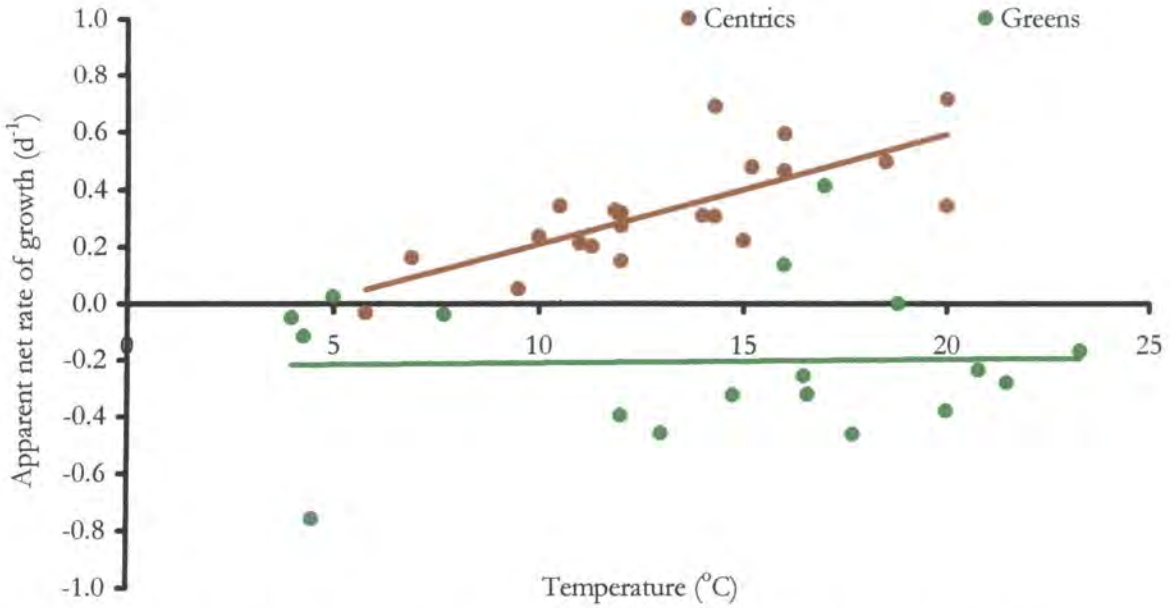

Figure 6.4 Relationship between downstream increase or decrease in phytoplankton chlorophyll *a* and river temperature. Data are separated into populations dominated by centric diatoms or green algae. A significant positive relationship exists between temperature and downstream growth of the centric diatom dominated population ($r=0.75$, $P<0.001$, $n=22$). The relationship was not significant for green algae.

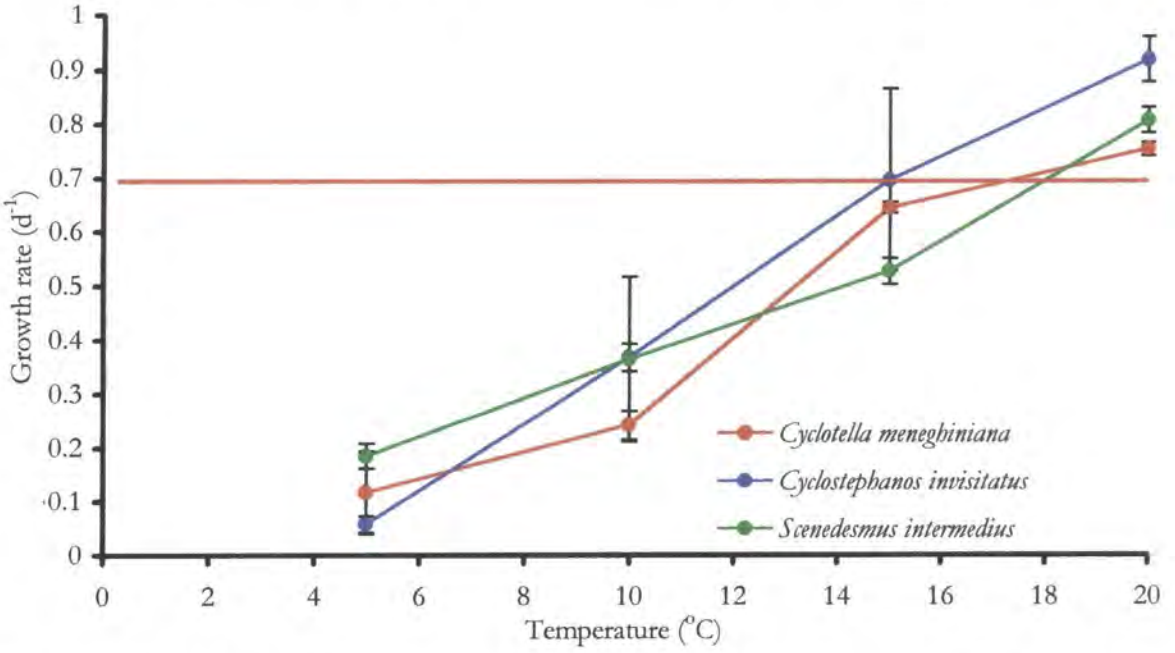

Figure 6.5 Growth rates of three phytoplankton species in culture; two centric diatoms and one green at four temperatures and at saturating light (40-50 µmol m^{-2} s^{-1} for 5 & 10°C, 70-80 µmol m^{-2} s^{-1} for 15 and 20°C) under a 16:8 hour L:D photoperiod. Incubations were performed in triplicate. Bars show standard deviation. Red horizontal line shows doubling rate per day.

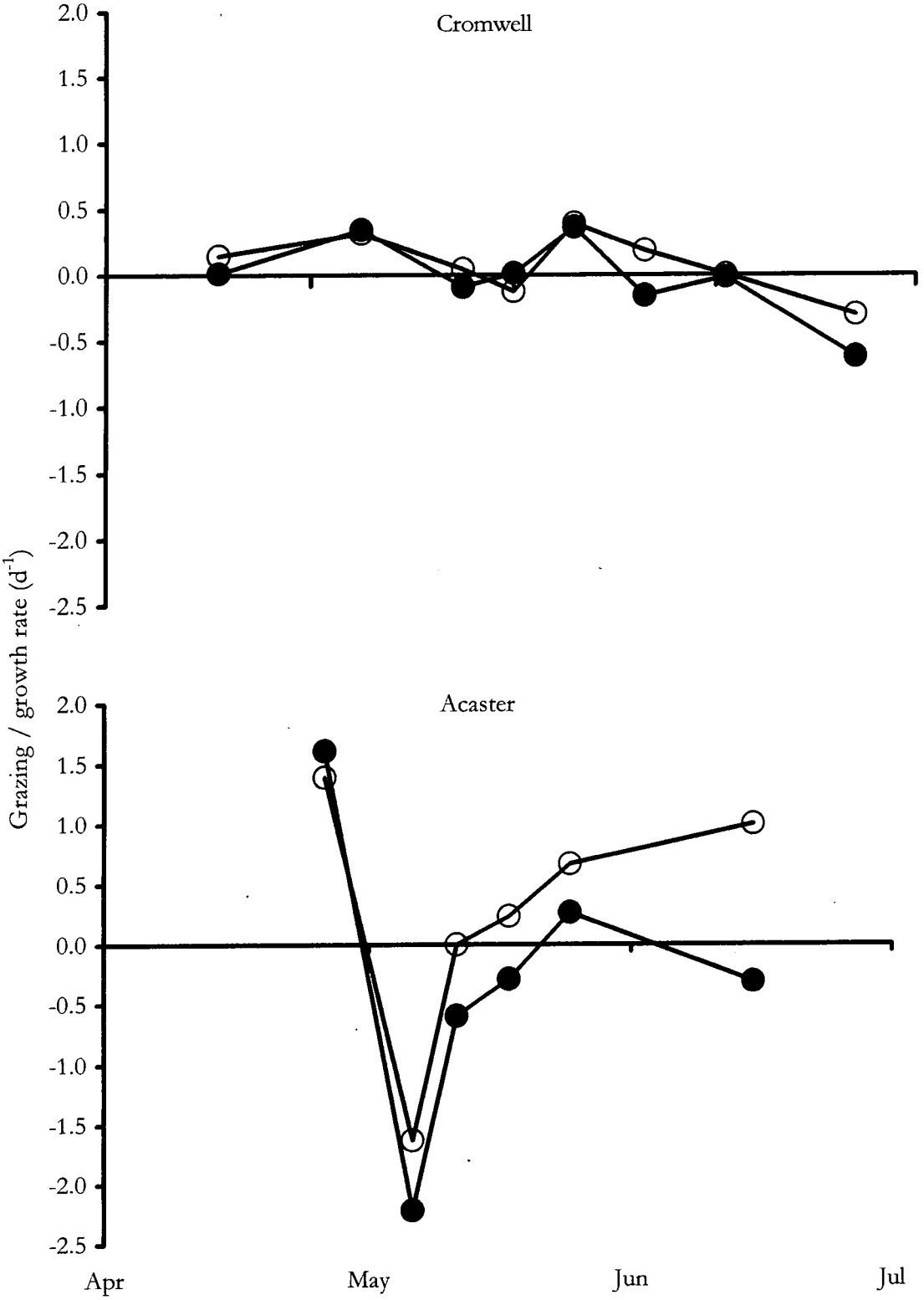

Figure 6.6 Grazing (closed circles) and growth rates (open circles) derived from a series of dilutions of river water for the tidal limits of the Trent and Ouse at Cromwell and Acaster, respectively during 1996. Dilutions were incubated for between 24 and 48 hours.

6.2 Growth of phytoplankton in culture as a function of temperature

To complement *in situ* estimations of growth, the growth rates of three species of phytoplankton isolated for the Trent and Ouse were estimated in culture at four temperatures and at saturating light (Section 3.73). Figure 6.5 shows the growth rates of these three species in culture. All three species exhibit increased growth rates with increasing temperature. The growth rate of *Cyclotella meneghiniana* increased from 0.12 d^{-1} at 5°C to 0.75 d^{-1} at 20°C ($r=0.96$, $P<0.01$, $Q_{10}=5.69$; Fig. 6.5). Growth of *Cyclostephanos invisitatus* increased from 0.06 d^{-1} at 5°C to 0.92 d^{-1} at 20°C ($r=0.97$, $P<0.001$, $Q_{10}=4.91$) and growth of *Scenedesmus intermedius* increased from 0.18 d^{-1} at 5°C to 0.81 d^{-1} at 20°C ($r=0.78$, $P<0.1$, $Q_{10}=2.29$; Fig. 6.5). Analysis of the data (ANOVA) showed that there was no overall difference between growth of any of the species over the 5 to 20°C temperature range. However, at 5°C a significant difference existed between growth of the Chlorophyta (*S. intermedius*) and the two species of centric diatoms (*C. meneghiniana* and *C. invisitatus*) with *S. intermedius* exhibiting higher growth rates than both *C. meneghiniana* (ANOVA, $P=0.004$) and *C. invisitatus* (ANOVA, $P=0.002$). Interpolation of the data showed that growth rates of a doubling per day (0.69 d^{-1}) were achieved at similar temperatures of 15, 17 and 18°C for *C. invisitatus, C. meneghiniana* and *S. intermedius* respectively (Fig. 6.5). This highlights the similar growth rate of the three species in culture.

6.3 Growth and loss rates derived from grazing rate estimations

Growth rates were also calculated when investigating the loss from zooplankton grazing (Section 3.74). Figure 6.6 shows the estimated growth rates and apparent grazing rates measured as an increase or decrease in phytoplankton chlorophyll *a*. Rates of growth and grazing were closely correlated for both Cromwell ($r=0.92$, $p<0.001$, $n=32$) and Acaster ($r=0.92$, $p<0.001$, $n=24$), shown in Figure 6.7.

The magnitude and temporal pattern of growth and grazing rates differed between the Trent and Ouse. Two grazing and growth peaks occurred at Cromwell. On 30 April and 21 May 1996, growth rates reached 0.32 and 0.39 d^{-1} respectively while grazing rates showed a similar pattern and similar rates and reached 0.35 and 0.37 d^{-1} respectively. Grazing and growth both decreased between 30 April and 21 May 1996. After 21 May, growth decreased to a minimum of -0.3 d^{-1} and grazing to a minimum of -0.62 d^{-1} on 18 June 1996.

For the Ouse at Acaster, maximal growth and grazing rates of 1.39 and 1.61 d^{-1} respectively occurred on 30 April 1996. Both growth and grazing rates decreased rapidly to mimima of -1.63 and -2.2 d^{-1} respectively. Growth rates then steadily increased to 1.0 d^{-1} on 18 June 1996. Grazing also increased to 0.26 d^{-1} on 28 May but declined to -0.31 d^{-1} on 18 June 1996 as the growth rate increased.

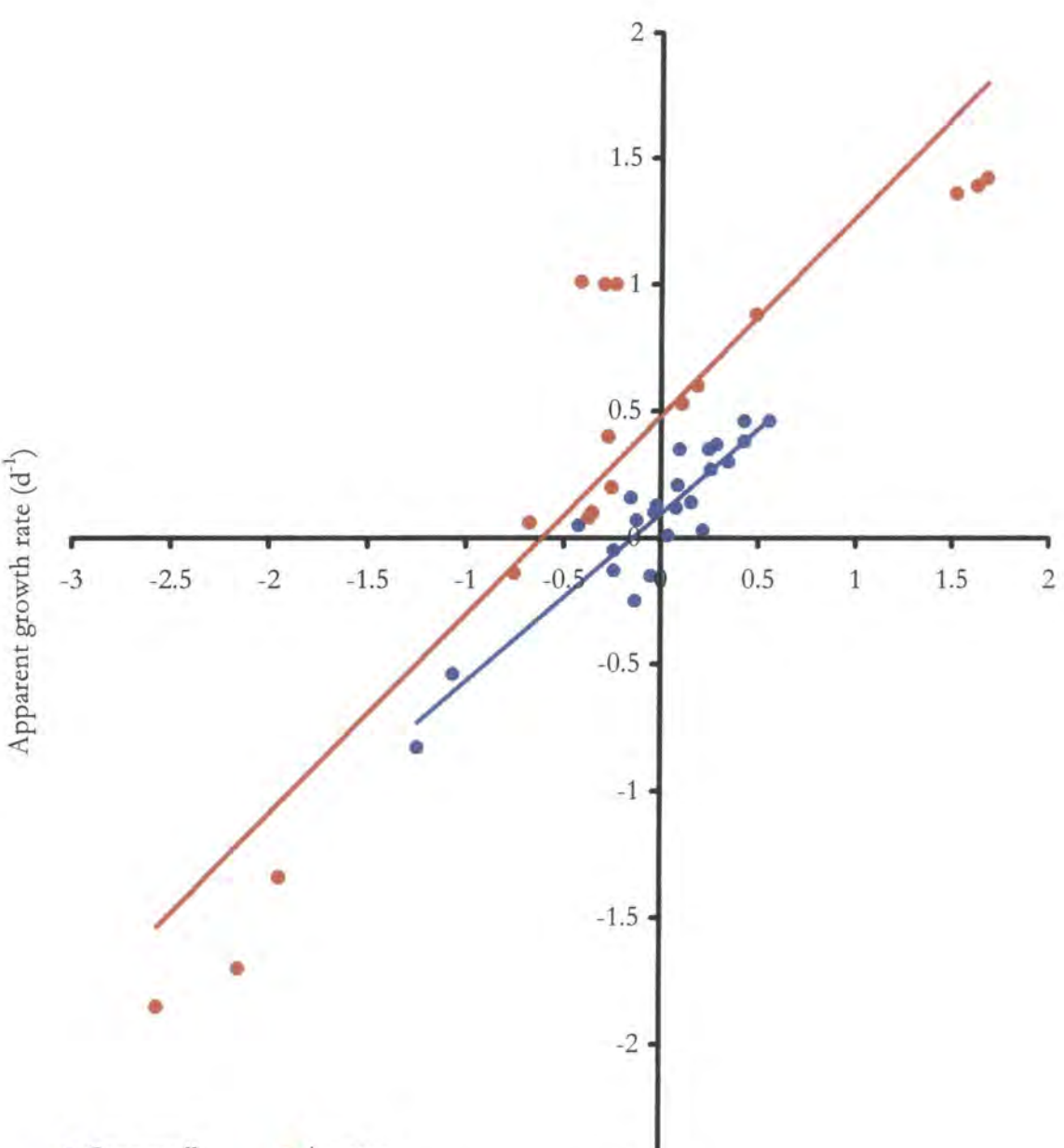

Figure 6.7 Relationship betweent apparent growth rate of phytoplankton and grazing rate by zooplankton for the Trent at Cromwell and Ouse at Acaster derived from data in Figure 6.6. Data are plotted for incubations made in triplicate on each occasion. A positive correlation exists for both Cromwell ($r=0.92$, $P<0.001$, $n=32$) and Acaster $r=0.92$, $P<0.001$, $n=24$).

Negative grazing rates (Fig. 6.6) were unexpected as it was assumed that if no grazing occurred then a grazing rate with a value of zero would result. These negative rates are discussed in Section 8.33. Where a positive grazing rate occurred, grazing by zooplankton could account for the loss of between 1.3 (16 April 1996) and 44.3 % (21 May 1996) of phytoplankton chlorophyll *a* for the Trent and between 30 (28 May 1996) and 400 % (30 April 1996) of the phytoplankton chlorophyll *a* for the Ouse. A significant negative correlation between grazing and temperature ($r=0.4$, $P<0.02$, $n=32$) and a positive correlation between grazing and discharge ($r=0.48$, $P<0.01$, $n=32$) existed for the Trent at Cromwell. A significant relationship was only observed for grazing rate and discharge for the Ouse at Acaster where a negative correlation existed ($r=0.37$, $P<0.1$, $n=24$).

Relationships between growth rate and environmental variables (calculated from grazing rate estimations) were similar to those observed between grazing rate and environmental variables. For the Trent at Cromwell, a negative correlation was observed between growth rate and temperature ($r=0.36$, $P<0.05$, $n=32$) and a positive correlation ($r=0.56$, $P<0.001$, $n=32$) between growth rate and discharge. In contrast, for the Ouse at Acaster, a negative relationship between growth rate and discharge was observed ($r=0.68$, $P<0.001$, $n=24$).

Although data for zooplankton species composition, population density or biomass were not available for this study, preliminary investigations showed that rotifers such as *Keratella* spp. and protozoans such as *Strobilidium* spp. dominated the zooplankton at both Cromwell and Acaster. Benthic filter feeders may also play an important role in the loss of phytoplankton to grazing. Although no quantitative data exists for this subject, large numbers of *Unio* sp. were found on gravel spoil, dredged from the Trent upstream of Cromwell.

6.4 Comparison of growth rates derived from various methods

Growth rates were also calculated from modelled rates of phytoplankton production (Section 5.4). Figure 6.8 compares these results with growth rates estimated from the grazing rate experiments, *in situ* downstream growth estimates and temperature dependent growth rates of phytoplankton in culture.

Growth rates obtained from all four methods of estimation showed a similar pattern (Fig. 6.8). For *in situ* calculations, growth rates increased during spring, reaching similar maximal values of 0.33, 0.39 and 0.59 d^{-1} for production modelled, grazing rate calculated growth and growth calculated from downstream changes in chlorophyll *a* respectively (Fig. 6.8). The growth rates of species in culture (Section 6.2) are plotted as a mean of all three species investigated and are plotted at the time of year when the temperatures used in the experiment (5, 10, 15, 20°C) were experienced *in situ*. These represent the maximal rates attainable at nutrient saturation, light saturation and 16 hours of light per day at a given temperature.

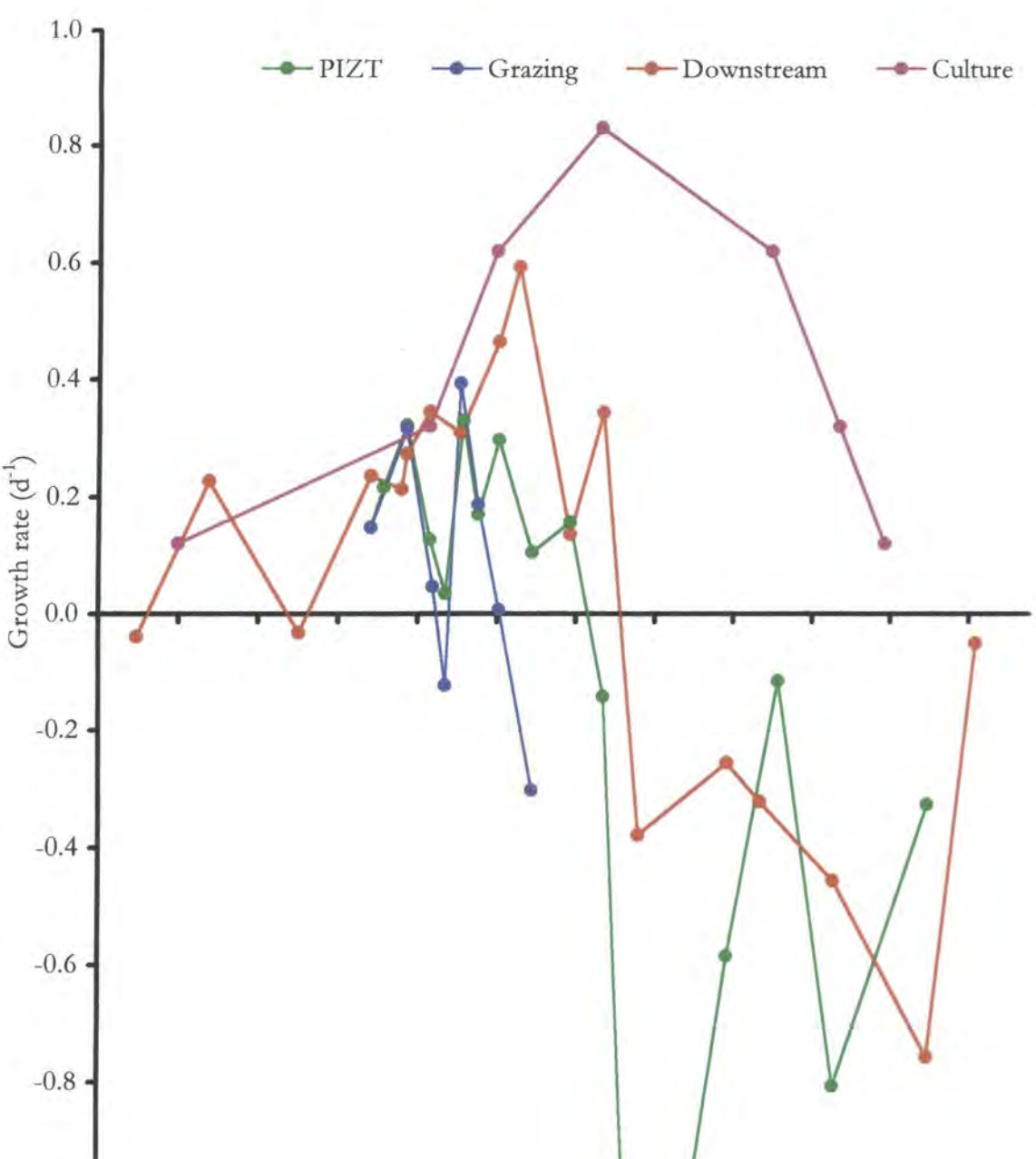

Figure 6.8 Comparison of estimated rates of growth derived from different methods; production modelled by PIZT, grazing rate experiments, downstream increase in chlorophyll *a* and mean temperature dependance of three phytoplankton species grown in culture for the Trent at Cromwell during 1996.

The growth rates of species in culture increased with temperature, but unlike the rates calculated from *in situ* measurements, did not decrease during summer. In fact, they attained a maximum growth rate of 0.83 d^{-1} on 18 June 1996 at a temperature of 20°C (Fig. 6.8). After the spring maxima, growth rates decreased during summer and declined to summer minima of –1.59, -0.3 and –0.76 d^{-1} for production modelled growth, grazing rate calculated growth and growth calculated from downstream changes in chlorophyll *a* respectively (Fig. 6.8). Growth rate estimates, calculated from grazing experiments, also declined during summer. This was not expected as light was never limiting during the grazing experiment incubations. However, growth rates calculated from grazing experiments did not decline to levels as low as other *in situ* calculations (Fig. 6.8). This may be because grazing was only measured up to the early summer, (18 June 1996).

Although growth rates calculated by different *in situ* methods differed slightly, especially during summer, rates of growth during spring were similar and the similar pattern of spring maximal rates and late summer minima (Fig. 6.8). The fact that the majority of growth rates estimated from *in situ* measurements are lower than the rates obtained for phytoplankton under ideal, laboratory conditions (Fig. 6.8) adds confidence to the *in situ* data.

6.5 Discussion

For the Trent at Cromwell *in situ* rates of growth and loss followed a similar seasonal pattern throughout the period of investigation. During spring and early summer, rates of growth increased, reaching yearly maxima in spring. During this period, the phytoplankton population was dominated by centric diatoms. Investigations concluded that the increase in growth rate upon journey downstream was correlated with temperature. Laboratory work also showed the increase in growth rate of two dominant species of centric diatom with temperature. Therefore, maximal rates of growth in spring were a result of increasing temperature and the ability of centrics to grow rapidly downstream when tempertures increase.

Rate of growth decreased during late summer and became negative, that is, net loss of phytoplankton was evident with journey downstream. During this period phytoplankton populations were dominated by green algae. During summer, water temperature increased. Laboratory studies showed the increase in growth rate of a species of green algae with increasing temperature, even when temperatures reached those experienced by *in situ* populations during the rapid decline in phytoplankton biomass during summer. However, no relationship was observed between downstream change in phytoplankton biomass and temperature for the green algal dominated populations. It was concluded that the increase in temperature influenced rates of grazing and respiration and these proceses were responsible for the downstream loss of phytoplankton from the system during summer.

Rates of growth were also negative for the majority of the winter period. This was attributable to high discharge and low light and temperature resultiung in poor conditions for phytoplankton growth.

Grazing by zooplankton was considered as unimportant apart from a couple of occasions when it was responsible for the loss of 44% of the phytoplankton of the Trent and 400% of phytoplankton of the Ouse at their respective tidal limits. Conditions responsible for the growth of phytoplankton were considered as equally important for the proliferation of zooplankton. It was considered that zooplankton was influenced by the abundance of phytoplankton rather than phytoplankton being influenced to a great degree by zooplankton. The importance of protozoa and benthic filter feeders were considered and their importance has still to be adequately quantified.

Comparison of growth of phytoplankton using calculations from downstream changes in biomass, grazing rate estimations, estimates of production and laboratory work showed a similar seasonal pattern and similar rates of growth. It was concluded that estimates of *in situ* growth were possible when compared to rates of production for all but the highest rates of growth calculated. *In situ* estimations of growth were also lower than rates calculated in the laboratory under ideal conditions. This added further confidence both *in situ* estimates of growth and production.

The last three chapters have been successful in meeting the first, second, third, and to some extent, fourth aims of the project (Section 1.11). It is now necessary to complement these data by estimating the flux of phytoplkankton in the form of phytoplankton carbon to the Humber Estuary. This will consider the fourth aim more fully and offer a comparison of phytoplankton flux from the Trent and Ouse to the Humber Estuary.

6.6 Summary

1. During spring, phytoplankton chlorophyll *a* increased downstream at up to 66% over 63 km in 1995 and up to 293 % over 103 km in 1996. Apparent growth rates of phytoplankton chlorophyll *a*, moving downstream, reached maxima of 0.48, 0.59 and 0.70 d^{-1} in 1995, 1996 and 1997, respectively.

2. During summer, phytoplankton chlorophyll *a* decreased downstream with maximal rates of loss of 0.46 and 0.76 d^{-1} in 1995 and 1996, respectively.

3. Temperature was the major environmental factor controlling the rate of growth and loss of phytoplankton chlorophyll *a* during transport downstream. During spring, when the population was dominated by centric diatoms, a positive relationship existed between temperature and growth rate ($r=0.77$, $P<0.001$, $n=21$). During summer, when the population was dominated by Chlorophyta, no significant relationship between temperature and growth rate existed. However, downstream decrease in phytoplankton chlorophyll *a* was mostly evident during times of a Chlorophyta dominated population.

4. Growth rates of three phytoplankton species in culture showed a significant positive correlation with temperature. Growth rates increased up to 20°C, whereas *in situ* growth rates decreased after rivers reached this temperature. Two centric diatoms; *Cyclotella meneghiniana* and *Cyclostephanos invisitatus*, and one Chlorophyta; *Scenedesmus intermedius*, all showed similar increased rates of growth with temperature.

5. A close positive relationship existed between estimated rates of phytoplankton growth and zooplankton grazing, estimated from grazing rate coefficients for Cromwell ($r=0.92$, $P< 0.001$, $n=32$) and Acaster ($r=0.92$, $P<0.001$, $n=24$). Grazing accounted for between 1.3 and 44.3% and between 30 and 400% of phytoplankton chlorophyll at Cromwell and Acaster, respectively.

6. Grazing was controlled primarily by temperature and discharge. At Cromwell a significant but weak negative relationship existed between grazing and temperature ($r=0.4$, $P<0.02$, $n=32$) and a positive relationship existed between grazing and discharge ($r=0.48$, $P<0.01$, $n=32$). At Acaster a negative relationship between grazing and discharge ($r=0.37$, $P<0.1$, $n=24$) was observed.

7. Growth rates, calculated from grazing experiments showed similar relationships to environmental variables as grazing rates. At Cromwell, growth rate decreased with increasing temperature ($r=0.56$, $p<0.001$, $n=32$) and increased with increasing discharge ($r=0.56$, $p<0.001$, $n=32$). However, at Acaster a negative relationship was observed between growth rate and discharge ($r=0.68$, $p<0.001$, $n=24$).

8. When compared, *in situ* apparent rates of growth calculated from productivity, grazing experiments, change in chlorophyll with movement downstream and from species in culture showed a similar pattern and similar rates of growth in spring. It was concluded that in situ rates of growth estimated during the project were reliable.

7. PHYTOPLANKTON CARBON FLUX

7.1 Estimation of the carbon to chlorophyll ratio

To estimate the flux of autochthonous carbon to the estuarine waters of the Humber Estuary the flux of phytoplankton carbon was calculated for the tidal limits of the Trent and Ouse. These calculations would give an overall picture of the importance of phytoplankton to the riverine carbon budget as well as providing an estimation of the contribution of phytoplankton carbon to the particulate carbon loading to the Humber Estuary.

The flux of phytoplankton or 'living' carbon from the Trent and Ouse out to the Humber Estuary was estimated from discharge, chlorophyll *a* concentration and an estimation of the carbon to chlorophyll ratio of the phytoplankton population (Section 3.71). Estimates concentrated on the tidal limits of the Trent and Ouse at Cromwell and Acaster, respectively, as these were the points where riverine carbon would enter the tidal section of the rivers.

An estimation of the carbon to chlorophyll ratio was needed to calculate the flux of carbon from the flux of phytoplankton chlorophyll *a*. Figure 7.1 shows the relationship between chlorophyll *a* concentration and particulate organic carbon (POC) determined according to the method of Tipping *et al.* (1997). A significant relationship existed between chlorophyll *a* concentration and POC for Cromwell ($r=0.69$, $p<0.001$, $n=104$; Fig. 7.1) but no significant relationship existed for the Ouse at Acaster. The gradient of the line of linear regression was used as an estimate of the carbon to chlorophyll ratio of the phytoplankton population. At Cromwell, from June 1995 to May 1997, a ratio of 33:1 was calculated (Fig 7.1). As no significant relationship existed for Acaster, the value calculated for Cromwell was also used as an estimate of the carbon to chlorophyll ratio at Acaster. As no POC data were available for the Trent at Cavendish Bridge and Gunthorpe the carbon to chlorophyll ratio calculated for Cromwell was also used in subsequent calculations of phytoplankton flux for these sites.

7.2 Time series of phytoplankton carbon flux

The carbon to chlorophyll ratio was used, along with average weekly discharge for each site and chlorophyll *a* concentration, to calculate weekly and annual phytoplankton carbon fluxes. Figure 7.2 shows the calculated weekly phytoplankton carbon fluxes for three sites on the Trent; Cavendish Bridge, Gunthorpe and Cromwell, and one site on the Ouse; Acaster. The average weekly discharge for Cromwell and Acaster is also shown.

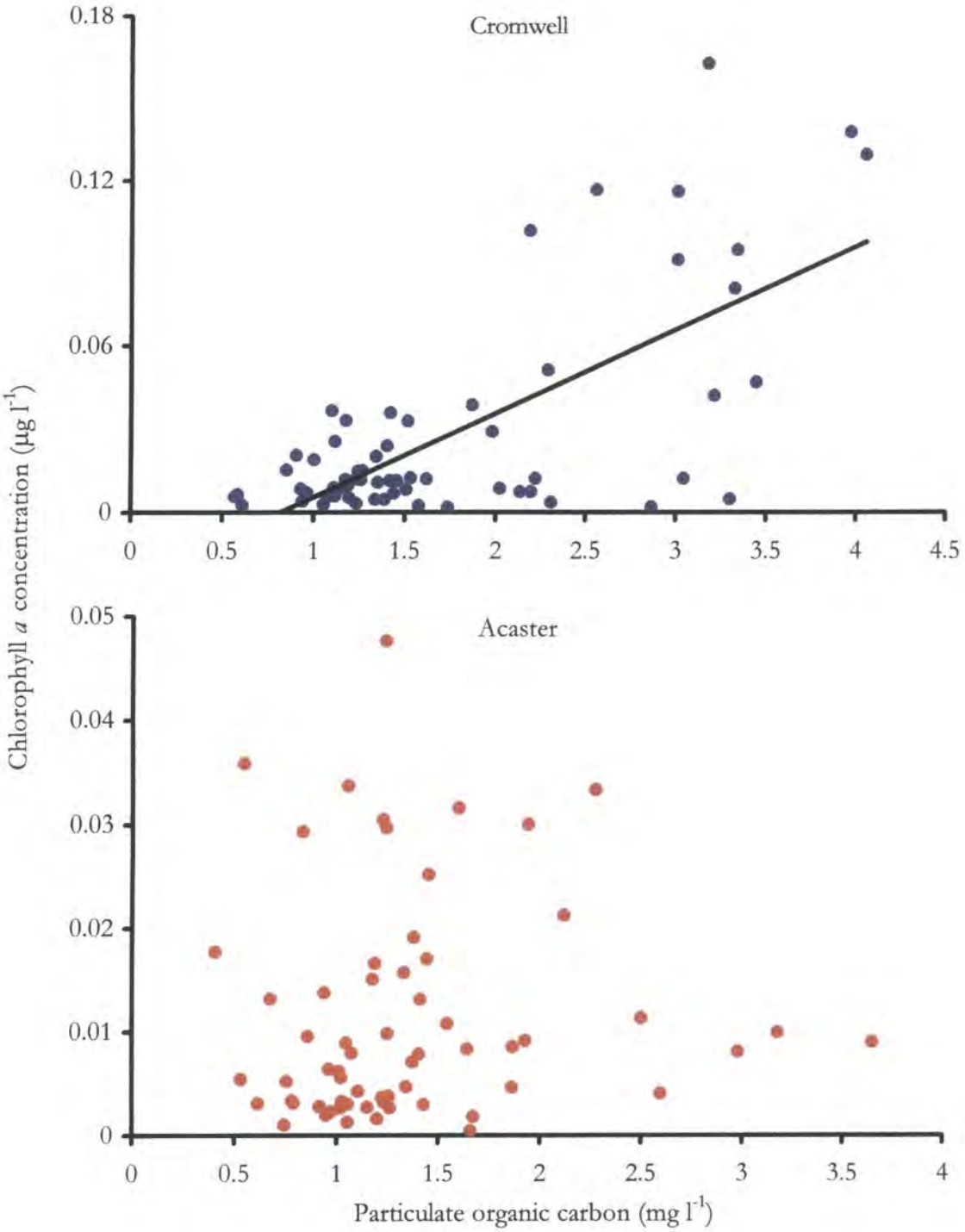

Figure 7.1 Relationship between suspended chlorophyll *a* concentration and POC for the tidal limits of the Trent (top figure) and Ouse at (bottom figure) from June 1995 to May 1997. A carbon to chlorophyll ratio of 33:1 was calculated for Cromwell ($r=0.69$, $P<0.001$).

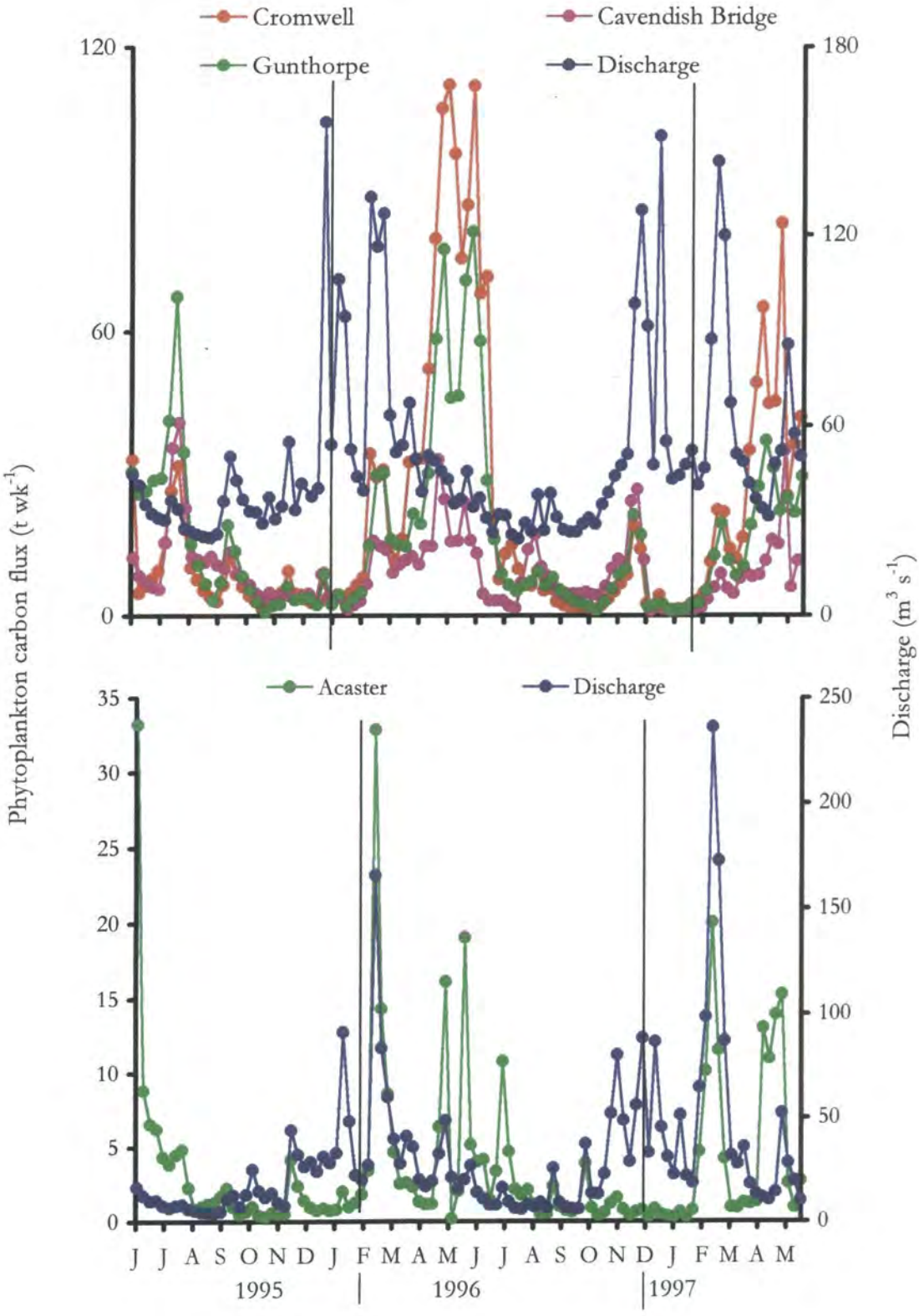

Figure 7.2 Weekly phytoplankton carbon flux for the Trent (top figure) and Ouse (bottom figure). Weekly average discharge is also shown for the tidal limits of the Trent and Ouse.

For both the Trent and Ouse, three major peak events occurred. At the uppermost site on the Trent; Cavendish Bridge, maximal phytoplankton carbon fluxes of 19, 32 and 57 t wk^{-1} occurred on 23 July 1995, 28 April 1996 and 11 May 1997, respectively (Fig. 7.2). The flux of phytoplankton carbon increased with increasing distance down the Trent. At Gunthorpe, maximal fluxes of 33, 33 and 32 t wk^{-1} occurred on 19 July 1995, 3 June 1996 and 19 April 1997, respectively (Fig. 7.2). At Cromwell, the tidal limit, maximal fluxes of 45, 43 and 52 t wk^{-1} were observed on 3 June 1995, 8 May 1996 and 7 May 1997, respectively (Fig. 7.2). The peaks in phytoplankton carbon flux for the Trent occurred during times of low discharge and high chlorophyll *a* concentration in spring (Fig. 7.2). In contrast, at Acaster, two out of the three large peaks in phytoplankton carbon flux occurred during high discharge periods during winter (Fig. 7.2). Maximal fluxes of 33, 33 and 20 t wk^{-1} were calculated for 3 June 1995, 17 February 1996 and 22 February 1997, respectively (Fig. 7.2). The two peaks in February 1996 and 1997 corresponded with peak discharge events of 165.9 and 236.2 m^3 s^{-1}, respectively (Fig. 7.2).

For the Trent, minimum fluxes of phytoplankton carbon occurred during the autumn and winter months. At Cromwell, minimum fluxes of 1.5, 1.1 and 1.4 t wk^{-1} occurred on 21 October 1995, 17 October 1996 and 22 January 1997 (Fig. 7.2). At Gunthorpe, minimum fluxes of 0.7, 1.1 and 1.3 t wk^{-1} were calculated and at Cavendish Bridge, concentrations of 3, 1.3 and 0.9 t wk^{-1} were the minimum fluxes calculated on 17 October 1995, 21 January 1996 and 12 January 1997, respectively (Fig. 7.2). For the Ouse, minimum fluxes of phytoplankton carbon were calculated during both winter and spring periods. Minimum fluxes of 0.3, 0.2 and 0.3 t wk^{-1} were calculated for the Ouse at Acaster on 21 October 1995, 11 May 1996 and 25 January 1997 (Fig. 7.2).

7.3 Contribution of phytoplankton carbon to POC

The contribution of phytoplankton carbon to POC was greatest during the spring and summer months in the Trent. Figure 7.3 shows the relationship between phytoplankton carbon concentration and POC concentration. During the spring and summer months, the flux of phytoplankton carbon increased with increasing POC concentration ($r=0.82$, $p<0.001$, $n=33$; Fig. 7.3). However, no such relationship existed for the Trent during the autumn and winter months (Fig. 7.3) or for the Ouse at Acaster. This suggests that sources other than phytoplankton carbon were more important in the contribution to POC on these occasions. On six occasions, the phytoplankton carbon flux was greater than the flux of POC. This is a result of a slight overestimation of the carbon to chlorophyll ratio.

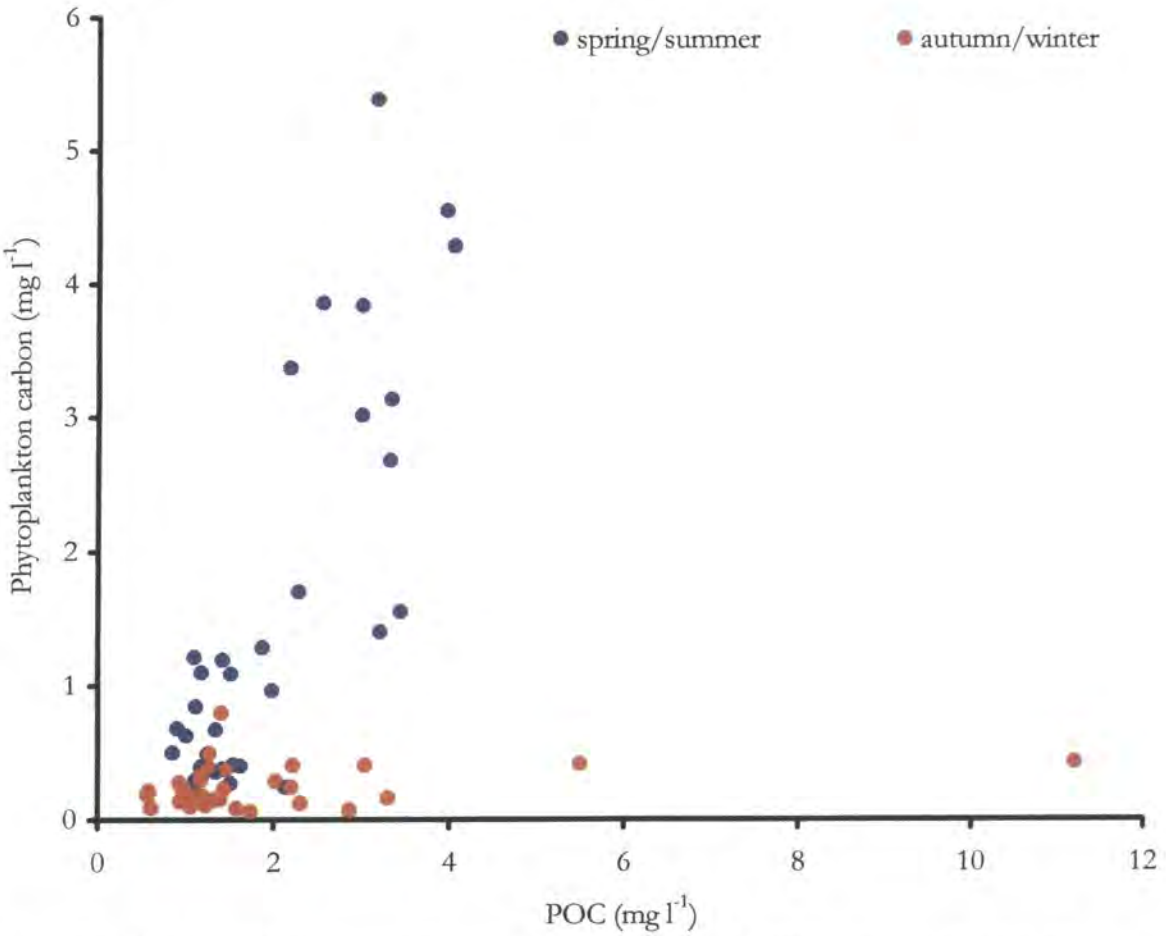

Figure 7.3 Relationship between phytoplankton carbon and POC from June 1995 to May 1997 for the Trent at Cromwell.

For the Trent at Cromwell, phytoplankton carbon contributed 77% of all spring and summer POC and 11% of autumn and winter POC during June 1995 to 31 May 1997. Phytoplankton carbon contributed to 49% of spring and summer POC for the Ouse at Acaster which was a lower contribution than for the Trent at Cromwell. The contribution, 11%, of autumn and winter POC was comparable to the Trent at Cromwell.

7.4 Factors influencing phytoplankton carbon flux

Phytoplankton carbon flux was controlled mainly by the chlorophyll *a* concentration in the Trent and Ouse. Chlorophyll *a* concentration accounted for 69, 89, 92 and 42% of the variation in phytoplankton carbon flux for the Trent at Cavendish bridge, Gunthorpe, Cromwell and the Ouse at Acaster, respectively (Fig. 7.4). Chlorophyll *a* concentration was, together with discharge, used to calculate phytoplankton carbon flux and so a relationship would be expected. The relationship does, however, indicate the influence of both chlorophyll and discharge upon phytoplankton carbon flux. A linear relationship, however, was not found between discharge and phytoplankton carbon flux at any of the sites on the Trent. However, a general trend of a decrease in phytoplankton carbon with an increase in discharge was shown for the Trent (Fig. 7.4). Discharge accounted for only 20% of the variation of phytoplankton carbon flux for the Ouse (Fig. 7.4). This suggests that phytoplankton carbon flux was regulated mainly by the concentration of chlorophyll *a* in the Trent (Fig. 7.4). For the Ouse at Acaster, chlorophyll *a* primarily controlled phytoplankton carbon flux, although discharge was also an important factor (Fig. 7.4). The combined data of Figures 7.2, 7.3 and 7.4 suggest that large fluxes of phytoplankton carbon occurred in the Trent during periods of low discharge and high chlorophyll *a* concentration, during high phytoplankton populations blooms.

For the Ouse at Acaster, no clear pattern existed although both chlorophyll *a* and discharge appeared to be important in controlling the flux of phytoplankton carbon. Large fluxes often occurred when the concentration of chlorophyll *a* was low as a result of increased discharge during large flood events (Fig. 7.2).

7.5 Annual phytoplankton carbon flux

Figure 7.5 shows the total phytoplankton carbon flux on an annual basis, calculated for three sites on the Trent; Cavendish Bridge, Gunthorpe and Cromwell, and the Ouse at Acaster. Flux is calculated for two years data; June 1995 to May 1996 and June 1996 to May 1997. For the Trent, flux increased on movement downstream during both years. An increase from 571 to 1141 t yr^{-1} during the first year (June 1995 to May 1996) and from 410 to 967 t yr^{-1} during the second year (June 1996 to May 1997) from Cavendish Bridge to Cromwell represents an increase of 200 and 236%, respectively, over the 63 km stretch of river studied.

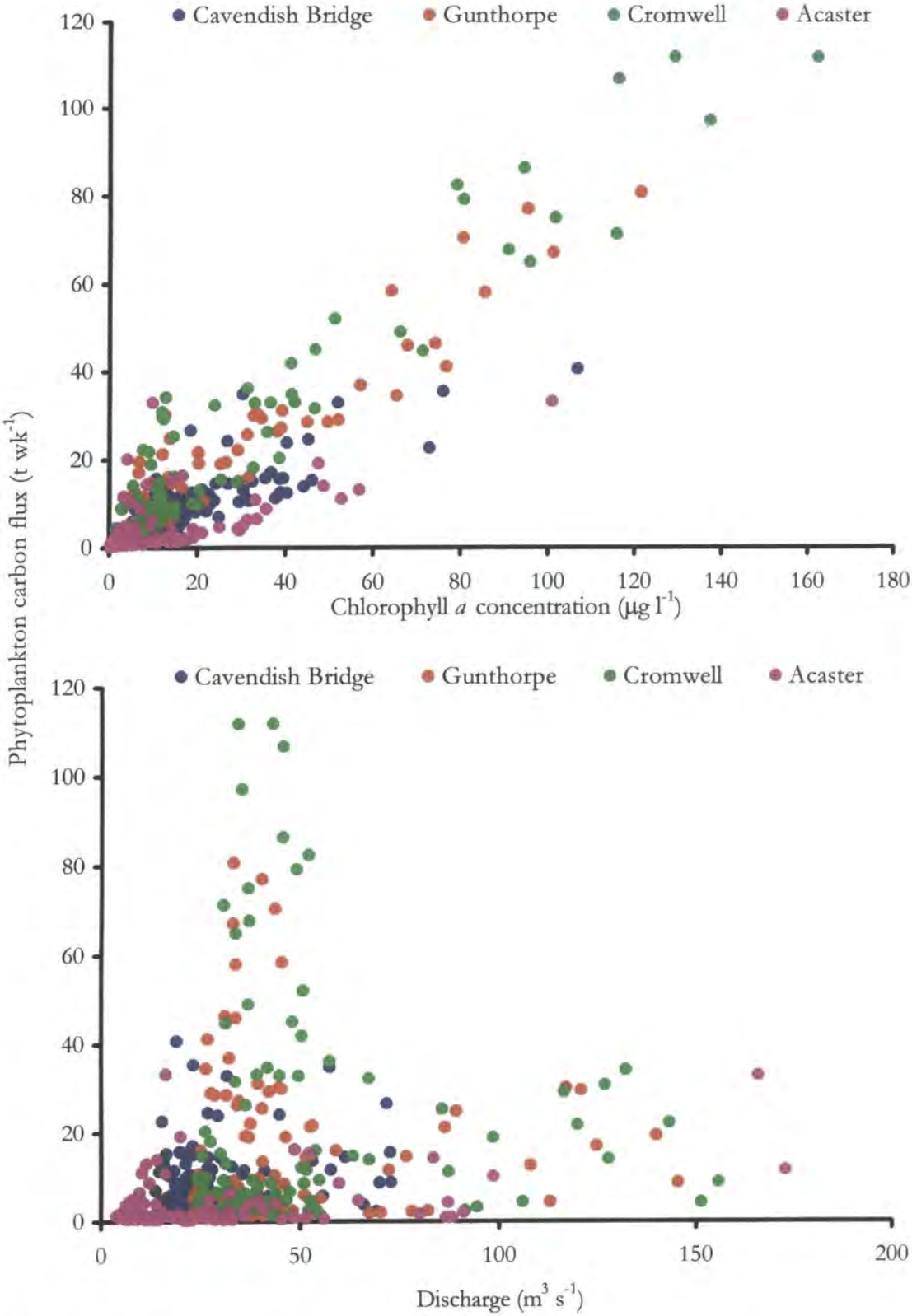

Figure 7.4 Relationship between phytoplankton carbon flux and chlorophyll *a* concentration (top figure) and phytoplankton carbon flux and discharge (bottom figure) for the Trent at Cavendish Bridge, Gunthorpe and Cromwell, and the Ouse at Acaster.

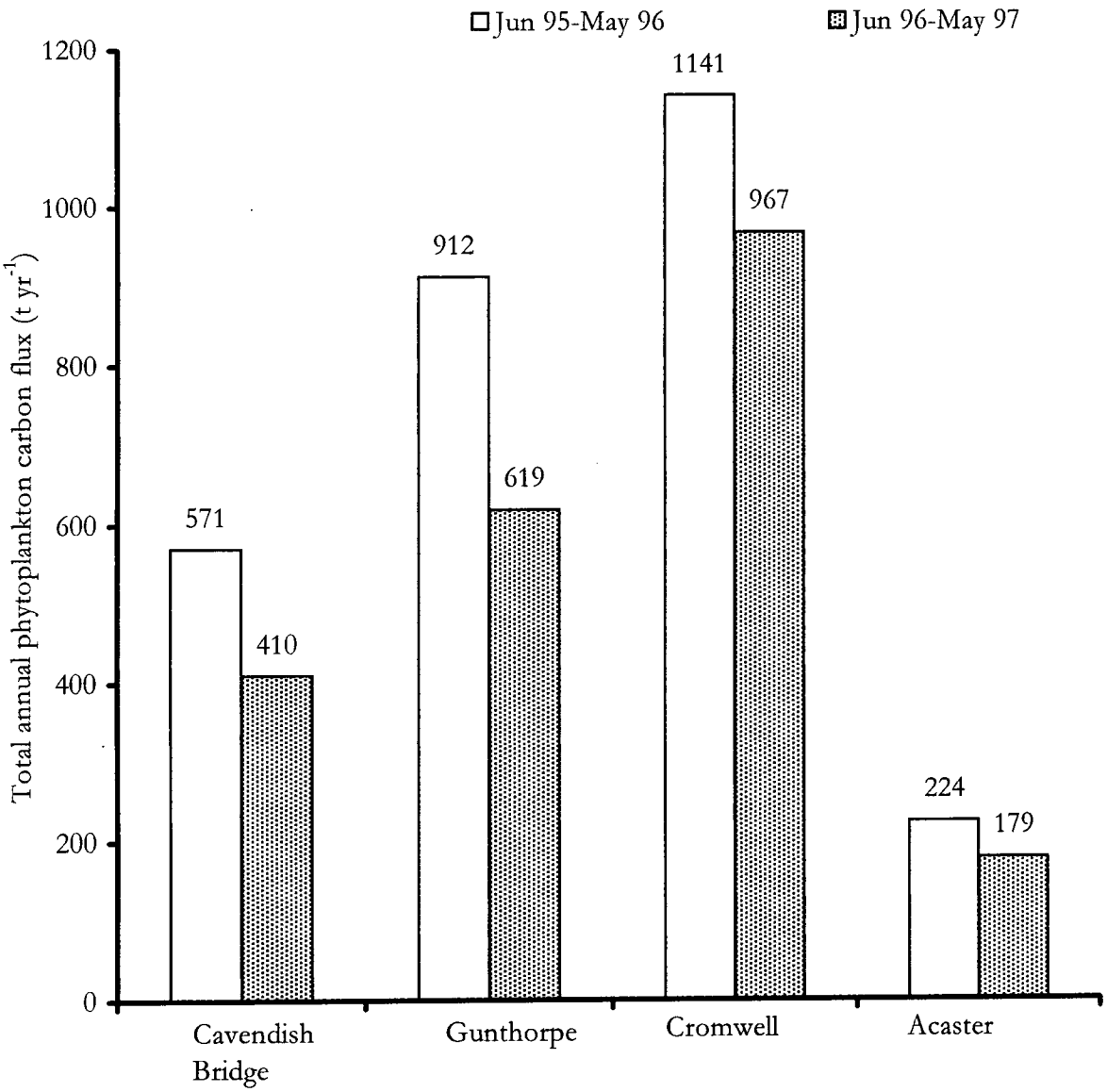

Figure 7.5 Annual phytoplankton carbon flux estimates for the Trent and Ouse. Data shown for three sites on the Trent; Cavendish Bridge, Gunthorpe and Cromwell, and one on the Ouse; Acaster. Estimates were made on a yearly basis, from June 1995 to May 1996 and from June 1996 to May 1997. Values are shown above blocks.

Phytoplankton carbon flux was lower during the second year by between 28, 32 and 15% for Cavendish Bridge, Gunthorpe and Cromwell was calculated. For the Ouse at Acaster, the flux of phytoplankton carbon decreased from 224 to 179 t yr^{-1}, a decrease of 20%.

The annual phytoplankton carbon flux for the tidal limit of the Trent at Cromwell was five times the flux at the tidal limit of the Ouse at Acaster during both years (Fig. 7.5). This highlights the importance of the Trent as a source of riverine phytoplankton carbon to the Humber Estuary.

7.6 Discussion

The estimation of the carbon to chlorophyll ratio, however crude (more sophisticated methods could have been employed; Section 8.5), allowed an estimation of phytoplankton flux from the Trent and Ouse to the Humber Estuary. The data suggest that autochthonous carbon flux is influenced primarily by chlorophyll *a* concentration and discharge in the Trent and Ouse. Maximum flux occurred for the Trent when discharge was low and chlorophyll a concentration high. This suggests that high rates of phytoplankton growth and production in spring are primarily responsible for high fluxes of autochthonous carbon in the Trent. In contrast, high discharge was primarily responsible for autochthonous flux maxima in the Ouse. Therefore, the sheer volume of material (i.e. water with low concentrations of chlorophyll *a*) and not the concentration is responsible for autochthonous carbon flux in the Ouse. This highlights the differences in phytoplankton carbon flux dynamics in the two rivers.

Phytoplankton contributed a maximum of 77% of the POC concentration during spring and summer. Maximal contributions of only 49% were observed for the Ouse. It can therefore be suggested that phytoplankton contribute the majority of the autochthonous carbon flux during spring and summer in the Trent. In the Ouse, however, they only comprise half of the flux. Therefore other sources of carbon, either autochthonous, such as bacteria and zooplankton or allochthonous must also be equally important in the flux of autochthonous carbon for the Ouse.

A decrease in annual phytoplankton carbon flux was evident during the second year of study. The 15 and 20% decrease for the tidal limits of the Trent and Ouse, respectively, is probably a result of a decrease in phytoplankton biomass in spring 1997 when compared to spring 1995 and 1996. During both years the Trent contributed over five times the annual phytoplankton carbon flux of the Ouse. This highlights the importance of the Trent as a source of autochthonous carbon to the Humber Estuary. It also suggests that to concentrate investigations of phytoplankton growth and production to the Trent was an astute decision.

7.7 Summary

1. A significant, positive relationship existed between particulate organic carbon (POC) and chlorophyll *a* concentration for the Trent at Cromwell ($r=0.69$, $P<0.001$, $n=104$). The gradient of the line of linear regression gave an estimated carbon to chlorophyll ratio of 33:1. No relationship existed for the Ouse at Acaster so the ratio estimated for the Trent at Cromwell was used.

2. For the Trent, phytoplankton carbon flux was highest (52 t wk^{-1}) during low flow events when chlorophyll *a* concentration was high. For the Ouse, the highest concentrations of phytoplankton carbon (33 t wk^{-1}) coincided with high discharge although a relationship between chlorophyll *a* concentration was also evident ($r=0.65$, $P<0.001$).

3. Minimal concentrations of phytoplankton carbon were calculated during the winter months for both the Trent and Ouse although one minimum concentration event was evident during the spring at Acaster.

4. Phytoplankton carbon contributed to 77.3% of the POC during spring and summer for the Trent at Cromwell and 48.9% for the Ouse at Acaster. Contribution during the autumn and winter months was lower with values of 11.5 and 11.4% at Cromwell and Acaster respectively.

5. Chlorophyll *a* was the major variable influencing the flux of phytoplankton carbon with significant positive relationships existing for both the Trent and Ouse. An increase in discharge resulted in a decrease in the flux of phytoplankton carbon in the Trent but resulted in an increase in the Ouse.

6. Annual phytoplankton carbon flux passing through the tidal limits of the Trent and Ouse during the second year of sampling decreased by 15% (from 1141 to 967 t yr^{-1}) and 20% (from 224 to 179 t yr^{-1}), respectively, when compared to the first year.

7. The flux of phytoplankton or 'living' carbon passing through the tidal limit of the Trent was five times that passing through the tidal limit of the Ouse. This shows the importance of the Trent as a source of riverine carbon to the Humber Estuary.

8 Discussion

8.1 Comparison of the Trent and Ouse with other European rivers

A large dataset has now been collected with regards to phytoplankton of the Trent and Ouse. It is important to assess to what extent this is typical of other temperate, European rivers. Temporal changes in chlorophyll *a* concentration (4.3) and phytoplankton density (4.2) were similar to those reported for other larger European rivers. Maximum chlorophyll *a* concentration for the Trent and Ouse were comparable to larger rivers such as the Thames, Spree and Danube (Table 8.1).

Table 8.1 Maximal chlorophyll *a* concentration, phytoplankton density and dominant centric diatom species for the Trent and Ouse compared to some other European rivers.

River	Max. chl *a* concentration ($\mu g\ l^{-1}$)	Max. cell density ($x10^3$ cells ml^{-1})	Dominant taxa	Reference
Thames	100	22.3	*Stephanodiscus hantzschii*	Lack *et al* (1978)
Severn	-	46	*S. hantzschii, Cyclotella meneghiniana*	Swale (1969)
Wye	137	277	*C. pseudostelligera*	Jones (1984)
Ebro	45	73	*S. hantzschii, C. meneghiniana, Skeletonema potamos*	Sabater & Munoz (1990)
Spree	115	-	*S. hantzschii, C. meneghiniana, C. radiosa*	Köhler (1993)
Danube	100	60	Centric diatoms	Kiss (1994)
Ouse	70	-	*S. hantzschii, C. meneghiniana,*	Marker *et al.* (1993)
Trent	150	14	*S. hantzschii, C. meneghiniana,*	Marker *et al.* (1993)
Meuse	60	30	*S. hantzschii,*	Gosselain *et al.* (1994)
Rhine	140	70	*S. hantzschii, C. meneghiniana, S. parvus*	Admiraal *et al.* (1994)
Ouse	166	50	*S. hantzschii, C. meneghiniana,*	This study
Trent	162	54	*S. hantzschii, C. meneghiniana, Cyclostephanos invisitatus*	This study

Concentrations of chlorophyll *a* in the Trent were similar to those reported by Marker *et al.* (1993; Table 8.1). However, maximal concentrations reported for the Ouse in 1995 in the present study were over twice the maximal concentration reported by Marker *et al.* (1993; Table 8.1). The

hydrodynamically responsive nature of the Ouse system may be responsible for comparatively low maxima reported for 1996 and 1997 and is discussed later (Sections 8.21, 8.31).

Surprisingly, maximum concentrations of chlorophyll *a* for the Trent and Ouse were over twice those reported for the Ebro and Meuse (Table 8.1) which are large European rivers. Maximal concentrations of chlorophyll *a* were observed during spring and minima during winter (Section 4.22). However, despite apparently favourable growth conditions during summer, chlorophyll *a* and phytoplankton abundance in the Trent and Ouse was much lower than in spring (Sections 4.1, 4.22, 6.1). This is a common feature of lowland rivers (e.g. Köhler, 1993; Admiraal *et al.*, 1994), although not universal (Kiss, 1994; Baker and Baker, 1979) and is discussed later (Section 8.35).

Maximal cell densities for European rivers vary greatly (Table 8.1). Even so, densities for the Trent and Ouse were within the limits reported for other rivers (Table 8.1). Surprisingly, low phytoplankton density was reported for the Trent by Marker *et al.* (1993; Table 8.1) even though maximum chlorophyll *a* concentration was similar to that reported for the present study. The reason for this is unclear as the dominant species were the same as in the present study (Table 8.1). The reason for the large population density recorded for the Wye for a relatively low chlorophyll *a* concentration (Table 8.1) is unclear. The small size of *Cyclotella pseudostelligera* cells dominating the population (Table 8.1) can only partially account for the relatively high density.

A strong, positive relationship was observed between chlorophyll *a* concentration and phytoplankton density (Section 4.21). As the relationship was highly significant, it was supposed that chlorophyll *a* was a reasonable estimate of phytoplankton biomass. The variation of the data was the result of the variability in the chlorophyll *a* content of different species of phytoplankton. The chlorophyll *a* content per cell is dependent upon cell size, physiological state of the cell and the environmental conditions imposed upon cells (Kirk, 1994). The chlorophyll *a* content of between 2.8 and 1.4 pg chl *a* $cell^{-1}$ for the Trent at Cromwell and Ouse at Acaster, respectively (Fig. 4.7) was similar to 2.9 pg chl a $cell^{-1}$ found for the Thames (Lack *et al.* 1978). The chlorophyll *a* content per cell for the Trent at Cromwell was twice that calculated for the Ouse at Acaster. This may have been the result of populations of larger cells occurring at Acaster than at Cromwell although phytoplankton species composition was similar for both Cromwell and Acaster (Section 4.1). A factor contributing to the difference in chlorophyll *a* content of individuals may have been light adaptation. Cells tend to increase their chlorophyll *a* content in response to a low light regime (Descy & Gosselain, 1994). This is unlikely to have been a factor in the case of the Trent and Ouse. The Ouse was on average 2 m deeper than the Trent at the tidal limits. It was therefore more likely that cells would use light more efficiently in the Ouse and therefore have higher concentrations of chlorophyll *a* per cell.

The seasonal switch from a spring phytoplankton population dominated by centrics to a population dominated by green algae in the Trent and Ouse (Section 4.1) is well documented for

other rivers (see Holmes & Whitton, 1981). This switch in algal dominance coincided with a decrease in phytoplankton density and biomass (Sections 4.1, 4.22) a switch from net growth in spring to net loss in summer (Section 6.1) and a switch from an autotrophic to a heterotrophic system (Section 5.4). Although no explanation is offered for this switch in dominance, the resulting changes in growth and production dynamics are discussed later (Section 8.34).

Species of centric diatoms recorded for the Trent and Ouse during the chlorophyll *a* maxima are similar for those reported for other European rivers (Table 8.1). The species of green algae recorded for the Trent and Ouse are also similar to those recorded for many other European rivers (Reynolds & Descy, 1996). Species of *Actinastrum, Chlorella* and *Scenedesmus* were the numerically dominant components of green algal dominated phytoplankton populations (Section 4.1). It appears, therefore, that the dominant species of temperate, European rivers are cosmopolitan. The similarity of species composition is indicative of a strong selection pressure induced by riverine environmental conditions.

Rates of production for the Trent and Ouse, expressed on a gross areal basis, were similar to other European rivers (Table 8.2). Variation between rivers may be a result of different techniques used for measuring photosynthesis. Using different models to estimate column production also causes variation in results. Sampling of the Trent and Ouse was frequent; weekly during spring. It was therefore more likely to sample during periods of peak production. Differences also occur as different environmental pressures are more important to different rivers. Overall, chlorophyll *a* concentration, phytoplankton density and production for the Trent and Ouse are similar to those reported for other European rivers.

Table 8.2 Minimum and maximum rates of gross areal production for the Trent and Ouse compared to some other European rivers

River	Gross primary production (g C m^{-2} d^{-1})		Reference
	Minimum	Maximum	
Itchen	0.2	11.7	Butcher *et al.* (1930)
Thames	0	4.5	Wetzel (1975)
Danube	0	4.8	Dvihally (1975)
Loire	0.1	3.9	Billen *et al.* (1984)
Meuse	0.1	5.8	Descy *et al.* (1987)
Rhine	2.1	3.4	Admiraal *et al.* (1994)
Ouse	0	5.9	This study
Trent	0	8.5	This study

8.2 Growth processes

8.21 Discharge

To understand the processes governing the flux of autochthonous carbon in rivers it is necessary to comprehend the environmental factors influencing the growth and production of riverine phytoplankton. Growth and production are primarily influenced by discharge, light and temperature. For the Trent and Ouse maximal concentrations of chlorophyll *a* (Section 4.22), phytoplankton cell density (Section 4.1) rates of growth (Section 6.1) and production (Section 5.4) were measured during spring when discharge was low. Reduced discharge during spring increases river retentivity and reduces dilution of phytoplankton populations. Decreased discharge reduces the rate of hydraulic flushing, an important loss process for all 'potamoplankton' (Reynolds, 1988; Pinder *et al.*, 1997). It has been suggested that discharge is the most important factor influencing phytoplankton growth in rivers (Baker & Baker, 1979). Decreased river velocity, rather than the actual discharge, increases river retentivity, allowing time for phytoplankton to grow. A river must flow slowly enough for populations to develop. For example, a velocity of 5 m s^{-1} has been suggested as the threshold for the centric diatom *Stephanodiscus hantzschii* to proliferate (Swale, 1969). Low discharge and high river retentivity allow more time for populations to establish and develop during their travel downstream. Rapid growth rates exhibited by centrics (Knoechel & Kalff, 1978) may explain why they proliferate in spring when discharge and velocity are decreasing but not as low as they are in summer. A species with a rapid growth rate will be able to proliferate in rivers before being washed out to the estuary as they will have a competitive advantage over larger, slower growing species. The downstream increase in phytoplankton populations during spring is discussed later (Section 8.24).

The increased temporal resolution offered by day to day (Section 4.25) and daily (Section 4.26) sampling of chlorophyll *a* showed the importance of hydraulic flushing upon spring phytoplankton density. As discharge decreased during the early spring months, chlorophyll *a* concentration increased to yearly maximum concentrations (see also Section 4.24). Spring floods interrupted the yearly chlorophyll *a* maximum as a result of dilution and rapid washout of phytoplankton from the river (Section 4.26). However, as discharge decreased, chlorophyll *a* concentration rapidly increased again, often reaching concentrations observed before the flood event (Section 4.26). Phytoplankton populations are able to recover from spring floods if favourable conditions return after the flood (Swale, 1969). It is obvious from the work on the Trent that spring floods are a major factor influencing spring phytoplankton development. The stochastic flood events during spring imposed an unpredictable climate upon spring phytoplankton populations. Environmental conditions rapidly change from those optimal for growth to those unfavourable for growth and

rapidly back again. We suggest that this unpredictable underwater climate favoured the development of some species and not others.

The spring maxima in phytoplankton density and chlorophyll *a* concentration comprised mainlycentric diatoms (Section 4.1). Centric diatoms also chiefly comprised the spring maximum in other temperate rivers (Table 8.1). It is assumed that centric diatoms are low temperature, low light adapted species with high growth rates (Reynolds, 1989). They take advantage of and proliferate in rivers when conditions are becoming favourable for growth but are not yet favourable for other phytoplankton groups such as green algae. Although no thorough detailed analysis of centric diatom species was conducted during this investigation, preliminary work identified three species (Table 8.1) as dominant during spring blooms. These species are common spring species in many temperate rivers (Table 8.1). They are small, with diameters from 4 to 30 μm and large surface-area-to-volume ratios. The ability of these species to grow rapidly and pre-adapt to their environment (Reynolds, 1984) gives them a competitive edge over other species. Large populations are able to develop before being transported to the sea. It is interesting to note that net growth was only observed in the Trent during spring when centric diatoms dominated the phytoplankton (Section 6.1). When the population became dominated by green algae, negative growth followed. This coincided with a decline in chlorophyll *a* concentration and rates of production (Sections 4.22, 5.4) and is discussed later (Section 8.34).

Although discharge during spring was low, the water column was usually well mixed as variability studies showed (Section 4.23). Mixing results in decreased rates of sedimentation of phytoplankton cells and the re-suspension of cells which have sedimented. During spring, as cells are actively growing, they exhibit low sedimentation rates (Tilman & Kilham, 1976)). Therefore only minimal losses of phytoplankton to sedimentation would be expected during spring.

Mixing also exposes cells to an intermittent light regime. This is thought to benefit centric diatoms (Reynolds, 1994) and is discussed later (Section 8.22). Centric diatoms could theoretically dominate throughout the season in deeper, turbid rivers as a result of their competitive advantage under these environmental conditions (Reynolds & Descy, 1996). Indeed, centric diatoms may be more important in the deeper, more turbid, downstream reaches of a river whilst green algae are more important in the shallower, less turbid, upstream reaches (Sabater & Muñoz, 1990; Descy, 1987).

Despite chlorophyll *a* maxima corresponding with low discharge in spring, winter flood events often coincided with an increase in chlorophyll *a* during winter (Section 4.22). This may have been the result of re-suspension of benthic diatoms. The re-suspension of benthic material during flood events often results in an increase in benthic diatoms in the water column (e.g. Jones & Barrington, 1985). However, there was no such relationship observed for the Trent and Ouse. An increased contribution of green algae to the population corresponded with winter floods. This

suggests that green algae inhabiting the benthos were washed into suspension. It further suggests that these green phytoplankton species exhibit a meroplanktonic existence; undergoing a benthic survival phase. Large proportions of pennate species, described as typically benthic (Reynolds & Descy, 1996) found in the Trent and Ouse, such as *Navicula, Nitzschia* and *Synedra* were observed during spring and summer when discharge was relatively low. This suggests that the influx of diatoms, particularly pennate diatoms, from the benthos was a result of removal by high O_2 production (Moore, 1976) with O_2 bubbles dislodging benthic communities (B.A. Whitton, pers. comm.).

The evidence suggests that discharge related environmental factors during spring; decreasing flow, increasing retentivity and mixing benefits centric diatoms. They have a competitive advantage over other species and proliferate during spring. Although a uniform pattern of centric diatom waxing and waning exists, the mechanism which favours centrics in spring is unknown.

During summer, when discharge reached the seasonal minimum, conditions no longer allowed centrics to be competitive. This resulted in a loss from the system and other species, particularly green algae were able to take over.

As well as a decrease in hydraulic wash out, re-suspension and dilution of phytoplankton populations, decreased discharge improves the underwater light climate.

8.22 Light

Once nutrient requirements of phytoplankton are sustained, light is the primary factor controlling production (Wetzel, 1975). Therefore, the amount of light available to phytoplankton influences primary productivity, the production of new biomass and the growth of phytoplankton populations.

Other than flood events, when attenuation was high as a result of suspended material, the underwater light climate in the Trent was primarily influenced by phytoplankton biomass (Section 5.1). High values of K_d, calculated during spring, coincided with large populations of centric diatoms (Section 5.11). This phenomenon has also been reported for other aquatic systems (Kirk, 1994; Jones, 1977). However, development of large phytoplankton populations, particularly centric diatom, rarely results in self-shading (Dokulil, 1994). No relationship between K_d and phytoplankton biomass was observed for the Ouse (Section 5.11). It is considered that dissolved humic and fulvic acids, originating from the peaty catchments of the tributary rivers Swale and Ure, may have been important in light attenuation in the Ouse. High values of K_d coincided with occasions when the Ouse was peaty-brown in colour (author's unpublished data). The importance of dissolved substances upon the underwater light climate has been well documented in other aquatic systems (Kirk 1976, 1980) as has the effect of mineral turbidity (Threlkeld & Søballe, 1988).

Spectroradiometric investigations (Section 5.12) showed that light at the red part of the spectrum was least attenuated throughout the year. The high attenuation of blue wavebands in both rivers, particularly in the Ouse, is further evidence for a large contribution of humic substances to light attenuation. During periods when phytoplankton biomass was high, light was increasingly attenuated at 675 nm by phytoplankton (Section 5.12). This was the wavelength most strongly absorbed by chlorophyll *a in vivo*.

Both the Trent and Ouse and the Ouse tributaries experienced an increase in the attenuation of light during high discharge events, particularly in winter (Section 5.11). This was probably a result of an increase in non-algal suspended solids originating from allochthonous and benthic sources and has been documented for other systems (Kirk, 1980, 1994). The Ouse system was more responsive to floods than the Trent system (D.V. Leach, pers. comm.). This implies that non-algal suspended solids were probably more important in attenuating light in the Ouse than the Trent as they would be incorporated into the water column by the scouring action of floods. Overall, non-algal turbidity is regarded as the primary cause of light attenuation in turbid systems (Owens & Crumpton, 1995; Reynolds & Descy, 1996).

During spring and summer, reduced discharge resulted in an improved underwater light climate. This resulted from decreased turbidity by a decrease in suspended particles (Kiss, 1994), so increasing the euphotic depth. Decreased river depth resulted in phytoplankton being exposed to higher irradiances for longer periods of time than in a deeper water column. In addition, the daily average and total amount of light at the water surface was also increasing.

Irradiance influenced values of the P vs I parameters and the shape of the P vs I curve for the Trent and Ouse (Section 52). The rate of P_{max}(net) was greatest during spring and summer when irradiance was high and daylength long and when the phytoplankton population was dominated by centric diatoms (Section 5.2). For the Trent and Ouse, the rate of P_{max}(net) increased with increasing average daily irradiance. This is a common response (Henley, 1993). High P_{max}(net) rates imply that phytoplankton attain high rates of photosynthesis for long periods of time (Harris, 1984). During spring and summer, with decreased discharge and increased irradiance and temperature, conditions were ideal for photosynthesis. Therefore, maximum rates of P_{max}(net) were expected at this time of year.

Rates of P_{max}(net) also depend upon temperature and species composition (Descy *et al.*, 1987). The small size of centrics found in this study (c. 5-15 μm diameter; Section 4.1) may account, in part, for the high rates of P_{max}(net) when compared to periods when green algae were dominant. Banse (1976) explains that rates of P_{max}(net) decrease on a size specific basis as cell size increases. As rates of P_{max}(net) in this study were expressed on a chlorophyll *a* basis, size may contribute to variation in rates of P_{max}(net) between populations dominated by centrics and green algae. Although maximal rates of P_{max}(net) coincided with dominance by centric diatoms (Section 4.2),

green algae often exhibit higher rates of P_{max}(net) (Jones, 1977).

Rates of P_{max}(net) are also temperature dependent. It has been suggested that temperature is the primary variable controlling P_{max}(net) (Baker & Baker, 1979). Even so, increased irradiance usually coincides with increased temperature so it is difficult to separate the effects of both upon rates of P_{max}(net). A combination of cell size, increasing temperature and irradiance resulted in maximum rates of P_{max}(net) during spring.

No clear relationship existed between α and irradiance for the Trent and Ouse (Section 5.2). However, α was positively correlated with K_d for the Trent and β with K_d for the Ouse (Section 5.2). Values of α increased with increasing K_d for the Trent, indicating adaptation to low light. Values of α decrease with increasing cell size (Banse, 1976) although no seasonal pattern or difference between values of α and species composition was evident. It is difficult to relate any photo-adaptation of cells to environmental factors. Even so, it has been suggested that phytoplankton must photoadapt in order to survive in turbid systems where the light climate is far from optimal (Reynolds & Descy, 1996).

Values of β increased with increasing K_d for the Ouse, indicating increased photoinhibition with decreasing light. This may be a result of experimental design. Samples were taken from the turbid water column and transferred to static incubation bottles under high light (Section 3.61). Incubation of samples over long periods can result in increased photoinhibition (Takahashi *et al.*, 1971). If not a result of experimental design, increased photoinhibition may be species dependent (Harris, 1984) with diatoms being more susceptible than other species (Goldman & Dennett, 1984). However, there was no clear relationship between values of β and species composition for the Trent and Ouse.

Photoinhibition may be a function of temperature. Although no significant relationship existed between β and temperature a significant relationship existed between I_b and temperature for the Trent. This suggests that at low temperature, photoinhibition is initiated at a lower irradiance. This is consistent with the theory that photoinhibition occurs when photon capture exceeds the capacity to deal with the energy (Henley, 1993).

In this study, column production was greatest during spring and early summer when irradiance was high and respiration rates low (Section 5.4). Low respiration rates in spring corresponded with low temperature and increased euphotic depth. Respiration as a source of phytoplankton loss is discussed later (Section 8.34). Decreased light attenuation and river depth contributed to increased average daily column productivity when modelled for the Trent and Ouse (Section 5.4).

The light climate for a phytoplankton cell during spring improves as surface irradiance and daylength increase (Kirk, 1994) and river depth decreases. Increased irradiance results in increased rates of daily column production in other rivers (Kowalczewski & Lack, 1971; Gosselain *et al.*,

1994) and estuaries (D'Avanzo *et al.*, 1995). Increased irradiance should promote gross production for phytoplankton populations as a whole (Dokulil, 1994), if surface photoinhibition of cells adapted to low light is not a major factor (Reynolds & Descy, 1996). Modelling of average daily column production when omitting the effect of photoinhibition showed little change in actual rates of production in the Trent and Ouse (Sections 5.412, 5.522). This suggests that photoinhibition had little effect on productivity of these turbid, deep rivers. As a result of turbidity, depth and mixing in turbid rivers such as the Trent and Ouse, cells are rarely subjected to irradiances high enough for photoinhibition to be important (Grande *et al.*, 1990; Mallin & Paerl, 1992).

Mixing may stimulate rates of production by mitigating light limitation in turbid systems (Grobbelaar, 1990; Dokulil, 1994; Cole *et al*, 1992). The euphotic depth to mixing depth ratio is the most important factor influencing production in turbid systems (Grobbelaar, 1985). The ratio is usually small in many rivers and the mixing depth is often larger than the compensation depth (Grobbelaar, 1990). As a result, cells experience a lot of time in the aphotic zone. During spring and summer, low discharge and high irradiance increases the euphotic to mixing depth ratio and phytoplankton are subjected to a greater amount of time in the euphotic zone. Therefore, production is less likely to be offset by high respiration rates.

Centrics dominated during spring (Section 4.1) when maximum rates of column production were achieved (Section 5.4). A rapidly fluctuating high then low light, experienced during spring, may favour centric diatoms (Reynolds, 1994; Reynolds & Descy, 1996). Conversely, intermittent mixing of the water column and the more stable light climate experienced during summer may favour green algae and blue-greens (Reynolds, 1994). High densities of blue-greens were not observed in either the Trent or Ouse (Section 4.1). This may be the result of river turbidity and turbulence suppressing blue-green development, even in summer. Another possibility is that blue-greens were washed out of the system before they could attain significant populations.

The combination of increased irradiance, mixing and a phytoplankton dominated by small centric diatoms, coupled with low respiration rates resulted in maximum rates of photosynthesis and column production during spring and early summer.

8.23 Temperature

An increase in temperature, experienced during spring and summer resulted in increased rates of *in situ* growth (Section 6.1), growth of phytoplankton in culture (Section 6.2) and production (Section 5.4). Increased temperature increases rates of chemical reactions up to the optimum temperature, after which rates decrease. An increase in growth and production with increasing temperature has been reported in other studies (Reynolds, 1984; Kirk, 1994). Even so, it is difficult to isolate temperature as primarily controlling processes as an increase in temperature coincides with

increased irradiance, decreased river depth and velocity. Increased temperature also results in increased rates of loss such as respiration and grazing as discussed later (Section 8.34).

Rates of growth of three species of algae in culture showed an increase up to 20°C; the highest temperature tested (Section 6.2). However, in the rivers, when temperatures approached 20°C, rates of *in situ* growth decreased and became negative. This highlights the importance of *in situ* loss processes which species in culture are not subjected to and is discussed later (Section 8.3).

8.24 Downstream growth

Downstream rates of change in phytoplankton chlorophyll *a* were estimated for the Trent (Section 3.71). Estimates were not made for the Ouse as too few sites were sampled along the length of the river to allow suitable data to be collected. Spring maxima in phytoplankton biomass and density in the Trent coincided with an increase in phytoplankton chlorophyll *a* with distance downstream (Section 6.1). Downstream increase in phytoplankton density and chlorophyll *a* has been reported for other rivers, for example, the Lee (Swale, 1964), Spree (Köhler, 1994) and Meuse (Descy & Gosselain, 1994) to name but a few. Skidmore *et al.* (1998) relate the spring, downstream increase in phytoplankton chlorophyll *a* in the Trent to *in situ* growth resulting from decreasing discharge and improving light quality. The increase in rates of phytoplankton production and growth to maxima in spring has been discussed earlier (Sections 8.21, 8.22, 8.23). The maximal growth rate reported in this study falls within the previously reported range for other rivers (Table 8.3).

Table 8.3 Comparison of maximum growth rates reported for the Trent and other European rivers

River	Maximum growth rate (day^{-1})	Reference
Lot	0.23	Capblancq & Décamps (1978)
Rhine	0.70	Reynolds & Glaister (1993)
Severn	0.53	Reynolds & Glaister (1993)
Meuse	0.28	Gosselain *et al.* (1994)
Trent	0.57	This study

It has been suggested that a series of 'dead zones' must be present along some rivers to allow sufficient time for large phytoplankton populations to grow over relatively short river lengths (Reynolds & Glaister, 1993; Reynolds, 1994). In the Trent, annual maximum growth rates of 0.48, 0.59 and 0.70 d^{-1} in 1995, 1996 and 1997, respectively, (Section 6.1) are equivalent to doubling

times of between 1.0 and 1.5 days. These maximal growth rates were produced between mid-May and mid-June when daylength was between 15.4 and 16.6 h and river temperature between 10 and 20 °C. Given the high soluble N and P concentrations in the Trent (House *et al.*, 1997) and reported growth rates of centric diatoms in culture of up to 0.92 d^{-1} (Section 6.2), it is possible that the calculated growth rates in the field could have been achieved without needing to invoke the existence of 'dead zones'. The study of intra-site variability suggested relative homogeneity of the Trent at the sites sampled (Section 4.25) and that 'dead zones' were unimportant here. However, the PIZT model predicted growth rates lower than those calculated from downstream increase in chlorophyll *a*, particularly during 1997. This discrepancy may result from dead zones.

Increase in phytoplankton biomass, resulting from *in situ* growth in spring (Section 6.1) was a result of favourable growth conditions. During spring, river retentivity allowed populations to develop before they were eventually washed into the estuary. The underwater light climate improved as decreased river depth and suspended sediment load coincided with increased irradiance and daylength. Species able to take advantage of these improving conditions, such as centric diatoms, rapidly proliferated as they travelled downstream. The evidence for downstream growth during spring in the Trent shows that centric diatoms were best suited to riverine conditions experienced during spring.

8.3 Loss processes

8.31 Discharge

Loss of phytoplankton from river systems is primarily controlled by discharge, temperature and grazing. For the Trent and Ouse, chlorophyll *a* concentration (Section 4.22), phytoplankton density (Section 4.1) and rates of growth (Section 6.1) and production (Section 5.4) all rapidly declined during summer. Increased rates of sedimentation with decreasing discharge was possibly an important loss process in summer. Sedimentation in rivers is primarily controlled by physical factors attributable to turbulence and not by chemical or biological factors as in lakes (Rust, 1982). Decreased discharge during summer results in decreased river depth and turbulence. Experiments have shown that sedimentation increases as channel depth decreases (Reynolds *et al.*, 1990). Diatoms are likely to be especially sensitive to sedimentation given their high specific gravity. As centric diatoms dominated spring populations (Section 4.1), the rapid decrease in the population during summer may have been a result of sedimentation. Decreased turbulence also results in decreased re-suspension of cells. This may have resulted in increased rates of benthic grazing upon sedimented cells. If other environmental stresses, for example nutrient limitation or bacterial attack contributed to cell scenescence then rates of sedimentation would have been expected to increase further.

No attempt was made to quantify sedimentation as a loss rate during this study. Attempts to estimate rates of sedimentation using trapping techniques (Section 1.8) often overestimate sedimentation in turbulent environments (Kozerski, 1994). Even so, sedimentation as a loss is particularly likely in summer when river depth and turbulence are usually at a seasonal minimum. The relationship between times when sedimentation rates are likely to be high and the loss of high centric diatom populations suggest a link between the two and warrants further investigation.

In contrast, during winter, increased discharge results in increased re-suspension and decreased sedimentation. However, river retentivity decreases and cells are washed out of the system before large populations are able to develop. Chlorophyll *a* (Section 4.22) and phytoplankton density (Section 4.1) minima were recorded during the winter for the Trent and Ouse, corresponding with high discharge. Rates of growth for the Trent (Section 6.1) and production for the Trent and Ouse (Section 5.4) were negative during the winter. The use of the PIZT model showed that an increase in depth and K_d resulted in low and often negative rates of production (Sections 5.511, 5.513, 5.521, 5.523) as the respiratory burden was increased. Negative rates indicated a loss of phytoplankton from the system. If there was no *in situ* growth or production of new biomass then an external or alternative source must be responsible for winter populations. The most plausible source would have been re-suspended cells from the benthos which often contained typical phytoplankton species, such as centric diatoms and green algae, undergoing a benthic survival stage (Kowe *et al.*, 1997). Meroplanktony would also explain why typical benthic algae, such as pennate diatoms were not a major component of re-suspended material during winter flood events.

8.32 Nutrients

Limiting N and P, suppressing phytoplankton growth and production is common in freshwaters (Doering *et al.*, 1995). Nutrient limitation affecting the growth of benthic and attached algae in smaller, upland rivers has also been reported (Christmas *et al.*, 1997). However, concentrations of N and P rarely fall to levels where phytoplankton growth and production is limited in larger temperate rivers (Reynolds & Descy, 1996). N and P concentrations were always high for the Trent Ouse during the period of study an so were unlikely to have ever limited phytoplankton growth. However, the fall in silica concentrations in spring with the increase in centric diatom density (Section 4.1) was apparently sufficient to suppress further growth of centric diatoms at the tidal limits of the Trent and Ouse, particularly in 1995 and 1996. Silica limitation of centric diatom growth has also been reported for other rivers (Section 1.4). Silica limitation may have imposed increased environmental stress upon growing phytoplankton populations. If they were unable to grow actively then rates of sedimentation may have increased. Another stress may be pathogenic attack. If centric diatoms continued to grow under times of silica stress then they may have

formed thinner silica frustules. This may have made them more susceptible to pathogenic attack and is discussed further later (Section 8.33). However, silica limitation only occurred over a short period. During summer, concentrations increased again and so the silica limitation during spring can not explain low numbers of centrics and the continued dominance of greens during summer (Section 4.1).

8.33 Grazing

Earlier investigations into grazing and ways in which grazing influences phytoplankton biomass and species composition have already been discussed (Section 1.9). Regression analysis suggested that grazing increased in response to an increase in phytoplankton growth rate and not vice versa (Section 6.3). This was concordant with the literature which reports that high zooplankton populations coincide with high phytoplankton populations (e.g. Admiraal *et al.*, 1994). Apparent negative grazing (Section 6.3) was unexpected. It was thought that a negative grazing rate may have resulted from predation of grazers by predatory zooplankton such as *Polyarthra* and *Asplancna*. An alternative theory is that particulate turbidity resulted in reduced grazing rate (A. Bothár pers. comm.). As the grazing rate was calculated as the slope of dilution against change in chlorophyll *a* (Section 3.74), increased turbidity in less diluted samples could result in negative grazing rates.

The occurrence of species of zooplankton common to many European rivers has been discussed earlier (Section 1.9). In the Trent, ciliate species such as *Strobolidium* spp. were dominant throughout the spring and summer months. Rotifers, mainly *Keratella* spp. were also found in samples although no Cladocerans or Copepods were found in the Trent or Ouse (Section 6.3). During this investigation, only one zooplankton specimen was found for the Ouse; a ciliate resembling *Strobolidium* spp. This suggested that zooplankton grazing pressure was potentially greater in the Trent than in the Ouse.

As with phytoplankton, zooplankton are lost from the river system by the unidirectional flow towards the sea. To develop large populations and exert significant grazing pressure upon phytoplankton populations, smaller, faster growing species are usually more important in river systems than larger, slow growing species (de Ruyter van Steveninck *et al.*, 1992). Discharge influences the development of crustaceans (Bothár & Ráth, 1994) although it has been suggested that ciliates are unaffected (Bereczky & Nosek, 1993; Nosek & Bereczky, 1994). Even so, in the present study, maximal grazing rates were observed during spring and summer. During this period, discharge was low and temperature high; conditions which are optimal for both phytoplankton and zooplankton development (van Dijk & van Zanten, 1995; Gosselain *et al.*, 1998).

The hydrodynamically responsive nature of the Ouse when compared to the Trent may explain why zooplankton density was low in the Ouse. However, this does not fully explain the lack of ciliates in the Ouse system. Increasing temperature, during spring and summer result in increasing rates of grazing in many species (Section 1.9). Even though experimental evidence suggests that grazing is unimportant in the Trent and Ouse is possible that summer temperatures resulted in increased grazing pressure upon the phytoplankton and may be partly responsible for the rapid decline of spring blooms.

A misunderstood source of grazing and perhaps the least understood is that from protozoa, benthic grazers, fungal, bacterial and viral infection (Section 1.9). Ciliates are considered to be important in the Trent as they contributed most of the zooplankton biomass. The importance of protozoa has been considered in other studies but never quantified.

Although chytrid infestation of phytoplankton has been mentioned in previous studies (Canter & Lund, 1951), few studies have considered it an important factor in the loss of phytoplankton from rivers. Although quantitative data is not available for this study, Chytrids were found on centric diatom cells in 1995 and 1996 during the centric diatom maxima in spring in both the Trent and Ouse. This coincided with low levels of SiO_2-Si (Section 4.1) which is consistent with the idea that silica stress made cells more vulnerable to pathogen attack. In this way, bacterial and viral attack may have been important. Few studies have also considered the importance of these in freshwaters (e.g. Reisser, 1993) although viral attack of marine algae has been more extensively studied (Boehme *et al.*, 1993). Pathogenic attack may be a major source of phytoplankton loss, particularly under nutrient or other environmental stress and is an area requiring further research.

The removal of phytoplankton by benthic grazers such as freshwater mussels is an area receiving more attention in recent papers (Section 1.9). In the Trent, large numbers of *Unio* sp. were found in dredged spoil, indicating the possible importance of mussels as grazers. During late spring and early summer, high temperature, increased sedimentation and decreased turbulence may have resulted in more phytoplankton being available to benthic grazers. Benthic grazing remains a potentially important source of phytoplankton loss during summer. Again, this is an area requiring more quantitative research.

Zooplankton are subjected to similar environmental constrains as phytoplankton, particularly discharge and temperature (Section 1.9). In the Trent and Ouse, grazing by zooplankton may be relatively unimportant when compared to pathogens and benthic grazers.

8.34 Temperature

Although not a loss process in itself, temperature can affect rates of loss. Increased temperature during summer may result in increased loss of phytoplankton through increased grazing pressure (Section 8.33). However, a more significant form of phytoplankton loss could be increased rates

of respiration in turbid rivers such as the Trent and Ouse (Section 5.4). The importance of light and temperature upon phytoplankton growth and production has been discussed earlier (Sections 8.22, 8.23, 8.34). For the Trent, *in situ* respiration rates increased with temperature (Sections 5.2, 5.4). A rapid increase in respiration was also observed over 15 to 20°C for three phytoplankton species in culture (Section 5.3). During summer, increased temperature corresponded with decreased and negative rates of productivity, particularly in the Trent (Section 5.41). An increase in the rate of respiration was therefore potentially a major factor influencing column productivity. Increased rates of respiration also corresponded with a rapid decline in chlorophyll *a* concentration (Section 5.41).

To compliment data collected *in situ*, column productivity was modelled using a low, average rate of respiration of 25 μmol O^2 (mg chl *a*)$^{-1}$ h^{-1} observed during spring when temperatures were typically between 12 and 16 °C (Sections 5.514, 5.524). The result was that increased rates of net productivity were observed with net productivity continuing throughout the summer. In this study, community respiration was measured. Therefore, bacterial, fungal and zooplankton respiration was included with phytoplankton respiration. However, respiration rates of phytoplankton in culture were similar at 20°C (Section 4.3) to *in situ* rates (Sections 5.2, 5.3). Species in culture were not axenic although bacteria were scarce and no protozoa were present. Therefore, most of the respiration was attributable to phytoplankton. This theory has also been put forward by Dokulil (1994).

High rates of respiration corresponding with low temperature (Sections 5.2, 5.4) during winter are harder to explain. This may have been a result of bacterial respiration although other factors such as oxidation of humic substances may be important, especially in the Ouse.

8.35 Downstream loss

Downstream loss of phytoplankton during summer and winter can be explained using the discussion formulated above. Phytoplankton chlorophyll *a* maxima in spring were followed by a rapid decline in phytoplankton chlorophyll *a* in summer (Section 4.2). This resulted from increased rates of loss from sedimentation, grazing and respiration.

With decreased discharge during summer, rates of sedimentation, particularly of centric diatoms increased (Section 8.31). If cells were also senescent, rates of sedimentation would increase further. With decreased mixing of the water column, sedimented cells would have had little opportunity to return to the water column. They would have then been subjected to benthic grazing and light limitation.

Rates of grazing, from zooplankton, benthic animals and pathogens increased with increasing temperature (Section 8.33). Therefore, grazing pressure upon phytoplankton, if important, would have increased. As discharge decreased and the rivers become more retentive, zooplankton

populations would be able to develop larger populations during their travel downstream so increasing the grazing pressure upon phytoplankton. Benthic grazing pressure may have increased if rates of phytoplankton sedimentation increased downstream during summer.

Light climate of the Trent and Ouse became more favourable for phytoplankton growth during spring and summer (Section 8.22). However, this was offset by increased rates of respiration induced by increased temperature (Section 8.34). As populations travelled downstream, river depth increased. Therefore, cells would have been subjected to longer periods in the dark when downstream than when upstream. As a result, the respiratory burden upon phytoplankton increased as they travelled downstream. This burden increased with increased temperature during summer and increased rates of production would have been offset. The respiratory burden upon phytoplankton was particularly marked during summer in the turbid Trent and Ouse (Section 5.4).

Loss of phytoplankton downstream during summer was probably a result of processes responsible for temporal loss of phytoplankton during summer. Evidence produced by this study suggests that respiration is a majr loss process. However, theoretically, sedimentation and grazing by protozoa and the benthos may contribute a substantial loss. Losses during winter were a result of low retentivity and an unfavourable underwater light climate, coupled with low temperature.

8.4 Short term changes in chlorophyll *a*

The *in situ* fluorometry work at Cromwell (Section 4.26) offered data of finer spatial resolution than offered previously by weekly or even daily sampling. The change in the fluorometric response of phytoplankton was associated with a change in chlorophyll *a* and hence a growth in the phytoplankton population. It is possible that the fluorometric response measured processes other than changes in chlorophyll *a*. Pigments such as antennae pigments may have contributed to absorption of fluorescence (Ernst, 1988) and so influenced the fluorometric response of phytoplankton. A more accurate estimate of chlorophyll *a* content would have been obtained by blocking the electon transport chain with CMU or DCMU, offering an explanation of 80% of the fluorometric response attributable to chlorophyll *a* content (Ernst, 1988). Even so, significant correlations existed between chlorophyll *a* concentration and fluorometric response for every calibration (Section 4.26) so the current method was deemed suitable.

Other work has attempted to show the daily pattern of changing phytoplankton chlorophyll *a* concentration. Studies have been carried out for the Rivers Danube (Kiss, 1996) and Welland (D. Balbi, pers. comm.). The general pattern shown during this study is one of an early morning minimum and an early evening maximum in chlorophyll *a* concentration. This has also been shown in other studies (Kiss, 1996; Harris, 1984). The apparent increase in chlorophyll *a* during the day may have been a result of growth in response to increased irradiance during the day. Many species of phytoplankton are able to divide twice per day under optimal conditions (see Reynolds, 1984; Kirk; 1994). Experimental work (Section 4.26) showed an increase in the chlorophyll based fluorometric response of phytoplankton with increased irradiance up between 50 and 70 $\mu mol\ m^{-2}\ s^{-1}$ (Section 4.26). Over this range, flourometric response decreased with increasing irradiance. The fluorometric response was also time dependent. Cells exposed to high light over longer periods exhibited a decrease in the fluorometric response. This decrease in fluorometric response is difficult to explain as it contradicts the literature. Cell damage and scenescence at higher irradiances may result in decreased fluorometric response.

The fluorometric response of phytoplankton increases with increasing light and is species dependent (Yentsch, 1980) and may not indicate an increase in chlorophyll *a*. An increase in fluorescence also results from nutrient limitation (Yentsch, 1980) although this is unlikely to be the case in the eutrophic Trent and Ouse.

The apparent chlorophyll *a* maxima during late afternoon or early evening was followed by a decrease during the night. The related phenomenon was the 'flattening' of the fluorometric response. That is, the fluorometric response increased as chlorophyll *a* increased althpough it is difficult to understand why the signal decreased during the night, indicating loss of biomass, only to rise again the next day. One theory is that during the day, when light was favourable and photosynthetic rate was high, new biomass production was able to offset loss processes such as

sedimentation and grazing. At night, when photosynthesis stopped and respiration was the governing process, not only was respiration adding to the loss but no further biomass was being produced. Therefore, loss processes acting together reduced the phytoplankton biomass as they continued through the night.

Alternatively, after photosynthesis during the day, cells may have broken down photosynthetic apparatus and used the amino acids elsewhere overnight. The photosynthetic apparatus may have been remade in the morning when they were needed (Kirk, 1994).

A decrease in water temperature overnight may also have contributed to a decrease in chlorophyll *a* (Harris, 1984). The fluorometric response also decreases per unit chlorophyll *a* with increasing phaeopigment concentration (Yentsch, 1980). As daily phaeopigment data were not available it was difficult to say whether or not phaeopigment concentration influenced the fluorometric response during this study.

The fluorometric response of phytoplankton may have been largely a result of physiological changes with increasing availability of light. However, studies mentioned previously have shown that actual chlorophyll *a* and cell density follows a familiar daily pattern to the one shown in this study. Morning minima increased during the day as a result of increased irradiance and cell growth and division and the production of chlorophyll *a*. The increase continued to the maxima in the late afternoon or early evening. During the night, chlorophyll *a* decreased as a result of loss from respiration, grazing and the breakdown and utilisation of photosynthetic material.

8.5 Phytoplankton carbon flux

A primary aim of this study was to estimate the autochthonous carbon flux to the Humber Estuary (Section 1.11). In order to do this, the carbon content of the phytoplankton was estimated, and using a measure of the gradient of chlorophyll *a* vs POC, an average carbon-to-chlorophyll *a* ratio of 33:1 mg mg^{-1} was calculated (Section 3.8). This was similar to ratios reported for other rivers (Table 8.3).

This method was slightly inaccurate as background POC from non-algal sources was included. For a more accurate calculation, phytoplankton carbon may have been calculated from volume (Smayda, 1978). When using this method, shrinkage of cells when preserving must be accounted for (Montagnes *et al.*, 1994). A dilution incubation procedure (Gallegos & Vant, 1996) or modelling approach (Cloern *et al.*, 1995) may also have been used. However, the approach taken in this study was similar to that for other rivers (e.g. Descy & Gosselain, 1994) and as comparable estimates were calculated it was deemed suitable to use this ratio to calculate the phytoplankton carbon flux.

Table 8.4 Comparison of carbon-to-chlorophyll ratios reported in some riverine studies.

System	Carbon/Chlorophyll *a* ($mg\ mg^{-1}$)	Reference
Oostershelde Estuary (Netherlands)	30	Westeyn & Kromcamp (1994)
River Meuse	37	Descy & Gosselain (1994)
River Rhine	50	Admiraal & van Zanten (1988)
Humber rivers	50	Tipping *et al.* (1997)
River Meuse	40	Descy *et al.* (1987)
River Trent	33	This study

Maximal carbon fluxes in the Trent corresponded with low discharge and high chlorophyll *a* concentration (Sections 7.2, 7.4). Minimum fluxes corresponded with high discharge and low chlorophyll *a* concentration (Section 7.4). In contrast, for the Ouse, maximal fluxes corresponded with winter flood events (Sections 7.2, 7.4). Therefore, it can be deduced that phytoplankton carbon flux for the Trent was dominated by chemical, physical and biological processes which influence phytoplankton growth and production. However, for the Ouse, discharge and the sheer volume of water entering the Estuary was more important in regulating the phytoplankton carbon flux in the Ouse. This was because large populations were able to develop *in situ* in the Trent over the spring months (Section 4.22). In contrast, the Ouse was highly responsive to floods and although large populations were able to develop they were often rapidly interrupted by floods and were not able to re-establish. Even so, phytoplankton carbon accounted for 49% of spring and summer POC for the Ouse (Section 7.3). However, the proportion was higher in the Trent with a contribution of 77 % during spring and summer (Section 7.3). These figures are comparable to other European rivers. During summer, phytoplankton contributed between 15 and 65% of POC for the Rhine (Admiraal *et al.*, 1992) and an annual contribution of 12% for the Humber rivers (Tipping *et al.*, 1997) and around 20% for the Westerschelde estuary (Soetaert & Herman, 1995) have been reported.

Phytoplankton were therefore important to the flux of autochthonously produced carbon, particularly in the Trent, during spring and summer. In shallower reaches of the Trent and Ouse, benthic and macrophytic production may have been more important then they were in other systems (Soetaert & Herman, 1995). However, macrophytes and benthic material are rarely transported downstream in quantities large enough to be important in spring and summer. Phytoplankton was the major contributor of autochthonous POC in the Trent and is important in

the Ouse during spring and summer. It is therefore important that the processes regulating phytoplankton carbon flux have been identified and quantified and the processes involved have been investigated.

Predicted changes in river discharge in the future indicate an increase in winter discharges in northern areas of the UK (Arnell, 1992). This may have little effect upon phytoplankton carbon flux in the Trent and Ouse as minima are already experienced in winter (Section 7.2). Flux may increase as a result of increased water volume passing through to the Estuary. If the increase in rainfall also occurred in spring, however, fluxes may decrease as phytoplankton development and production were hindered by loss processes resulting from increased discharge (Section 8.31).

Further studies of interest would be to develop a mass balance model to identify and quantify different sources of autochthonously produced carbon from macrophytes and the benthos during the year. The importance of each at different times of the year, at different stretches of the river and under varying environmental conditions, could be used to predict changes with predicted changes in riverine environmental parameters over the next few decades.

9 SUMMARY

1. Although subtle differences exist between the Trent and Ouse, the same processes generally had a similar effect upon phytoplankton growth, production and development in both rivers.

2. During spring , when discharge was low, maximal phytoplankton density was observed for both the Trent (53000 individuals ml^{-1}) and Ouse (62700 individuals ml^{-1}). The spring maxima comprised mainly centric diatoms, contributing a maximum of 83% of the phytoplankton of the Trent and 85% for the Ouse. Centric diatoms were considered able to efficiently utilise the environment experienced during spring.

3. 85 taxa were recored for the Trent at Cromwell and 82 for the Ouse at Acaster. The majority of these taxa were Chlorophyta. Species recorded were similar to those recorded for other European rivers.

4. Maximal chlorophyll *a* concentrations were also observed for the Trent (162 $\mu g\ l^{-1}$) and Ouse (166 $\mu g\ l^{-1}$) during spring. Chlorophyll *a* maxima were often disrupted by floods, especially for the Trent.

5. Maximal rates of column production were evident during spring for the Trent (1114 $\mu mol\ O_2$ (mg chl *a*)$^{-1}$ d^{-1}) and Ouse (2721 $\mu mol\ O_2$ (mg chl *a*)$^{-1}$ d^{-1}). During this period, maximum rates of areal production were also observed (546 $\mu mol\ O_2 m^2\ d^{-1}$ for the Trent and 536 $\mu mol\ O_2 m^2\ d^{-1}$ for the Ouse). Maximum rates were a result of minimum rates of phytoplankton respiration during spring (13 $\mu mol\ O_2$ (mg chl *a*)$^{-1}$ h^{-1} for the Trent and 10 $\mu mol\ O_2$ (mg chl *a*)$^{-1}$ h^{-1} for the Ouse). Rates of production were similar to those recorded for other European rivers.

6. A downstream increase in chlorophyll *a* was evident for the Trent during spring and early summer. Estimated rates of phytoplankton growth attained a maximum of 0.70 d^{-1}. Again, this maximum rate of growth was similar to those recored for other European rivers.

7. Overall, during spring, the Trent experienced a pattern of phytoplankton density, chlorophyll *a*, production and growth maxima. A similar pattern existed for the Ouse although it was not as pronounced as for the Trent. Growth and production maxima were attributable to favourable conditions of high river retentivity, increasing irradiance, daylength and

temperature. Low rates of loss from sedimentation, grazing and respiration also contributed to the maxima.

8. During summer, phytoplankton density decreased for then Trent (3000 to 6000 individuals ml^{-1}) and Ouse (2000 to 6000 individuals ml^{-1}). This corresponded with a rapid decline in cenric diatom density and the switch from a centric dominated population to a green algal dominated one. Silica depletion may partly have contributed to the decline of centric diatoms during spring.

9. Chlorophyll *a* concentration also rapidly declined during summer for both the Trent (c. 6$\mu g\ l^{-1}$) and Ouse (c. 2 to 7 $\mu g\ l^{-1}$). However, this decline was most marked for the Trent at Cromwell.

10. The decline in phytoplankton density and chlorophyll *a* during summer corresponded with declining rates of production. This was more pronounced for the Trent than for the Ouse. Rates of column production declined during summer for the Trent (-1954 $\mu mol\ O_2\ (mg\ chl\ a)^{-1}\ d^{-1}$) and Ouse (-5026 $\mu mol\ O_2\ (mg\ chl\ a)^{-1}\ d^{-1}$) as did rates of areal production. However, minimum rates of production for the Ouse were thought to be unrealistic and the result of unexplained processes. The decline in rates production was a result of a combination of increased repiratory burden caused by an increase in temperature and of river turbidity. The PIZT model suggested that respiration, river depth and attenuation coefficient were the most important factors influencing phytoplankton production in the Trent and Ouse.

11. A downstream decrease in chlorophyll *a* was observed during late summer. Rates of growth estimated from this downstream change declined to a minimum of 0.76 d^{-1} for the Trent. This phenomenom has been reported for other European rivers and was a reuslt of increasing pressure form loss processes such as respiration and grazing downstream relative to upstream.

12. Loss of phytoplankton populations during summer was considered primarily as a result of an increased respiratory burden resulting from increased temperature. Other processes considered as being possibly important were sedimentation, benthic grazing and pathenogenic attack. Experimental work suggested that the green algae dominating the summer populations were more responsive to increased rates of respiration than centric diatoms. This may partly explain the rapid decline in rates of production and growth during summer. However, the reason for a switch from a spring population dominated by centrics to a summer population dominated by green algae has still to be sufficiently explained.

13. During winter, high discharge, low irradiance and low temperatures resulted in a climate unfavourable for phytoplankton growth. Phytoplankton density decreased to minima of c. 60 individuals ml^{-1} for both the Trent and Ouse. Minimum concentrations of chlorophyll *a* were also observed during winter with concentrations falling below 2 $\mu g\ l^{-1}$ for the Trent and Ouse.

14. Although no singular environmental factor can be said to be ultimately important in influencing phytoplankton dynamics, the most important factors were discharge, temperature, and irradiance.

15. Phytoplankton was a major source of POC to the Humber Estuary, particularly during spring and summer where they contributed a maximum of 77% and 47 % of the POC for the Trent and Ouse, respectively. These contributions to the total POC load were similar to other European river systems. A minimum contribution of phytoplankton to POC was observed during winter when they contributed c. 11 % of the riverine POC.

16. Phytoplankton was the most important factor with regards to autochthonous carbon flux to the Humber Estuary in spring and early summer.

17. The Trent contributed between 967 and 1141 t yr^{-1} of autochthonous carbon to the Humber Estuary over the studied period. This was over 5 times the autochthonous carbon flux of the Ouse and highlights the importance of the Trent in the flux of autochthonous carbon to the Humber Estuary.

Bibliography

Admiraal W, Breebaart L, Tubbing GMJ, van Zenten B, De Ruyter van Steveninck ED, Bijkerk R (1994) Seasonal variation in composition and production of planktonic communities in the lower River Rhine. *Freshwat. Biol.* 32: 519-531.

Admiraal W, Jacobs DMLHA, Breugem P, de Ruyter van Steveninck ED (1992) Effects of phytoplankton on the elemental composition (C, N, P) of suspended particulate material in the lower river Rhine. *Hydrobiologia* 236: 479-489.

Admiraal W, van Zanten B (1988) Impact of biological activity on detritus transported in the lower River Rhine: an exercise in ecosystem analysis. *Freshwat. Biol.* 20: 215-225.

Arnell NW (1992) Impacts of climatic change on river flow regimes in the UK. *J. Instn Wat. Engrs. Scient.*. 6: 432-438.

Bainbridge R (1953) Studies on the interrelationships of zooplankton and phytoplankton. *J. Mar. biol. Ass. UK.* 32: 385-447.

Baker KS, Frouin R (1987) Relation between photosynthetically available radiation and total insolation at the ocean surface under clear skies. *Limnol. Ocenaogr.* 32:1370- 1376.

Baker AL, Kromer Baker K (1979) Effects of temperature and current discharge on the concentration and photosynthetic activity of the phytoplankton in the upper Mississippi River. *Freshwat. Biol.* 9: 191-198.

Baly ECC (1935) The kinetics of photosynthesis. *Proc. R. Soc.. B.* 117: 218-239.

Banse K (1976) Rates of growth, respiration and photosynthesis of unicellular algae as related to cell size – a review. *J.Phycol.* 12: 135-140.

Bastviken DTE, Caraco NF, Cole JJ (1998) Experimental measurements of zebra mussel (*Dreissena polymorpha*) impacts on phytoplankton community composition. *Freshwat. Biol.* 39: 375-386.

Baumert H (1996) On the theory of photosynthesis and growth in phytoplankton. Part I: Light limitation and constant temperature. *Int. Revue ges. Hydrobiol.* 81: 109-139.

Belcher H, Swale E (1978) *Freshwater Algae.* HMSO. London

Belcher H, Swale E (1979) *River Phytoplankton.* HMSO. London

Bereczky MC, Nosek JN (1993) The influence of ecological factors on the abundance of different ciliated protozoa populations in the Danube River. I. Investigation of the ecological amplitude. *Acta Protozool.* 32: 1-16.

Bereczky MC, Nosek JN (1994) Composition and feeding spectrum of protozoa in the River Danube, with particular reference to planktonic ciliata. *Limnologica* 24: 23-28.

Billen G, De Becker E, Lancelot C, Mathot S, Servais P, Stainier E (1984) Etude des processus de transfert, d'immobilisation et de transformation de l'azote dans cheminement depuis les sols agricoles jusqu'à la mer. *Contract C.C.E ENV-522-B(RS). 5ème raport.* Univ. Libre Bruxelles. 27pp.

Billen G, Garnier J, Hanset P (1994) Modelling phytoplankton development in whole drainage networks: the RIVERSTRAHLER model applied to the Seine river system. *Hydrobiologia* 289: 119-137.

Blatbak G, Egge JK, Heldal M (1993) Viral mortality of the marine alga *Emiliania huxleyi* (Hapatophyceae) and termination of algal bloom. *Mar. Ecol. Prog. Ser.* 93: 39-48.

Blum JL (1954) Evidence for a diurnal pulse in stream phytoplankton. *Science* 119: 732-734.

Boeme J, Frischer ME, Jiang SC, Kellogg CA, Pichard S, Rose JB (1993) Viruses, bacterioplankton and phytoplankton in the South-Eastern Gulf of Mexico: distribution and contribution to oceanic DNA pools. *Mar. Ecol. Prog. Ser.* 97: 1-10.

Bogdan KG, Gilbert JJ (1982) Seasonal patterns of feeding by natural populations of *Keratella, Polyarthra,* and *Bosmina.* Clearance rates, selectivities, and contributions to community grazing. *Limnol. Oceanogr.* 27: 918-934.

Bothár A (1987) The estimation of production and mortality of Bosminalongirostris (O.F. Müller) in the River Danube (Danubialia Hungarica, CIX). *Hydrobiologia* 145: 285-291.

Bothár A, Kiss KT (1990) Phytoplankton and zooplankton (Cladocera, Copepoda) relationship in the eutrophic River Danube (Danubialia Hungarica, CXI). *Hydrobiologia* 191: 165-171.

Bothàr A, Ràth B (1994) Abundance dynamics of crustaceans in different littoral biotopes of the "Szigetköz" side arm system, River Danube, Hungary. *Verh. Internat. Verein. Limnol.* 25: 1684-1687.

Bourrelly P (1966) Les Algues D'eau Douce. I: Les Algues verters. Booubée. Paris.

Bourrelly P (1968) Les Algues D'eau Douce. II: Les Algues jaunes et brunes. Booubée. Paris.

Bourrelly P (1970) Les Algues D'eau Douce. III: Les Algues bleues et rouges. Booubée. Paris.

Brunet C, Davoult D, Casotti R (1996) Physiological reactions to a change in light regime in cultured *Skeletonema costatum* (Bacillariophyta): implications for estimation of phytoplankton biomass. *Hydrobiologia* 333: 87-94.

Bryan JR, Riley JP, Williams PJ LeB (1976) A Winkler procedure for making precise measurements of oxygen concentration for productivity and related studies. *J. Exp. Mar. Biol. Ecol.* 21: 191-197.

Butcher RW (1924) The plankton of the River Wharfe. *The Naturalist*, Hull: April-June: 175-214.

Butcher RW, Pentelow, FTK, Woodley JWA (1930) Variations in compositions of river waters. *Int. Rev. Hydrobiol.* 24: 47-80.

Canter HM, Lund JWL (1951) Studies of plankton parasites. III: Examples of the interaction between parasites and other factors determining the growth of diatoms. *Annal. Bot.* 15: 359-371.

Capblancq J, Décamps H (1978) Dynamics of the phytoplankton of the River Lot. *Verh. Int. Verein. Limnol.* 20: 1479-1484.

Caraco NF, Cole JJ, Raymond PA, Strayer DL, Pace ML, Findlay SEG, Fischer DT (1997) Zebra mussel invasion in a large, turbid river: Phytoplankton response to increased grazing. *Ecology* 78: 588-602.

Carr OJ, Goulder R (1990) Fish-farm effluents in rivers. II. Effects on inorganic nutrients, algae and the macrophyte *Ranunculus penicillatus*. *Wat. Res.* 24: 639-647.

Carpenter JH (1965) The accuracy of the Winkler method for dissolved oxygen analysis. *Limnol. Oceanogr.* 10: 135-140.

Carpenter JH (1966) New measurements of oxygen stability in pure and natural water. *Limnol. Oceanogr.* 11: 264-277.

Chalker BE (1980) Modelling light saturation curves for photosynthesis: an exponential function. *J. Theor. Biol.* 84: 205-215.

Chisholm SW, Costello JC (1980) Influenceof environmental factors and population composition on the timing of cell division in Thallassiosira fluvitalis (Bacillariophyceae) grown on light/dark cycles. *J. Phycol.* 16: 375-383.

Christmas M, Whitton BA (1998) Phosphorus and aquatic bryophytes in the Swale-Ouse river system, north-east England. 1. Relationship between ambient phosphate, internal N:P ratio and surface phosphatase activity. *Sci. total Envir.* 21: 389-399.

Chu SP (1942) The influence of the mineral composition of the medium on the growth of planktonic algae. I. Methods and culture media. *Journal of Ecology* 30: 284-325.

Cloern JE, Grenz C, Vidergar-Lucas L (1995) An empirical model of the phytoplankton chlorophyll : carbon ratio – the conversion factor between productivity and growth rate. *Limnol. Oceanogr.* 40(7): 1313-1321.

Cole JJ, Caraco NF, Peierls BL (1991) Phytoplankton primary production in the tidal, freshwater Hudson River, New York (USA). Verh. Internat. Verein. Limnol. 24: 1715-1719.

Cole JJ, Caraco NF, Peierls BL (1992) Can phytoplankton maintain a positive carbon balance in a turbid, freshwater, tidal estuary? *Limnol. Oceanogr.* 37: 1608-1617.

D'Avanzo C, Kremer JN, Wainwright SC (1996) Ecosystem production and respiration in response to eutrophication in shallow temperate estuaries. *Mar. Ecol. Prog. Ser.* 141: 263-274.

De Ruyter van Steveninck ED, Admiraal W, Breebaart L, Tubbing GMJ, Van Zanten B (1992) Plankton in the River Rhine: structural and functional changes observed during downstream transport. *J. Plankton Res.* 14: 1351-1368.

De Ruyter van Steveninck ED, Van Zanten B, Admiraal W (1990) Phases in the development of riverine plankton: Examples from the Rivers Rhine and Meuse. *Hydrobiologia. Bull.* 24: 46-55.

del Giorgio PA, Vinocur AL, Lomardo RJ, Tell HG (1991) Progressive changes in the structure and dynamics of the phytoplankton community along a pollution gradient in a lowland river – a multivariate approach. *Hydrobiologia.* 224:129-154.

Descy JP (1987) Phytoplankton composition and dynamics in the River Meuse (Belgium). Arch. Hydrobiol. (Suppl.) 78: 225-245.

Descy JP (1993) Ecology of the phytoplankton of the River Moselle: effects of disturbances on community structure and diversity. *Hydrobiologia* 249: 111-116.

Descy JP, Everbecq E, Smitz JS (1988) Primary production in the River Meuse (Belgium). Verh. Internat. Verein. Limnol. 23: 1287-1293.

Descy JP, Gosselain V (1994) Development and ecological importance of phytoplankton in a large lowland river (river Meuse, Belgium). *Hydrobiologia* 289: 139-155.

Descy JP, Servias P, Smitz JS, Billen G, Everbecq (1987) Phytoplankton biomass and production in the River Meuse (Belgium). *Wat. Res.* 21 (12): 1557-1566.

Doering PH, Oviatt CA, Nowicki BL, Klos EG, Reed, LW (1993) Phosphorus and nitrogen limitation of primary production in a simulated estuarine gradient. *Mar. Ecol. Prog. Ser.* 124: 271-287.

Dokulil MT (1994) Environmental control of phytoplankton productivity in turbulent turbid systems. *Hydrobiologia* 289: 65-72.

Dvihally ST (1975) Primary Production of the Hungarian Danube. *Verh. Internat. Verein. Limnol.* 19: 1717-1722.

Eilers PHC, Peeters JCH (1988) A model for the relationship between light intensity and the rate of photosynthesis in phytoplankton. *Ecological Modelling.* 42: 199-215.

Ernst EW (1988) Applications of chlorophyll fluorescence in hydrobiology in: Lichtenthaler HK (ed) *Applications of Chlorophyll Fluorescence.* Kluwer Academic Publishers pp: 261-268.

Fee EJ (1973) Modelling primary production in water bodies: A numerical approach that allows vertical inhomogeneities. *J. Fish. Res. Board Can.* 30: 1469-1473.

Forsberg BR, Araujolima CARM, Martinelli LA, Victoria RL, Bonassi JA (1993) Autotrophic carbon-sources for fish of the central Amazon. *Ecology* 74: 643-652.

Friedrich G, Viehweg M (1984) Recent developments of the phytoplankton and its activity in the lower Rhine. *Verh. Internat. Verein. Limnol.* 22: 2029-2035.

Fritsch FE (1902) Algological notes. III. Preliminary report on the phytoplankton of the Thames. *Ann. Bot.* 16: 1-9.

Fritsch FE (1905) The plankton of some English Rivers. *Ann. Bot.* 19: 163-167.

Gallegos CL, Vant WN (1996) An incubation procedure for estimating carbon-to-chlorophyll ratios and growth-irradiance relationships of estuarine phytoplankton. *Mar. Ecol. Prog. Ser.* 138: 275-291.

Garnier J, Billen G, Coste M (1995) Seasonal succession of diatoms and Chlorophyceae in the drainage network of the Seine river: Observations and modelling. *Limnol. Oceanogr.* 40: 750-765.

Genkal SI, Korneva L (1992) A simple method to assess the number of diatoms using TEM. *Arch. Hydrobiol.* 124: 357-366.

Gilbert JJ, Bogdan KG (1981) Selectivity of *Polyarthra* and *Keratella* for flagellate and aflagellate cells. *Verh. Internat. Verein. Limnol.* 21: 1515-1521.

Goldman JC, Dennett MR (1984) Effect of photoinhibition during bottle incubations on the measurement of seasonal pri8masry production in a shallow coastal water. *Mar. Ecol. Prog. Ser.* 15: 169-180.

Gosselain V, Descy JP, Everbecq E (1994) The phytoplankton community of the River Meuse, Belgium: seasonal dynamics (year 1992) and the possible incidence of zooplankton grazing. *Hydrobiologia* 249: 179-191.

Gosselain V, Viroux L, Descy JP (1998) Can a community of small-bodied grazers control phytoplankton in rivers? *Freshwat. Biol.* 39: 9-24.

Grande KD, Bender ML, Irwin B, Platt T (1990) A comparison of net and gross rates of oxygen production as a function of light intensity in some natural plankton populations and in a *Synechoccus* culture. *J. Plankt. Res.* 13: 1-16.

Gregg WW, Carder KL (1990) A simple spectral solar irradiance model for cloudless maritime atmospheres. *Limnol. Ocenaogr.* 35:1657- 1675.

Grobbelaar JU (1985) Phytoplankton productivity in turbid waters. *J. Plankton Res.* 7:653-663.

Grobbelarr JU (1989) The contribution of phytoplankton productivity in turbid freshwaters to their trophic status. *Hydrobiologia* 173: 127-133.

Grobbelaar JU (1990) Modelling phytoplankton productivity in turbid waters with small euphotic to mixing depth ratios. *Journal of Plankton Research.* 12(5): 923-931.

Guillard RRl (1973) Methods for microflagellates and nannoplankton. In Stein, JR (ed) *Handbook of Phycological Methods.* Cambridge University Press. Cambridge. pp 69-86.

Håkansson H (1986) A taxanomic reappraisal of some *Stephanodiscus* species (Bacillariophyta). *Br. Phycol. J.* 21: 25-37.

Harris GP (1984) Phytoplankton productivity and growth measurements: past, present and future. *J. Plankton Res.* 6: 219-237.

Hasle GR, Fryxell GA (1970) Diatoms: cleaning and mounting for light and electron microscopy. *Trans. Amer. Microsc. Soc.* 89: 469-474.

Henley WJ (1993) Measurement and interpretation of photosynthetic light-response curves in algae in the context of photoinhibition and diel changes. *J. Phycol.* 29: 729-739.

Herrera-Silveira JA, Ramírez - Ramírez J (1996) Effects of natural phenolic material (tannin) on phytoplankton growth. *Limnol. Oceanogr.* 41: 1018-1023.

Holmes NTH ,Whitton BA (1984) Phytoplankton of four rivers, the Tyne, Wear, Tees and Swale. *Hydrobiologia* 80: 111-127.

Hoshaw RW, Rosowski JR (1973) Methods for Microscopic Algae, pp 53-67, In Stein, JR (ed) *Handbook of Phycological Methods.* Cambridge University Press. Cambridge. pp 448.

Hynes HBN (1970) *The Ecology of Running Waters.* Univ. Liverpool Press. Liverpool.

Ittekkot V, Laane RWPM (1991) Fate of riverine particulate organic matter. In: Degens ET, Kempe S, Richey JE (eds) Biogeochemistry of major World rivers. SCOPE. Wiley. Chichester. Pp 233-243.

Jarvie HP, Neal C, Robson AJ (1997) The geography of the Humber catchment. *Sci. Total Envir.* 194/195: 87-100.

Joaquimjusto C, Gosselain V, Decy JP, Thome JP (1995) Relative importance of the trophic and direct pathways of PCB contamination in the rotifer species *Brachionus calyciflorus* (Pallas). *Hydrobiologia* 313: 249-257.

Jones FH (1984) The dynamics of suspended algal populations in the lower Wye catchment. *Water Res.* 18: 25-35.

Jones RI, Barrington RJ (1985) A study of the suspended algae in the River Derwent, Derbyshire, UK. *Hydrobiologia* 128: 255-264.

Jones RI (1977) Factors controlling phytoplankton production and succession in a highly eutrophic lake (Kinnego Bay, Lough Neagh): ii. Phytoplankton production and its chief determinants. *J. Ecol.* 65: 561-577.

Kilham P, Kilham SS (1980) The Evolutionary Ecology of Phytoplankton. in Morris I ed (1980) *The Physiological Ecology of Phytoplankton.* Blackwell Scientific Publications. Oxford.

Kirk JTO (1976) Yellow substance (Gelbstoff) and its contribution to the attenuation of photosynthetically active radiation in some inland and coastal south-eastern Australian waters. *Aust. J. Mar. Freshwater Res.* 27: 61-71.

Kirk JTO (1980) Spectral absorption properties of natural waters: Contribution of the soluble and particulate fractions to light absorption in some inland waters of south-eastern Australia. *Aust. J. Mar. Freshwater Res.* 31:287-296.

Kirk JTO (1994) *Light and Photosynthesis in Aquatic Ecosystems.* 2nd edn. Cambridge University Press. Cambridge. 509 pp.

Kiss KT (1994) Trophic level and eutrophication of the River Danube in Hungary. *Verh. Internat. Verein. Limnol.*, 25: 1688-1691.

Kiss KT (1996) Diurnal changes of planktonic diatoms in the River Danube near Budapest (Hungary). *Algol. Stud.* 80: 113-122.

Kiss KT, Padisák J (1988) Species succession in the Thalassiosiraceae: Quantitative studies in the large, shallow Lake Balaton, Hungary. 10th Diatom-Symposium 1988.

Kiss KT, Szabó A (1975) Longitudinal profile investigation in the Tisza and Eastern Main Channel I. Quantitative changes in phytoplankton. *Tiscia* (Szeged) 10: 3-14.

Kiss KT, Genkal SI (1993) Winter blooms of centric diatoms in the River Danube and in its side-arms near Budapest (Hungary). *Hydrobiologia* 269/270: 317-325.

Kiss KT, Ács É, Kovács A (1994) Ecological observations on *Skeletonema potamos* (Weber) Hasle in the River Danube, near Budapest (1991-92, daily investigations). *Hydrobiologia* 289: 163-170.

Knoechel R, Kalff J (1978) An *in situ* study of the productivity and population dynamics of five freshwater planktonic diatom species. *Limnol. Oceanogr.* 23(2): 195-218.

Köhler J (1993) Growth, production and losses of phytoplankton in the lowland River Spree. I. Population dynamics. *J. Plankton Res.* 15: 335-349.

Köhler J (1994a) Dynamics of phytoplankton in the lowland River Spree (Germany). *Verh. Internat. Verein. Limnol.* 25: 1590-1594.

Köhler J (1994b) Origin and succession of phytoplankton in a river-lake system (Spree, Germany). *Hydrobiologia* 289: 73-83.

Köhler J (1995) Growth, production and losses of phytoplankton in the lowland River Spree: carbon balance. *Freshwater Biology* 34: 501-512.

Köhler J, Bosse S (1998) Growth and losses of phytoplankton studied with a new dialysis chamber technique along the river Spree. *Arch. Hydrobiol.* 142: 1-19.

Köhler J, Nixdorf B, Hoeg S (1993) Lake Müggelsee and the inflowing River Spree: comparison of phytoplankton communities 1980-1990. *Int. Revue ges. Hydrobiol.* 78: 345-358.

Kowalczewski A, Lack TJ (1971) Primary production and respiration of the phytoplankton of the rivers Thames and Kennet at Reading. *Freshwat. Biol.* 1: 197-212.

Kowe R, Skidmore RE, Whitton BA, Pinder AC (1998) Modelling phytoplankton dynamics in the River Swale, an upland river in NE England. *Sci. Total Environ.* 210/211: 535-546.

Kozerski HP (1994) Possibilities and limitations of sediment traps to measure sedimentation and resuspension. *Hydrobiologia* 284: 93-100.

Kramer K, Lange-Bertalot H (1991) *Süßwasserflora von Mittleeuropa. 3. Tierl: Centrales, Fragilariaceae, Eunotiaceae*. Gustav Fisher Verlag. Stuttgart.

Lack TJ (1971) Quantitative studies on the phytoplankton of the rivers Thames and Kennet at Reading. *Freshwat. Biol.* 1: 213-224.

Lack TJ, Youngman RE, Collingwood RW (1978) Observations on a spring diatom bloom in the River Thames. *Verh. Internat. Verein. Limnol.* 20: 1435-1439.

Lair N, Ali HO (1990) Grazing and assimilation rates of natural populations of planktonic rotifers *Keratella cochlearis*, *Keratella quadrat* and *Kellicottia longispina* in a eutrophic lake (Aydat, France). *Hydrobiologia* 194: 119-131.

Landrey MR, Hassett RP (1982) Estimating the grazing impact of marine micro-zooplankton. *Mar. Biol.* 67: 283-288.

Law M, Wass P, Grimshaw D (1997) The hydrology of the Humber catchment. *Sci. Total Environ.* 194/195: 119-128.

Leeks GJL, Jarvie HP (1998) Introduction to the Land-Ocean Interaction Study (LOIS): Rationale and international context. Sci. Total. Envir. 210/11: 5-20.:

Lester WF (1975) Polluted River: River Trent. In: BA Whitton (Ed.), *River Ecology.* Blackwell Scientific Publications. Oxford. pp 489-513.

Lowe RL (1975) Comparative ultrastructure of the valves of some *Cyclotella* species (Bacillariophyceae). *J. Phycol.* 11: 415-425.

Lund JWG, Kipling C, Le Cren ED (1958) The inverted microscope method of estimating algal numbers and the statistical basis of estimations by counting. *Hydrobiologia* 2: 142-171.

Lund JWG (1959) A simple counting chamber for nannoplankton. Limnol. Oceanogr.. 4: 57-65.

Mallin MA, Paerl HW (1992) Effects if variable irradiance on phytoplankton productivity in shallow estuaries. *Limnol. Oceanogr.* 37 (1): 54-62.

Marker AFH (1994) *Chlorophyll a – SCA Method Revision.* NRA Report. 64 pp.

Marker AFH, Gunn RJM (1977) The benthic algae of some streams in southern England. III. Seasonal variations in chlorophyll *a* in the seston. *Journal of Ecology* 65: 223-234.

Marker AFH, Butterwick C, Garbutt RA (1993) A short pilot study of the phytoplankton of rivers of the Humber catchment. *LOIS Report.* 50 pp.

McCollin TA (`1995) An investigation into the spatial variation and the interactions between the phytoplankton and zooplankton in the River Trent. MSc Napier University.

Mead R, Curnow RN (1983) *Statistical Methods in Agriculture and Experimental Biology.* Chapman and Hall. London.

Meybeck M (1993) Riverine transport of atmospheric carbon: sources, global typology and budget. *Wat. Air Soil Pollut.* 70: 443-463.

Meybeck M, Cauwet G, Dessery S, Somville M, Goleau D, Billen G (1988) Nutrients (organic C, P, N, Si) in the eutrophic River Loire (France) and its estuary. *Estuar. Coast. Mar. Sci.* 27: 595-624.

Montagnes DJS, Berges JA, Harrison PJ, Taylor FJR (1994) Estimating carbon, nitrogen, protein and chlorophyll *a* from volume in marine phytoplankton. *Limnol. Oceanogr.* 39(5): 1044-1060.

Moore JW (1976) Seasonal succession of algae in rivers. I. Examples from the Avon, a large slow flowing river. *J. Phycol.* 12: 342-349.

Morel A, Smith RC (1974) Relation between total quanta and total energy for aquatic photosynthesis. *Limnol. Ocenaogr.* 19: 591-600.

Moss B, Balls H, Booker I, Manso, K, Timms M (1984) The River Bure, United Kingdom: Patterns of change in chemistry and phytoplankton in a slow-flowing fertile river. *Verh. Internat. Verein. Limnol.* 22: 1959-1964.

Nienhuis PH (1993) Nutrient cycling and foodwebs in Dutch estuaries. *Hydrobiologia* 265: 15-44.

Nosek JN, Bereczky MC (1994) The effect of some environmental factors on protozoa populations of the River Danube. *Tiscia* 28: 29-36.

NRA (1995) The River Trent. NRA.

NRA (1994) Rivers Swale, Ure and Ouse catchment management plan consultation report. NRA.

Nusch EA (1987) Development of planktonic algae in the Ruhr River dependent on nutrient supply, waterflow, irradiance and temperature. *Verh. Int. Verein. Theor. Angew. Limnol.* 20: 1837-1843.

Ojala A (1993) Effects of temperature and irradiance on the growth of two freshwater photosynthetic Cryptophytes. *J. Phycol.* 29: 278-284.

Owens JL, Crumpton WG (1995). Primary production and light dynamics in an upper Mississippi River backwater. *Regulated Rivers: Research and Management.* 11: 185-192.

Pahl-Wost C, Imboden DM (1991) DYPHORA – a dynamic model for the rate of photosynthesis of algae. *J. Plankt. Res.* 12: 1207-1221.

Pinder A, Marker AFH, Pinder AC, Ingram JKG, Leach DV, Collett GD (1997) Concentrations of suspended chlorophyll a in the Humber Rivers. *Sci. Total Envir.* 194/195: 373-378.

Platt T, Gallegos CL, Harrison, WG (1980) Photoinhibition of photosynthesis in natural assemblages of marine phytoplankton. *J. Mar. Res.* 38: 687-701.

Potter IC, Cannon D, Moore JW (1975) The ecology of algae in the Moruya River, Australia. *Hydrobiologia* 47: 415-430.

Pourriot R (1977) Food and feeding habits of rotifera. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* 8: 243-260.

Prygiel J, Leitao M (1994) Cyanophycean blooms in the reservoir Val Joly (northern France) and their development in downstream rivers. *Hydrobiologia* 289: 85-96.

Reisser W (1993) Viruses and virus-like particles of freshwater and marine eukaryotic algae – a review. *Arch. Protistend.* 143: 257-265.

Reynolds CS (1984) *The Ecology of Freshwater Phytoplankton.* Cambridge University Press. Cambridge.

Reynolds CS (1988) Potamoplankton: paradigms, paradoxes, prognoses. In: Round FE (Ed) *Algae and the Aquatic Environment.* Biopress. Bristol. Pp 285-311.

Reynolds CS, White ML, Clarke RT, Marker AF (1990) Suspension and settlement of particles in flowing water: comparison of the effects of varying water depth and velocity in circulating channels. *Freshwat. Biol.* 24: 23-34.

Reynolds C S (1994) The long, the short and the stalled – on the attributes of phytoplankton selected by physical mixing in lakes and rivers. *Hydrobiologia* 289: 9-24.

Reynolds CS, Descy JP (1996) The production, biomass and structure of phytoplankton in large rivers. *Arch. Hydrobiol. Suppl.* 113: 161-187

Reynolds CS, Glaister MS (1993) Spatial and temporal changes in phytoplankton abundance in the upper and middle reaches of the River Severn. *Arch. Hydrobiol. Suppl.* 101: 1-22.

Robson A.J, Neal C (1997) A summary of regional water quality for Eastern UK rivers. *Sci. Total Environ.* 194/195: 15-38.

Roditi HA, Caraco NF, Cole JJ, Strayer DL (1996) Filtration of Hudson River water by the zebra mussel (*Dreissena polymorpha*). *Estuaries* 19: 824-832.

Rust BR (1982) Sedimentation in fluvial and lacustrine environments. *Hydrobiologia* 91: 59-70.

Ryder RA, Pesendorfer J (1989) Large rivers are more than flowing lakes: a comparative review. *Can. Spec. Publ. Fish. Aquat. Sci.* 106: 65-85.

Sabater S, Muñoz I (1990) Successional dynamics of the phytoplankton in the lower part of the River Ebro. *J. Plankton Res.* 12: 573-592.

Schlüter M, Groeneweg J, Soedeer CJ (1987) Impact of rotifer grazing on population dynamics of green microalgae in high-rate ponds. *Wat. Res.* 21: 1293-1297.

Schmidt A (1994) Main characteristics of the phytoplankton of the Southern Hungarian section of the River Danube. *Hydrobiologia* 289: 97-108.

Schroeder B (1989) Über das Plankton der Order. *Ber. Dt. Bot. Gesel.* 15: 479-492.

Sedjo RA (1993) The carbon cycle and global forest ecosystem. *Wat. Air Soil Pollut.* . 70: 295-307.

Seip KL, Reynolds CS (1995) Phytoplankton functional attributes along trophic gradient and season. *Limnol. Oceanogr.* 40: 589-597.

Shimeta J, Jumars PA, Lessard EJ (1995) Influences of turbulence on suspension feeding by planktonic protozoa; experiments in laminar sheer fields. *Limnol. Oceanogr.* 40: 845-859.

Skidmore RE, Maberly SC, Whitton BA (1998) Patterns of spatial and temporal variation in phytoplankton chlorophyll a in the River Trent and its tributaries. *Sci. Total Environ.* 210/211: 357-365.

Smayda TJ (1978) From phytoplankters to biomass. In: Sournia A (Ed) *Phytoplankton manual.* UNESCO. Pp 273-279.
Smayda T (1980) Phytoplankton Species Succession. in Morris I (Ed) The Physiological Ecology of Phytoplankton. Blackwell Scientific Publications. Oxford.

Speller FM (1990) A contribution to our knowledge of the taxonomy of discoidal centic diatoms based upon obervations of populations from the River thames, England. Hydrobiologia 190: 15-32.

Soetaert K, Herman PMJ (1995) Carbon flows in the Westerschelde estuary (the Netherlands) evaluated by means of an ecosystem model (MOSES). *Hydrobiologia* 311: 247-266.

Starkweather P (1980) Aspects of the feeding behaviour and trophic ecology of suspension-feeding rotifers. *Hydrobiologia* 73: 63-72.

Steeman-Nielsen E, Jensen A (1957) Primary oceanic production. The autotrophic production of organic matter in the oceans. *Galathea Rep.* 1: 49-136.

Stevenson RJ, White KD (1995) A comparison of natural and human determinants of phytoplankton communities in the Kentucky River basin, USA. *Hydrobiologia* 297: 201-216.

Stoyneva MP (1994) Shallows of the lower Danube as additional sources of potamoplankton. *Hydrobiologia* 289: 171-178.

Swale EMF (1964) A study of the phytoplankton of a calcareous river. *J. Ecol.* 52: 433-446.

Swale EMF (1969) Phytoplankton of two English Rivers. *J. Ecol.* 52: 1-23.

Takahashi M, Shimura S, Yamaguchi Y, Fujita Y (1971) Photoinhibition of phytoplankton photosynthesis as a function of exposure time. J. Oceanogr. Soc. Japan. 27: 43-50.

Talling JF (1957) The phytoplankton population as a compound photosynthetic system. New Phytol. 56: 133-149.

Talling JF, Rzóska J (1967) The development of plankton in relation to the hydrological regime in the Blue Nile. *J. Ecol.* 55: 637-662.

Threlkeld ST, Søballe DM (1988) Effects of mineral turbidity on freshwater phytoplankton communities: Three exploratory tank experiments of factorial design. *Hydrobiologia* 159:223-236.

Tikkanen T (1986) *Kasviplanktonopas.* Helsinki Suomen Luonnansuojelun Tuki Oy. Helsinki.

Tipping E, Marker AFH, Butterwick C, Collett GD, Cranwell PA, Ingram JKG, Leach DV, Lishman JPG, Pinder A, Rigg E, Simon BM (1997) Organic carbon in the Humber rivers. *Sci. Total Envir.* 194/195: 345-356.

Titman D, Kilham P (1976) Sinking in freshwater phytoplankton: some ecological implications of cell nutrient status and physical mixing. *Limnol. Oceanogr.* 21: 409-417.

Tubbing DMJ, DE Zwart D, Burger-Wiersma T (1995) Phytoplankton dynamics in the River Meuse as affected by pollution. *Netherlands Journal of Aquatic Ecology.* 29: 103-116.

Uncles RJ, Easton AE, Griffiths ML, Harris C, Howland RJM, Joint I, King RS, Morris AW, Plummer DH (1998) Concentrations of suspended chlorophyll in the tidal Yorkshire Ouse and Humber Estuary. *Sci. Total. Envir.* 210/11: 357-366.

Van Dijk GM, van Zanten B (1995) Seasonal changes in zooplankton abundance in the lower Rhine during 1987-1991. *Hydrobiologia* 304: 29-38.

Vannote RL, Minshall GW, Cummins KW, Sedell JR, Cushing CE (1980) The river continuum concept. *Can. J. Fish. Aquat. Sci.* 37: 130-137.

Viroux L (1997) Zooplankton development in two large lowland rivers, the Moselle (France) and the Meuse (Belgium), in 1993. *J. Plankton Res.* 19: 1743-1762.

Vollenweider RA (Ed)(1974) *A Manual on Methods for Measuring Primary Production in Aquatic Environments.* 2nd Edn. Blackwell Scientific Publications. Oxford.

Walsby AE (1997) Numerical integration of phytoplankton photosynthesis through time and depth in a water column. *New Phytol.* 136: 189-209.

Welch, EB (1952) Limnology (2nd Edn) McGraw-Hill. New York.

Westlake DF, Spence DHN, Clarke RT (1986) *The Direct Determination of Biomass of Aquatic Macrophytes and Measurement of Underwater Light.* HMSO. London Pp 45.

Wetsteyn LPMJ, Kromcamp JC (1994) Turbidity, nutrients and phytoplankton primary production in the Oosterschelde (The Netherlands) before, during and after a large-scale coastal engineering project (1980-1990). *Hydrobiologia* 282: 61-78.

Wetzel RG (1975) Primary production in: Whitton BA (Ed.) *River Ecology.* Blackwell Scientific Publications. Oxford. Pp 230-247.

Whitehead PG, Hornberger GM (1984) Modelling algal behaviour in the River Thames. *Water Res.* 18: 945-953.

Whitton BA, Lucas MC (1997) Biology of the Humber rivers. *Sci. Total Environ.* 194/195: 247-262.

Wilkinson WB, Leeks GJL, Morris A, Walling DE (1997) Rivers and coastal research in the Land Ocean Interaction Study. *Sci. Total Environ.* 194/195: 1-4.

Williams LG (1972) Plankton diatom species biomass and the quality of American rivers and the Great Lakes. *Ecology* 53: 1038-1050.

Williams PJ leB, Jenkinson NW (1982) A transportable microprocessor-controlled precise Winkler titration suitable for field station and shipboard use. *Limnol. Oceanogr.* 27: 576-584.

Yentsch CS (1980) Light attenuation and phytoplankton photosynthesis.. In: Morris I (ed.) *The Physiological Ecology of Phytoplankton.* Blackwell Scientific Publications. Oxford.

APPENDIX 1

APPENDIX 1 - Results of dilution experiements for Cromwell