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The importance of nutrient source in determining the influence of retention time on phytoplankton: an explorative modelling study of a naturally well-flushed lake.

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This paper has not been submitted elsewhere in identical or similar form, nor will it be during the first three months after its submission to Hydrobiologia.

Abstract

Two models were used to examine the relationship between hydraulic retention time, nutrient source and total chlorophyll in a shallow lake (Bassenthwaite Lake, UK). The first model was a derivation of the Vollenweider model and the second was the phytoplankton community model, PROTECH.

The adapted Vollenweider model produced two different responses to changing retention time that were phosphorus source dependent. If the phosphorus was totally from a point source, then annual mean chlorophyll steadily declined with increasing flushing rate. However, when a diffuse source was used, the chlorophyll changed little and even increased with short retention times (retention time <40 days).

The PROTECH model produced some similar responses but they were more season dependent. Winter mean chlorophyll always declined with decreasing retention time, regardless of nutrient source, but the summer mean curves were source dependent and similar to those produced by the adapted Vollenweider model. Further simulations with PROTECH using a standardised flow regime provided strong evidence as to the mechanisms behind these responses.

Analysis showed that the decline in chlorophyll with decreasing retention time was the prevalent response of the PROTECH simulations due to flushing loss of both nutrients and algae. Furthermore, the curve formed an asymptote at long retention times because other factors (e.g. light) limited growth; retention times >100 days had little effect on chlorophyll. However, with a diffuse phosphorus source and short retention times, an increase in biomass was observed when the nutrient was limiting for growth.

Introduction

The concept of lake retention (residence) time is well established in limnology, as is its importance in influencing lake ecology (Kalff, 2002). The rate at which water moves through a lake can affect the supply, and the loss, of nutrients, organic matter etc., making changes to this flushing rate a complex balance between the competing effects of gain and loss (Søballe & Kimmel, 1987). For many lakes, such changes in flushing rate are likely in the next few decades because of climate change and its associated effects on rainfall and snowmelt (IPCC, 2007). Therefore, it is important to understand the sensitivity of lakes to changes in retention time and, more importantly, the potential drivers that may lie behind any change.

Perhaps one of the most important mechanisms by which retention time (flushing rate) has been thought to affect phytoplankton in lakes is through determining the in-lake phosphorus (*P*) concentration. Interestingly, flushing rate was originally excluded as a factor in the Vollenweider (1968) model because most of the lakes originally used to derive the empirical relationship had very long retention times (i.e. 3 of 25 had retention times < 1 year; Dillon (1975)). Dillon's (1975) application of the model to a lake with a retention time of approximately 19-21 days highlighted this omission and subsequent versions of the Vollenweider model included flushing rate (Vollenweider, 1976; Larsen & Mercier, 1976; Vollenweider & Kerekes, 1980):

$$P = \frac{L_p / q_s}{(1 + \sqrt{\tau_w})}, \qquad (1)$$

where L_p is the annually and areally averaged phosphorus load (mg m^{-2} y^{-1}), q_s is the water discharge height (m y^{-1}) and τ_w (y) is the reciprocal of the flushing rate. In this version of the model, the flushing rate acts as a surrogate for the sedimentation of phosphorus from the water column (Kalff, 2002). In a recent review, Brett &

Benjamin (2008) re-emphasized the importance of retention time in the Vollenweider (1976) phosphorus loading model and its many derivatives. They also highlighted that the source of phosphorus in the Vollenweider model is non-specific and may account for some of the variation in the relationship i.e. internal loading of phosphorus can affect the relationship between external phosphorus supply and in-lake phosphorus.

The relationship between nutrient source and retention time has long been a relatively unexplored issue, despite its potential importance being highlighted in Edmondson's (1970) review of Vollenweider (1968); the former found issue with the latter's lack of consideration as to the source of the phosphorus in Vollenweider's model. Schindler (2006) recognized the importance of this factor in a comprehensive review of the state of eutrophication science, stating that the effect that retention time has on eutrophication is poorly understood when the nutrient load to the lake is split between point (e.g. sewage waste, sediment released phosphorus) and diffuse (e.g. agriculturally derived phosphorus) sources.

In an initial study examining precisely this issue, Jones & Elliott (2007) adapted the Vollenweider model in Equation 1 to demonstrate the theoretical basis for this point/diffuse effect. They rewrote the model in a form that could separate inflow dependent and inflow independent phosphorus sources thus:

$$P = \frac{P_i}{(1+\sqrt{V/Q})} + \frac{M_s}{(Q+\sqrt{QV})}, \qquad (2)$$

where P_i is the inflow phosphorus concentration (mg m^{-3}), V is the volume of the lake (m^3), Q is the discharge from the lake (m^3 y^{-1}) and M_s is the annual input mass from point sources (see Jones & Elliott (2007) for a full explanation and derivation). In this study, we make the approximation that the first and second terms of the right hand side of the above equation are analogous to diffuse and point source loading respectively. This simplification should be considered when interpreting the results of this study. Furthermore, P can be used to predict C, the annually averaged chlorophyll concentration (mg m^{-3}) with this equation from Vollenweider & Kerekes (1980):

$$C = 0.37(P^{0.91}), \quad (3)$$

Coupling these two equations allows the prediction of the annual mean chlorophyll of a given lake in response to different point and diffuse source ratios and retention times. Whilst it is simplistic and has its limitations, it does provide an important starting hypothesis of response for a given lake.

This study aims to expand upon the investigation of Jones & Elliott (2007) by testing a lake which naturally experiences a wide range of retention times. By using the phytoplankton community model, PROTECH, the study examines fully the impact of changing retention time, as well as considering the importance of annual discharge pattern, the relative effects in winter and summer and, of course, the importance of nutrient source. It compares these outputs to those predicted by Equations 2 and 3 and considers the implications of any differences in response.

Methods

Site description

Bassenthwaite Lake (54° 39.09' N, 3° 12.93' W) is situated to the north of the English Lake District. It is relatively shallow, with a mean depth of 5.3 m and a maximum depth of 19.0 m (Ramsbottom, 1976). Thermal stratification is episodic and readily broken down, and the average annual retention time is short, c. 19 days (Thackeray et al., 2006). Based on the annual average concentration of phytoplankton chlorophyll-*a* (13.4 mg m^{-3}, Thackeray et al., 2006), Bassenthwaite Lake may be considered eutrophic (OECD, 1982). Estimates of the relative importance of the sources for nutrients entering the lake suggest that approximately 60% of the total annual load comes from anthropogenic sources (treated sewage waste) with the rest derived from the catchment (Thackeray et al., 2006). In the UK, for example, this split can range from anywhere between 100% point source to virtually 0% (Anthony & Lyons, 2007).

Bassenthwaite Lake has been routinely monitored since 1991, with nutrient and phytoplankton samples taken every two weeks (the exception was during the 2001 foot and mouth incident which restricted access to the rural areas of the UK). Corresponding daily meteorological measurements for wind speed, air temperature and air humidity were available from a meteorological station approximately 4 km away from the lake. Daily cloud cover measurements were available from another meteorological station near Windermere, approximately 25 km away. Daily outflow discharges were available and the inflows were assumed to be the same as these values. Previous analysis (see Elliott et al., 2006) had identified that 1996 was the year during this study period with the longest annual retention time (c. 28.25 days), therefore this year was chosen for the subsequent sensitivity analysis in order to provide the widest range of retention times, and its corresponding observed discharge and meterological data were used to drive the simulations.

PROTECH model description

PROTECH (**P**hytoplankton **R**esp**O**nses **T**o **E**nvironmental **CH**ange) is a computer model that simulates the growth of multiple phytoplankton species types (see Reynolds et al., 2001 for full details of the equations and philosophies behind PROTECH). The biological component of the PROTECH model is the basic state variable equation determining the daily change in the chlorophyll *a* concentration (X) of each algal species:

$$\Delta X/\Delta t = (r' - S - G - D) X, \qquad (4)$$

where r' is the proportional growth rate over 24 h, S represents the losses due to settling, G the losses due to *Daphnia* grazing (see below for further details) and D those due to dilution. The growth rate for a species in the model is firstly determined by their morphology and then modified by the water temperature and daily photoperiod and can be limited further by lack of phosphorus, nitrogen or silicon. These nutrient concentrations in the water column are modified to reflect uptake due to growth and daily supply and loss via inflow/outflow exchange. For all the species simulated it is assumed that these nutrients are consumed from the water column in the following stoichiometric ratio of 82 g SiO_2 (only if diatom): 8.3 g nitrogen : 1.2 g phosphorus : 1g chlorophyll (Stumm & Morgan, 1981).

In this study eight phytoplankton species were modelled at one time and an analysis of Bassenthwaite Lake phytoplankton data was conducted in order to identify the dominant taxa that should be included in the simulations. They were *Chlorella*, *Cryptomonas*, *Aphanizomenon*, *Anabaena*, *Fragilaria*, *Aulacoseira*, *Asterionella formosa* Hass. and *Planktothrix* (Table 1). A species-specific movement function calculates the position of each species in the column, accounting for the movement of the water and Stoke's Law (movement down the water column), as well as the motile/buoyancy properties of some phytoplankton (positive movement up the water column, dependent upon light intensity for motile species) (Table 2).

As mentioned above, there is a simple grazing routine in PROTECH, adopting the temperature- and food-dependent growth and reproduction relationships developed for *Daphnia* by Reynolds (1984). This simulated grazing pressure is also affected by flushing loss and was applied to only three of the eight species simulated in this study (Table 1).

The physical structure of the water column is defined over vertical, morphologically-dependent 0.1 m slices. The extent of mixing within the water column is calculated by following the Monin-Obukhov length calculation (Imberger, 1985), which gives an instantaneous prediction of the depth at which the buoyancy forces (due to the heat flux) and the opposing dissipative forces (due to wind stress) are equal in magnitude. This point corresponds to the extent of the mixed layer, assuming initial uniformity. To test the resistance to mixing of an existing density structure, it is also necessary to apply a Wedderburn-test, which incorporates a term for the accumulated density difference between the water at the surface and at any nominated depth. At each iteration, the model works down the water column, incorporating each slice until the accumulated density difference resists the incorporation: this slice then corresponds to the depth of the thermocline (Reynolds et al., 2001).

The PROTECH model has had its key growth parameters verified (Elliott et al. 1999b), tested for sensitivity (Elliott et al. 1999a) and been validated at numerous sites (Elliott et al., 2000; Lewis et al., 2002; Elliott & Thackeray, 2004; Elliott et al., 2007; Bernhardt et al., 2008). Also, it has been successfully used to simulate Bassenthwaite Lake in a previous study (Elliott et al., 2006).

Retention time sensitivity

The biomass of the simulated phytoplankton was calculated at a daily temporal resolution in terms of an integrated 5-m concentration of chlorophyll-*a* per unit volume of lake water. This made the results comparable with observed data from Bassenthwaite Lake in 1996. The total chlorophyll output of PROTECH was compared with the observed data and tested both visually and statistically, using regression analysis for its "goodness-of-fit".

This 1996 simulation was then subjected to a detailed testing by the following method. Eleven nutrient supply ratios were calculated ranging from 100% diffuse to 100% point phosphorus source in 10% changes to the ratios (i.e. 90-10, 80-20, 30-70 etc.) and representing ratios commonly observed in UK water bodies (Anthony & Lyons, 2007). The point source was created by altering the measured inflow SRP concentration so that the daily load was the same regardless of the changes in daily discharge (i.e. a dilution). Conversely, a diffuse source was created by not changing SRP concentration with changes in discharge, so that the daily load would change with discharge. Finally, to create scenarios that had different ratios of point and diffuse nutrient sources, the alterations outlined above were applied in different relative proportions to SRP inflow input. 100 different retention time simulations for each nutrient scenario were then run, providing a range of annual retention times between 5.7 – 260.0 days. Annual, winter (defined as January-March and November-December) and summer (August-September) mean chlorophyll were calculated for each run.

The previous study of Jones & Elliott (2007) suggested that the seasonal pattern of discharge might have an influence on the simulated phytoplankton, thus additional runs were made for the two extreme cases of source scenarios (100% point and 100% diffuse) using a seasonal average discharge pattern. The latter was achieved by calculating the mean daily discharge for October-March and also for April-September, and then applying those means to the relevant time period of the simulations e.g. the October-March mean was used for all the days in the simulation during those months and, again, 100 different retention time scenarios were run for the two nutrient sources. Finally, in response to the results of these stepped-flow simulations, the runs were repeated but this time the phosphorus concentration of the inflow was reduced to 20% of its original value in 10% reductions and 100 different retention time scenarios were run for each of these changed nutrient concentrations. Only the mean summer chlorophyll values are shown for these latter simulations because this period showed the greatest sensitivity to the flow changes.

Results

Vollenweider model predicted response

By applying Equations 2 and 3 to Bassenthwaite Lake in 1996 for a range of annual discharge rates (Q), a theoretical response of annual mean chlorophyll to changing retention time was produced for the two extreme nutrient source scenarios of 100% point (i.e. P_i set to zero) and 100% diffuse (i.e. M_s set to zero) (Fig. 1). The figure shows clearly large differences between the two theoretical loading scenarios. If the source is totally point, then the supply of phosphorus is independent of discharge and is therefore flushed out at higher discharges (shorter retention times) and the mean annual chlorophyll response follows a bow shaped curve. In contrast, with only diffuse sources the relationship is relatively flat and unchanging because the increase in phosphorus supply is balanced by the nutrient's flushing loss and sedimentation. However, there is the notable exception that at very high discharges (c. <40 days retention time) more chlorophyll is produced, as the gain of phosphorus begins to outweigh the "sedimentation of phosphorus", as approximated by Equation 2.

PROTECH simulation of Bassenthwaite Lake in 1996

The total chlorophyll output of PROTECH (i.e. sum of the eight species' individual chlorophyll concentrations) was compared to the observed seasonal pattern (Fig. 2). The seasonal pattern was reproduced, particularly the spring bloom, although the single high summer value was not produced by PROTECH. Regression analysis between observed and simulated confirmed the "goodness-of-fit" of the simulation (R^2 = 0.67, P < 0.01).

Retention time sensitivity

Considering initially the two extreme nutrient supply scenarios, it was clear that the response of the mean total chlorophyll to retention time changes was greatly dependent upon the period of year examined (Fig. 3). The annual mean total chlorophyll showed that nutrient source did affect the response of chlorophyll to retention time change. Both scenarios showed a decline in the annual mean with increasing discharge at short retention times, although the response curve under the 100% diffuse scenario was flatter than the 100% point simulations above about 100 days (Fig. 3). In the summer, the different responses between the nutrient scenarios were much more pronounced. The point source scenario produced a steady decline from the maximum mean summer total chlorophyll of 30 to 12 mg m^{-3} (Fig. 3a) with shortening retention time, whereas the diffuse source scenario showed a steady increase in chlorophyll (Fig. 3b). It was also interesting that during the summer, for the point source scenario, a distinct step change in chlorophyll occurred at c. 90 days retention time (Fig. 3a). Finally, irrespective of nutrient source, the mean winter total chlorophyll response was virtually identical between the two nutrient scenarios, showing a slight decline with shorter retention times (Fig. 3).

The other nutrient source scenarios provided further information on these responses (Fig. 4). Each 10 % change in the point-diffuse ratio produced a relatively smooth transition between the two extreme mean annual chlorophyll response curves (Fig. 4a). The greatest rate of change occurred between the 100% diffuse scenario and 20-80 point-diffuse scenario. The summer mean chlorophyll values showed a similar response as the annual mean curves, with gradual changes in chlorophyll occurring as the resource ratios altered. It is interesting to note that the gain in chlorophyll that was seen at short retention times in the 100% diffuse scenario became a loss with only a 30% reduction in the diffuse source contribution (i.e. for ratios greater than 30-70 point-diffuse). Finally, the abrupt change in chlorophyll at c. 100 days retention time was hinted at in most ratios but was most pronounced at ratios greater than 70-30 point-diffuse.

For the 100% diffuse and point scenario, the day at which the total chlorophyll first and last passed 10 mg m^{-3} was recorded for all the retention time scenarios (Fig. 5); these points nominally represented the start of the spring bloom and the end of the summer/autumn bloom. Irrespective of nutrient source, the onset of the spring bloom became 14 days earlier with retention times shorter than 18 days but barely advanced further with longer retention times. The end of the bloom occurred later with increasing retention time but did show a nutrient source related effect. With a point source, the bloom end levelled out 60 days later (day 335) than that observed for the shortest retention time scenario (day 272). In contrast, the diffuse source scenarios levelled out about 40 days later at day 315.

The seasonal average discharge pattern scenarios produced response curves that were generally similar to those in Fig. 3 (Fig. 6). There was one notable exception to this: the summer mean chlorophyll for the diffuse scenario did not continue to increase at very short retention times, but instead declined sharply (Fig. 6b). This result warranted further consideration, thus the seasonal average simulations were repeated, but this time with decreasing inflow phosphorus concentrations and focusing solely on the summer means. The patterns produced were similar to those in Fig. 6 for the point source conditions (Fig. 7a), although the actual amount of chlorophyll produced naturally declined with decreasing inflow phosphorus. The same was not true for the diffuse source simulations (Fig. 7b) where the pattern of sharp decline in summer mean average seen in Fig. 6b was only apparent in the scenarios with more than 40-50% of the original inflow phosphorus concentration. Below this amount, the mean chlorophyll had a much flatter response with changing retention time, actually rising slightly with very short retention times in a way similar to the summer mean curve in Fig. 3b.

Discussion

The effects on phytoplankton of changing retention time can be varied and complex (Kalff, 2002). By using models, we can try to unravel this complexity to understand quantitatively the response of phytoplankton populations to these changes. If we consider first the results from equations 2 and 3, it would appear that changes in retention time seem to be able to produce large variations in annual phytoplankton biomass, but that the source of nutrients greatly determines the extent of variation, i.e. with a 100% point nutrient source, the change is greatest (Fig. 1). With this simple model, it is easy to understand why this is the case by examining Equation 2. If the nutrient load entering a lake is wholly proportional to the inflow ('100 % diffuse' source), then as river discharge increases, more nutrients are brought into the lake, but simultaneously, more nutrients are flushed out of the lake. This can be seen in the first part of the right hand side of Equation 2, which also indicates that this balance is slightly altered by sedimentation effects, albeit ones that are approximated empirically in this Equation. Conversely, if the nutrient load to a lake is from a point source only, then an increase in river discharge brings no extra nutrients to the lake, but the consequent increase in flushing still removes in-lake nutrients (i.e. increased dilution). This is represented by the second part of the right hand side of Equation 2, where the discharge is firmly within the denominator. Following Equation 3, a decrease in in-lake nutrient concentration leads directly to a decrease in phytoplankton biomass. Interestingly, this means that the Vollenweider equation does not account for the actual removal of biomass directly from flushing but rather via the loss of in-lake phosphorus. Of course, in order to explore these predictions for Bassenthwaite Lake, we used a second, more complex, model.

The PROTECH simulations produced a greater range of response curves than

Equation 3 and were less smooth in nature. The latter reflects the interactions between the eight species with their different traits and, whilst interesting, such competitive interactions were not the focus of this study. Rather the broad overall changes were compared to the simple Vollenweider responses. The winter curves showed little response, regardless of phosphorus source; under such poor environmental conditions (low temperatures and light levels), net growth was very low. In the summer, both curves agreed with those predicted by Equation 3, with shortening retention time causing a decrease in chlorophyll under point source conditions and an increase under diffuse conditions. The explanation for this lies in one of the fundamental assumptions behind the original Vollenweider model, namely that phosphorus is controlling the amount of chlorophyll in the lake (see Equation 3). In the PROTECH simulations, growth limiting concentrations of phosphorus (<3 mg m^{-3}, Reynolds (1984)) occurred only in the summer period. This meant that during the rest of the year, the supply of phosphorus to the lake was less important than the direct flushing of phytoplankton, leading to a decrease in biomass with increasing discharge. However, in the summer diffuse scenario, the increased flow brought with it vitally important extra phosphorus as well as a reduced sedimentation rate, leading to an increase in biomass; this is in accordance with the first term of the right-hand side of Equation 2.

Given the two different response curves for 100% diffuse or point sources and the fact that most lakes experience varying ratios of both types of nutrient source (Anthony & Lyons, 2007), it was important to see if altering the split between the two was a gradual, even transition or involved sudden changes. The evidence from this study suggested that the former was generally the case (Fig. 4) although other growth limiting factors in PROTECH made the transition with changing ratio less regular with longer retention times. The ratio scenarios (Fig. 4) illustrated that the increase in chlorophyll at short retention times was dependent on the diffuse supply being dominant; with only a 20-30% reduction in the diffuse source contribution, the biomass accumulation was no longer positive under high flushing conditions. This showed that even in the summer, the loss processes associated with high discharges were generally more dominant than the benefits of increased nutrient supply and reduced sedimentation. Finally, it is worth briefly commenting on the discontinuous change in summer mean chlorophyll observed around retention times of c. 90 days (Fig. 4b). The abruptness of the change was sharpest with the increasing proportion of the point source and was caused primarily by changes in *Planktothrix* biomass. Closer analysis of this threshold showed that the increase in *Planktothrix* with longer retention times was connected to more SRP being available, allowing *Planktothrix* to gradually establish a larger population, shading out the other species and reducing the total chlorophyll. This phytoplankton type in PROTECH has demonstrated rapid-change responses like this before, such as when the model was used to investigate the intermediate disturbance hypothesis (Elliott et al., 2001) and shows how more complex models can produced more complex outcomes.

The timing of the start and end of the blooms showed similar patterns of response to each other and to those observed in our Blelham Tarn study (Jones and Elliott, 2007). For the starting day of the bloom, the lack of difference between the nutrient source treatments was again due to the lake being replete with nutrients and the delay simply due to the increase flushing loss under the high discharge scenarios. The marked difference between the nutrient scenarios response curves for the end of the bloom was due to the scarcity of nutrients under the conditions of diffuse source and low flow i.e. low overall nutrient supply led to more rapid bloom termination.

With a point source and low flow, nutrients were largely not limiting, hence the bloom was more prolonged (Fig. 5a).

The seasonal average discharge pattern scenarios were introduced in this study to try and correct for any potential complexity that was being caused by the specific discharge pattern being used. They produced response curves that were similar to those derived from the observed 1996 discharge pattern except for the significant exception of the summer mean chlorophyll with a 100% diffuse phosphorus source (Fig. 6b). This curve declined with shortening retention time, in marked contrast to the curve in Figure 4b. It was suspected that this difference was, again, due to the phosphorus supply and indeed this was the case; the averaged summer discharge conditions simply supplied enough phosphorus to preventing it reaching persistent limiting levels and thus the effects implied in Equation 2 did not apply. Therefore, we also ran simulations where the overall inflow phosphorus concentration was reduced and saw a reduced rate of decrease in summer mean chlorophyll with increasing discharge and low nutrient (Fig. 7), thus clearly proving how important it was to have a limiting in-lake phosphorus concentration to produce the diffuse source curve of Equation 2 (Fig. 1).

Drawing together these various responses, it seems clear that Equations 2 and 3 have their limitations compared to the more complex PROTECH model when applied to a specific lake. Taking each nutrient source response curve in turn, the 100% point source relationship seemed the more robust in that its general shape was similar between the two models used. This is perhaps unsurprising, because it has the least complex driving factor of the two; the increasing discharge just flushes out more and more nutrients and phytoplankton. This latter effect is regarded as the most typical response by phytoplankton to an increasingly flushed system (Dickman, 1969;

Kalff, 2002). However, for 100% point source, the PROTECH model produced an upward sloping *asymptotic* curve compared to the continuingly rising curve of Equation 3. This happened because PROTECH, being a single lake model that calculates daily chlorophyll values, accounts for other growth limiting factors not present in the original, statistically derived, Vollenweider model which seeks to model a huge range of lake types and provide an annual mean value. In the case of the scenarios run in this study, the most important one was light limitation caused by self-shading. This was also found to be the case by Reynolds' (1992) assessment of the Vollenweider model which showed that the chlorophyll to phosphorus yield could not increase indefinitely and that some other factor would eventually cap the chlorophyll yield (e.g. light or nitrogen availability).

Understanding the effect of the diffuse source was more complex. It seems clear that the Equation 3 prediction of mean chlorophyll being fairly unresponsive at long retention times is supported by PROTECH, but at lower retention times there can be a marked difference. Thus, within the scope of the scenarios tested in this lake system, only under one set of circumstances can PROTECH produce a relationship comparable to Equation 3's output and, as was shown clearly with the seasonal average flow scenarios, this was dependent on phosphorus availability being limiting. Therefore, only under these precise circumstances would the increase in flow bring sufficient net-benefit to the phytoplankton populations.

Relating the modelled outputs of this study to specific case-studies was quite challenging because studies focusing on such high flushing in lakes, particularly in the summer, are rare (these rates are more typical of rivers). Nevertheless, there are some examples of increasing biomass production under very high flushing conditions. For example, the very shallow lakes (mean depth 1.1-1.2 m) of the Pampa Plain

(Argentina) were reported to have increased summer total chlorophyll and phosphorus (primarily from agriculture, i.e. diffuse sources) when the retention time decreased to < 15 days (Rennella & Quirós, 2006) and there have been similar responses observed in comparable systems that regularly experience such low retention times (Van den Brink et al., 1994; Walz & Welker, 1998). However, these systems are all considered hypertrophic, so nutrients are unlikely to be limiting, although there are other studies that show a similar response pattern and also nutrient limitation (Turner et al., 1983). Another study found an increase in in-lake phosphorus occurred with increasing discharge, but phytoplankton growth was curtailed by the raised turbidity caused by the flushing (Vanni et al., 2006). The influence on growth of other factors linked to changes in retention time again shows the limitations of a model as simple as equation 2. Clearly, though, there is still a need for further research on this topic, particularly at the species level.

Conclusions

It would appear that variations in retention time, irrespective of discharge pattern, can have large influences on phytoplankton populations under several combined conditions. These are when the dominant source of phosphorus is point and the retention time is < 90-100 days, or simply when the retention time is < c.30 days. These results find further support in that it has been often found that retention times greater than 100 days are inconsequential in terms of their influence on growth rate (Søballe & Kimmel, 1987; Kimmel, Lind & Paulson, 1990; Reynolds, 2006) and, secondly, that lakes regularly experiencing retention days < 30 days struggle to support *Planktothrix* populations (Reynolds, 2006). Finally, both models show that if future climate change causes the predicted reduction in rainfall that could be seen in mainly regions, the response of a lake to a change in its retention time will be greatly dependent on the nutrient source. Thus, if summer flows were low in a point source system limited by phosphorus, chlorophyll is likely to increase and conversely in a diffuse system, it would decrease.

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Tables

Table 1. The morphological and phylogenetic characteristics of the eight simulated species. The last three columns denote simple logic statements (True/False) which, if True, activate relevant functions in PROTECH.

Species	Surface Area (μm^2)	Volume (μm^3)	Maximum dimension (μm)	Diatom ?	Grazed ?	Nitrogen fixer?
Chlorella	**50**	**33**	**4**	**F**	**T**	**F**
Cryptomonas	**1030**	**2710**	**21**	**F**	**T**	**F**
Aulacoseira	**4350**	**2970**	**240**	**T**	**F**	**F**
Asterionella	**6690**	**5160**	**130**	**T**	**T**	**F**
Fragilaria	**11950**	**8100**	**70**	**T**	**F**	**F**
Planktothrix	**7350**	**13970**	**300**	**F**	**F**	**F**
Anabaena	**6200**	**29000**	**75**	**F**	**F**	**T**
Aphanizomenon	**5200**	**15400**	**125**	**F**	**F**	**T**

Table 2. Summary of PROTECH instructions governing vertical movements of phytoplankton. In all cases of either moving up or down, if the top or bottom layer (i.e. 0.1 m PROTECH layer) is encountered the movement is stopped; if it is the bottom layer the phytoplankton is lost.

Phytoplankton	Light condition (µmol photon m^{-2} s^{-1})	Movement (m d^{-1})
1. Nearly neutrally-buoyant, non-motile life-forms		
Chlorella	all	sink 0.1
2. Non-buoyant non-motile diatoms		
Aulacoseira	≤ 500	sink 0.8
	> 500	sink 1.0
Asterionella	≤ 500	sink 0.2
	> 500	sink 1.0
Flagilaria	>600	sink 1.0
	≤600	sink 0.3
3. Buoyancy-regulating Cyanobacteria		
Planktothrix	> 30	sink 0.1
	≤ 30 but > 10	no move
	≤ 10	rise 0.1
Anabaena, and	> 100	sink 0.3
Aphanizomenon	≤ 100 but > 30	sink 0.1
	≤ 30 but > 10	no move
	≤ 10	rise 0.1
4. Swimming flagellates		
Cryptomonas	> 100	rise 0.1
	≤ 100	rise 2.0

Figure Legends

Fig. 1. Illustration of the Equation 3 predicted response of annual mean total chlorophyll *a* (mg m^{-3}) in Bassenthwaite Lake in 1996 to changing retention time (days) with a point (solid line) and diffuse (dashed line) source of phosphorus.

Fig. 2. Comparison between the observed (crosses) total chlorophyll *a* (mg m^{-3}) in Bassenthwaite Lake in 1996 and that simulated by PROTECH (solid line).

Fig. 3. Response of the mean chlorophyll *a* (mg m^{-3}) for the winter (long dashed lines), summer (short dashed lines) and whole year (solid line) to changing retention time (days) with (a) point and (b) diffuse sources of phosphorus.

Fig. 4. Response of the mean chlorophyll *a* (mg m^{-3}) for (a) whole year and (b) the summer to changing retention time (days) with varying ratios of point-diffuse sources of phosphorus (e.g. 100_0 = 100% point).

Fig. 5. Variation in the timing (days from start of year) of the start (circles) and end of the bloom (crosses) with (a) point and (b) diffuse sources of phosphorus.

Fig. 6. Under the "stepped" average discharge pattern, the response of the mean chlorophyll *a* (mg m^{-3}) for the winter (long dashed lines), summer (short dashed lines) and whole year (solid line) to changing retention time (days) with (a) point and (b) diffuse sources of phosphorus.

Fig. 7. Under the “stepped” average discharge pattern, the response of the mean summer chlorophyll *a* (mg m^{-3}) to changing retention time (days) and inflow phosphorous concentration (from no change (1.0) to 80% reduction (0.2)) with (a) point and (b) diffuse sources of phosphorus.

Figures

Fig. 1

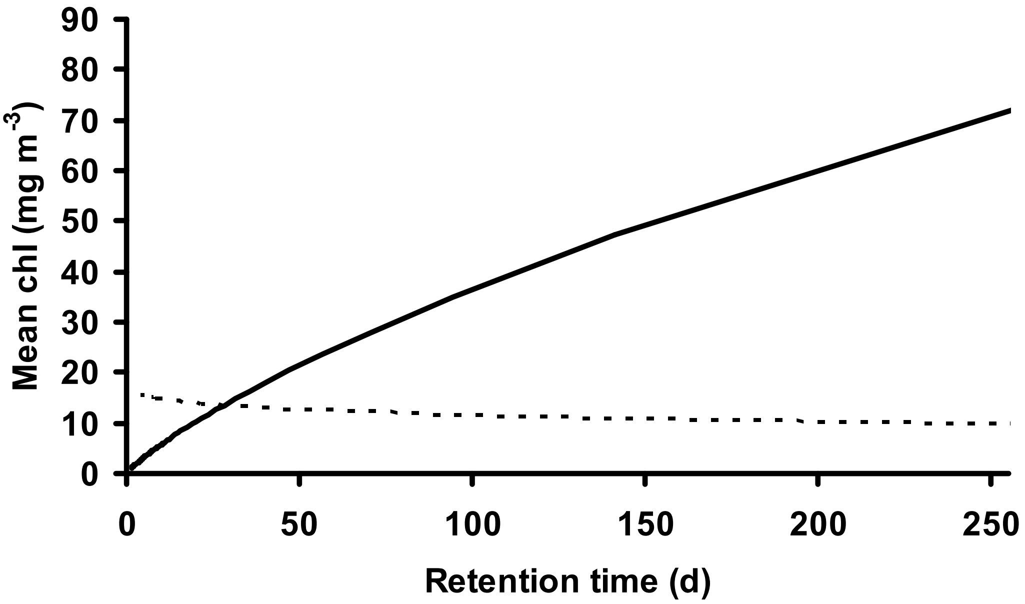
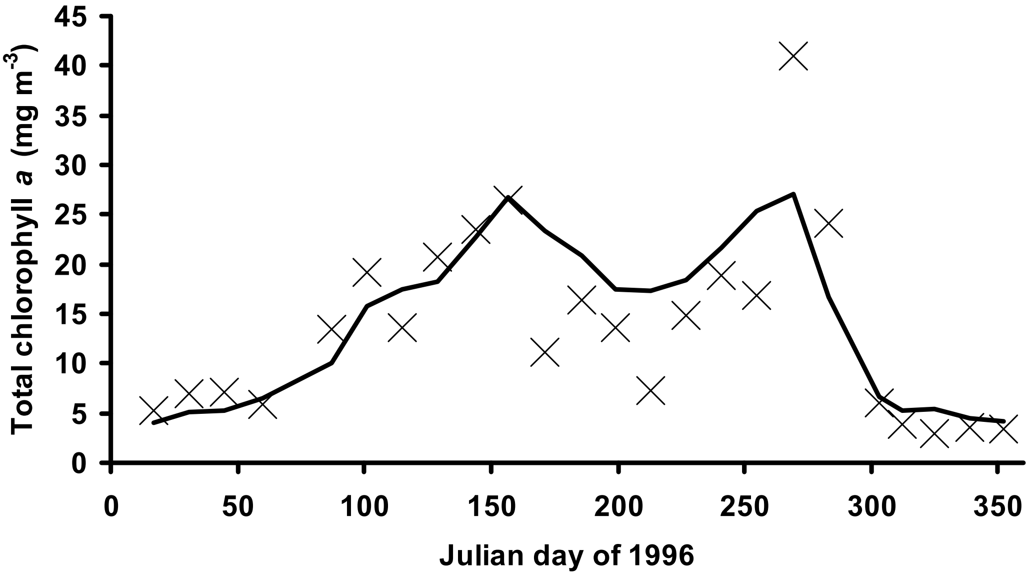


Fig. 2



Total chlorophyll a (mg m-3)
45
40
35
30
25
20
15
10
5
0
0
50
100
150
200
250
300
350
Julian day of 1996

Fig. 3

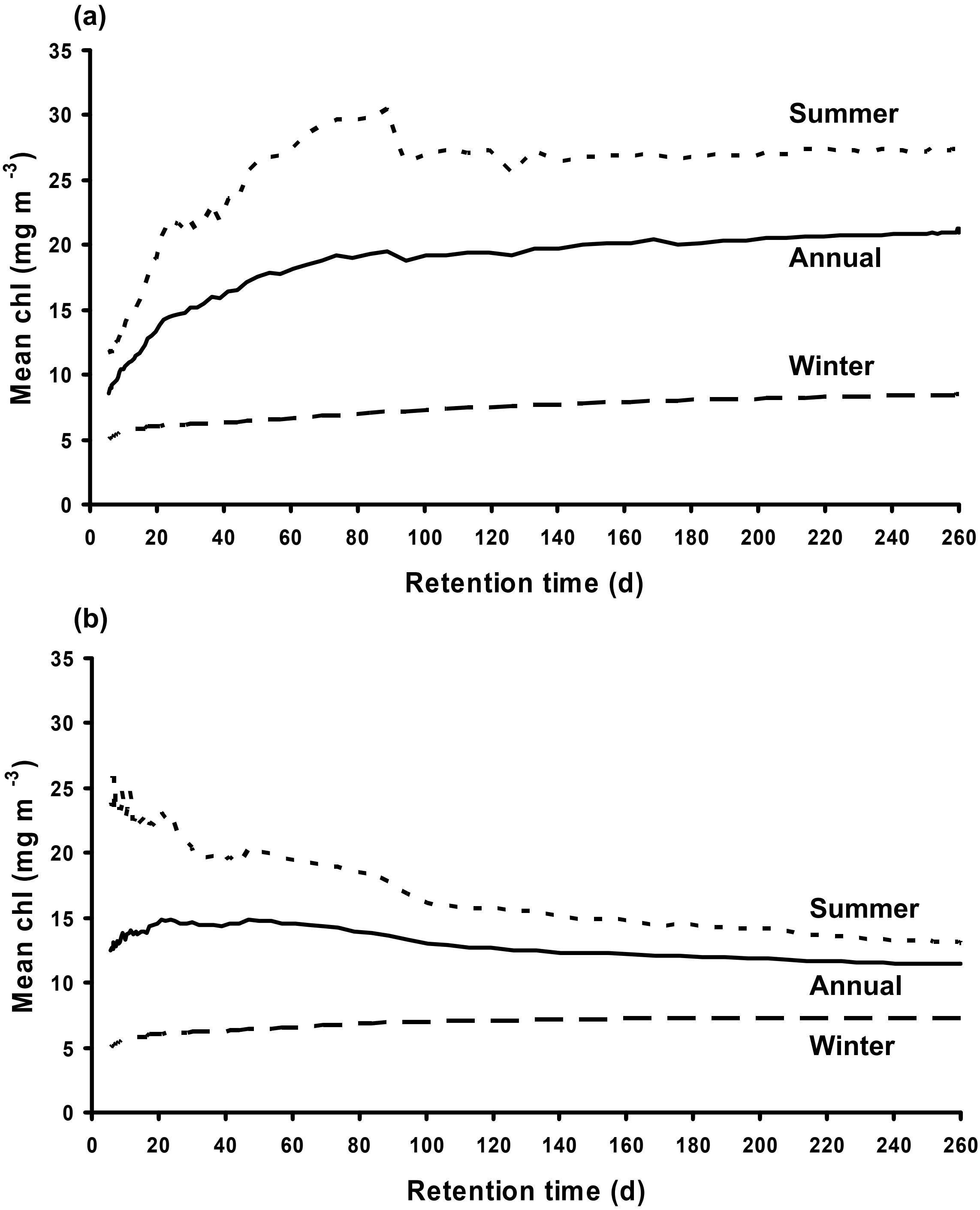

(a)
Mean chl (mg m -3)
35
30
25
20
15
10
5
0
0 20 40 60 80 100 120 140 160 180 200 220 240 260
Retention time (d)
Summer
Annual
Winter
(b)
Mean chl (mg m -3)
35
30
25
20
15
10
5
0
0 20 40 60 80 100 120 140 160 180 200 220 240 260
Retention time (d)
Summer
Annual
Winter

Fig. 4 (In colour)

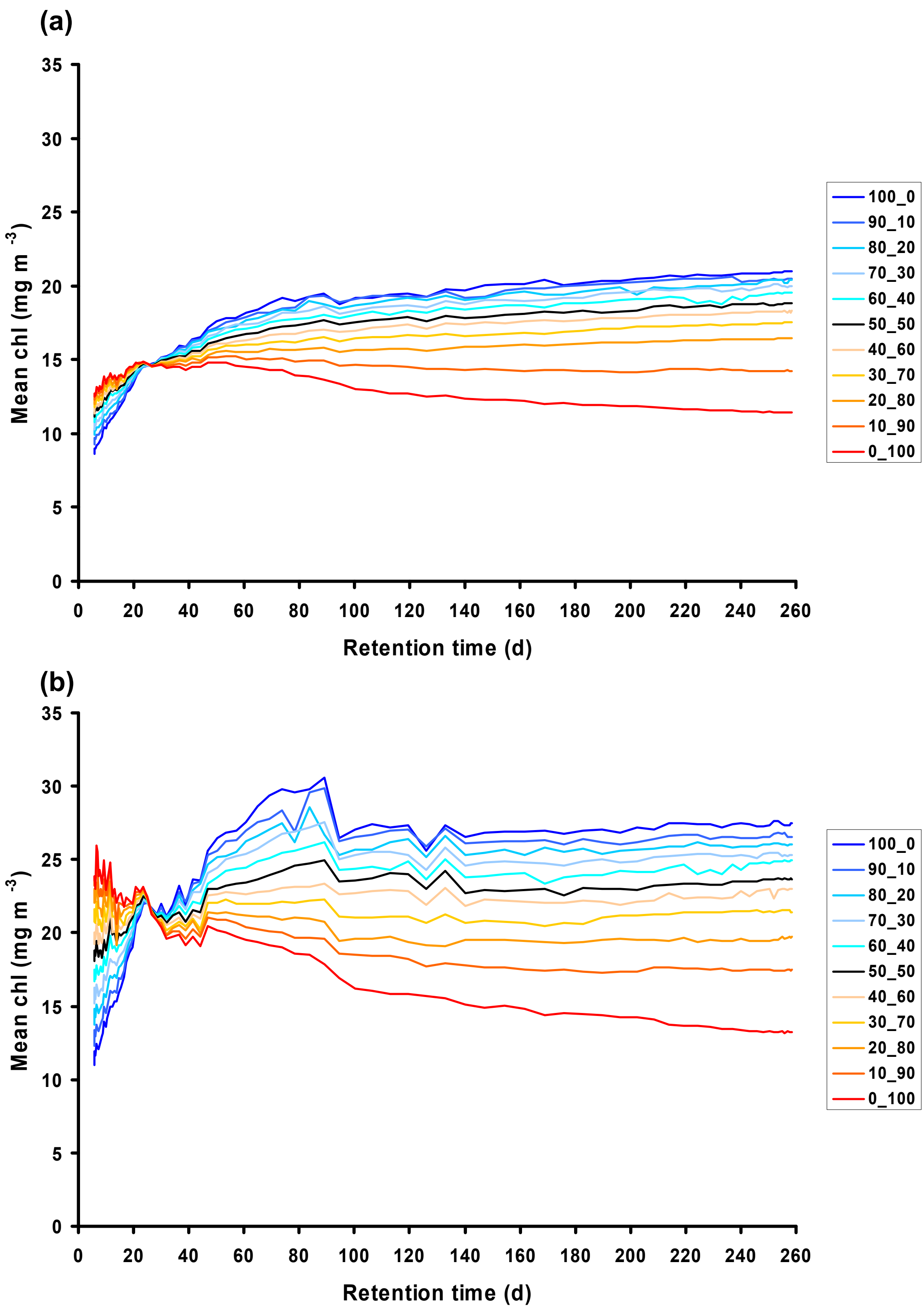
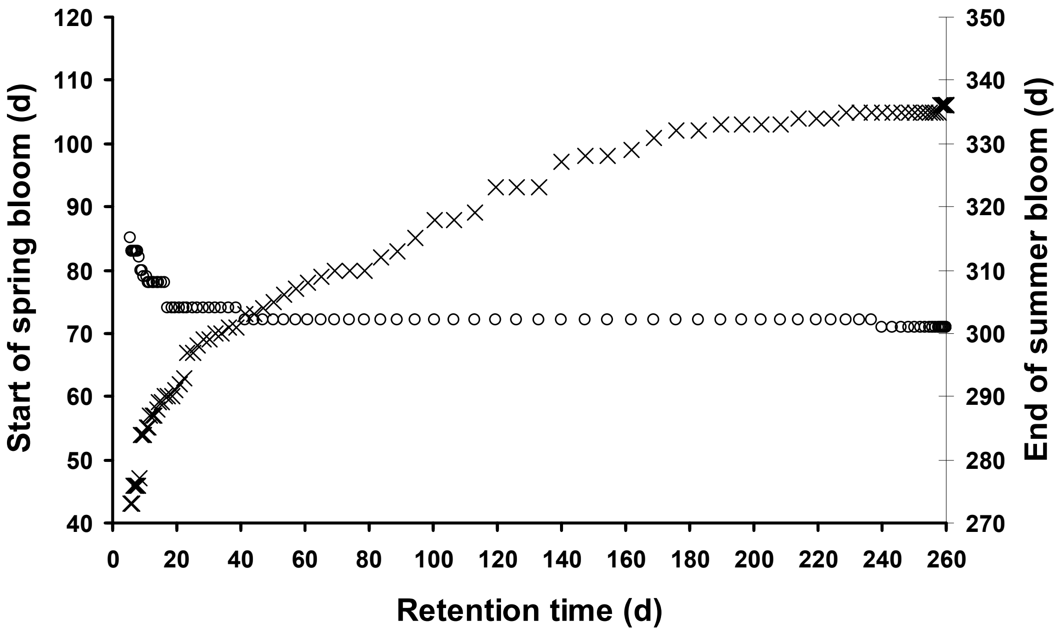


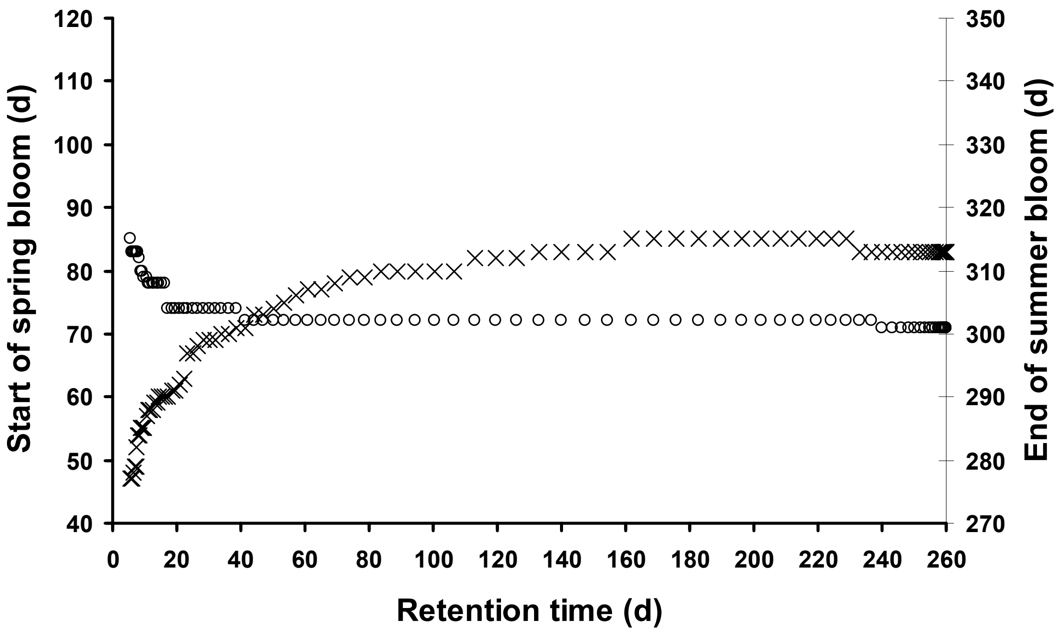
Fig. 5

(a)



Start of spring bloom (d)
End of summer bloom (d)
Retention time (d)
120
110
100
90
80
70
60
50
40
350
340
330
320
310
300
290
280
270
0 20 40 60 80 100 120 140 160 180 200 220 240 260

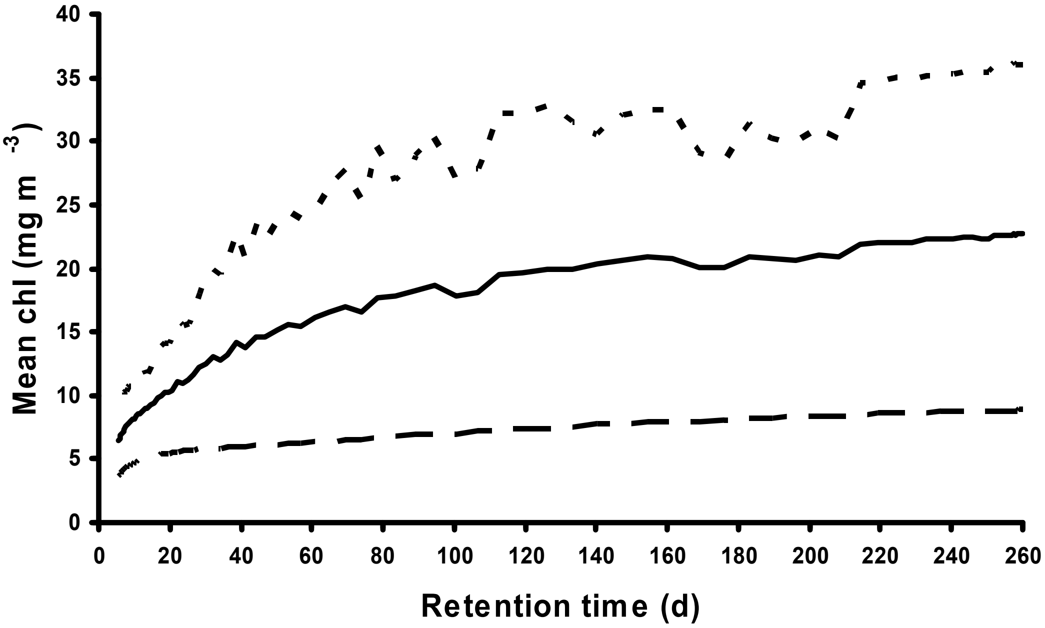
(b)



Start of spring bloom (d)
End of summer bloom (d)
Retention time (d)
120
110
100
90
80
70
60
50
40
350
340
330
320
310
300
290
280
270
0 20 40 60 80 100 120 140 160 180 200 220 240 260

Fig. 6

(a)


Mean chl (mg m -3)
Retention time (d)
0
5
10
15
20
25
30
35
40
0 20 40 60 80 100 120 140 160 180 200 220 240 260

(b)

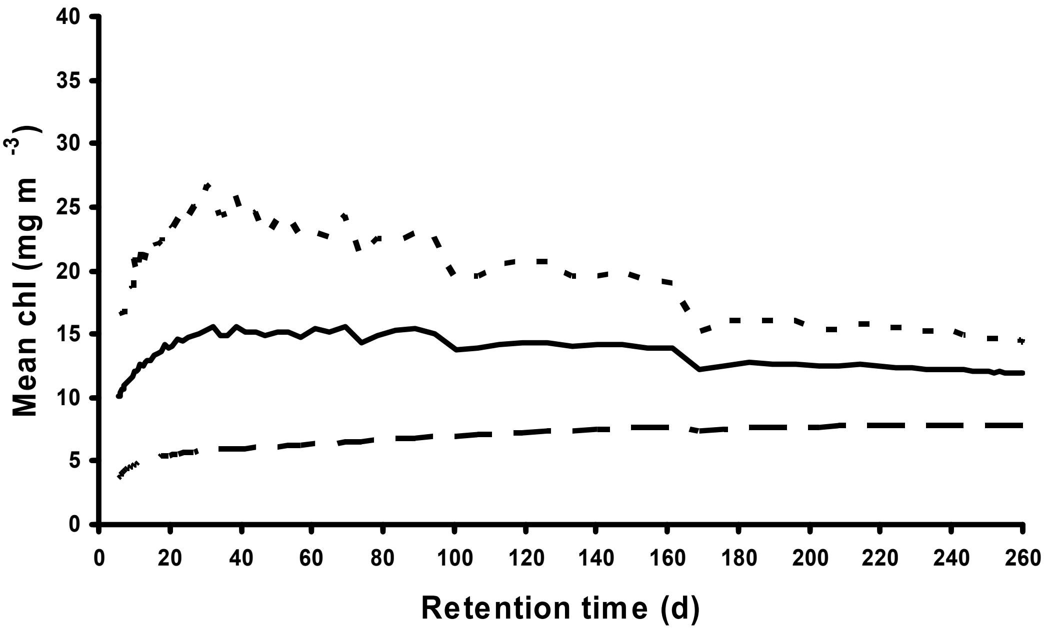

Mean chl (mg m -3)
Retention time (d)
0
5
10
15
20
25
30
35
40
0 20 40 60 80 100 120 140 160 180 200 220 240 260

Fig. 7 (In colour)