

A review: limnological management and biomanipulation in the London reservoirs

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Abstract

Low algal biomasses and high water transparencies are a feature of the storage reservoirs that supply most of London's treated water. This is a result of knowledgeable limnological management and biomanipulation and despite the eutrophic nature of the River Thames with its high nutrients (7 gN m^{-3} ; 1 gP m^{-3}) and particulate organic carbon (2 gC m^{-3}). Built-in possibilities of jetting input water are managed to prevent stratification, to ensure isothermy, to mix chemicals and plankton vertically and horizontally and to manipulate the mixed-depth of the algal populations such that their potential for biomass growth is reduced by light-energy limitation. Spring algal growth is delayed and the spring peak is reduced and curtailed by the grazing impact of considerable biomasses of large-bodied daphnid populations (*Daphnia magna*, *pulicaria* & *hyalina*) whose development is also supported by the continuous input of high riverine algal crops. The existence of a large-bodied daphnid zooplankton in the reservoirs is associated with low levels of fish predation since the late 1960s. Variations in the intensity and nature of this vertebrate predation during the subsequent twenty years (1968–88) are illustrated by the changes that have occurred in the relationship between the phytoplankton and zooplankton biomasses of the April–May–June quarter of the year. This example of the London reservoirs serves to illustrate biomanipulation in deep water bodies by bottom-up as well as top-down effects.

Introduction

One purpose of this review paper is to use the London Reservoirs to demonstrate that biomanipulation as a tool for management of water quality need not be confined either to shallow water bodies, but is applicable to deeper ones like the London reservoirs, or only to the manipulation of the fish/zooplankton interaction. There are also other possible applied limnological management procedures based on the manipulation of the underwater light regime to control planktonic primary production. Another purpose of the review is to illustrate and update long-term

changes in the relationship between the mean spring algal and zooplankton biomasses that have been investigated in one deep (15 m) reservoir during the twenty years from 1968 to 1988 and to discuss these in relation to what is known about the fish populations.

Vertical mixing, algal growth and biomasses: bottom-up effects

Low algal biomasses and high water transparency are a feature of the London reservoirs (Fig. 1), despite a continuous input ($1\text{--}2\% \text{ day}^{-1}$ of re-

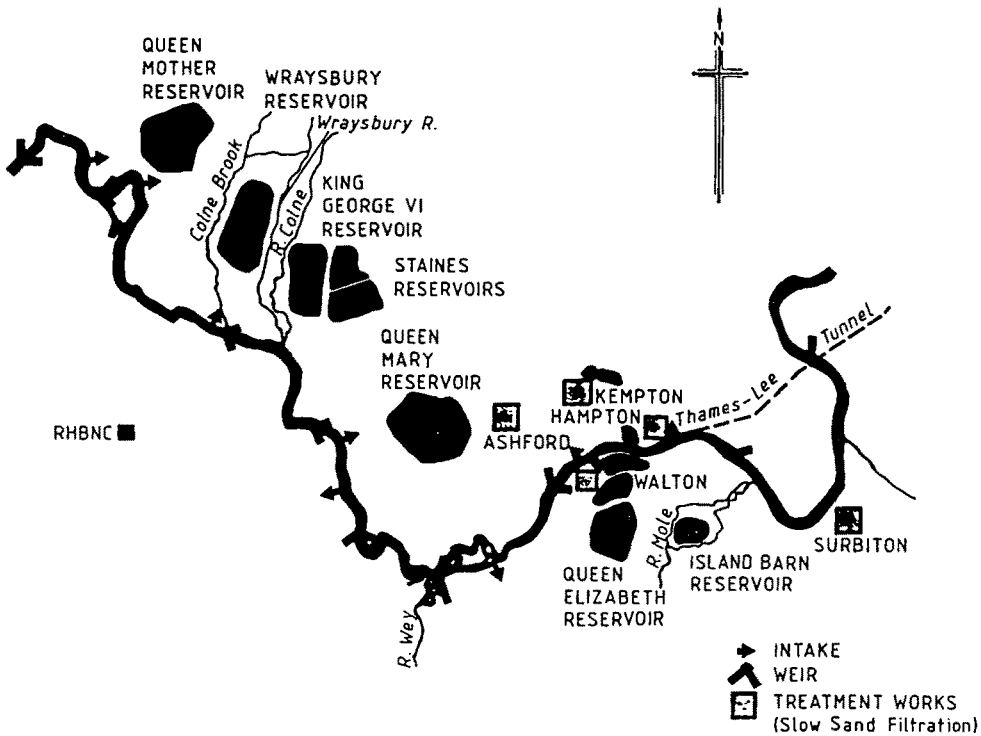


Fig. 1. River Thames, the London reservoirs and treatment works of the lower Thames Valley.

reservoir volume) of nutrient-rich water from the River Thames which ensures that dissolved phosphorus ($\text{PO}_4\text{-P}$ and nitrogen ($\text{NO}_3\text{-N}$) in the supply reservoirs are not less than 1 gP m^{-3} and 7 gN m^{-3} (Ridley & Steel, 1975). Therefore, the potential for algal growth is very great, judging from the Vollenweider (1968) relationship, but this potential productivity is prevented from expressing itself as large algal biomasses by the use of angled inlet 'jets' (Cooley & Harris, 1954) installed in the more recently built and deeper supply reservoirs (Queen Elizabeth II Reservoir, built in 1962; mean depth 15.3 m; Wraysbury Reservoir built in 1971; mean depth 16.8 m). The jetted input water produces an expanding jet plume from bottom to the surface and at a selected angle out of three available which 'entrains' reservoir water, thus helping to mix it vertically. The initial purpose of this 'jetted' input was to prevent the onset of thermal stratification and the ever-present danger of the development of anoxia in the hypolimnion, thus producing unpalatable

drinking water (Ridley *et al.*, 1966). Steel (1972) notes that the efficiency of the jets in vertical mixing is enhanced by the addition of wind mixing work to that of the jet plume. The success of artificial plus wind mixing is illustrated by published figures of time-depth distributions of isotherms and dissolved oxygen concentrations in Queen Elizabeth II Reservoir during 1974 (Steel, 1975; Fig. 3) and of isotherms and chlorophyll *a* concentrations in Wraysbury Reservoir in 1985/86 (Santos, 1989; Figs. 9, 11) but could be illustrated for any other year given access to the weekly monitored data of Thames Water Authority (TWA).

Although the potential for algal growth in these reservoirs is great, the maximal algal biomasses ($20\text{--}60 \text{ mg a m}^{-3}$) attained in the above two deeper, continuously flowing supply reservoirs tend to be low considering the nutrients available, together with high water transparencies (attenuation coefficients of 0.7 m^{-1}) and with euphotic depths of about 7 m (Steel, 1976, 1978a). Accord-

ing to Steel (1972), this desirable result is the consequence of biomanipulation of the underwater light regime of the phytoplankton by the efficient vertical mixing of the epilimnetic algal populations to below their compensation depth, such that photosynthetic rates are decreased in low light intensities, algal respiration forms a great portion of the gross areal primary production and algal growth rates and attainable algal biomasses are reduced. Another consequence of efficiently-managed vertical mixing in the deeper flow-through reservoirs is change in the seasonal pattern of their phytoplankton compared with the shallower flow-through reservoirs, such as Queen Mary Reservoir (12 m) which has similar high levels of nutrients and is largely wind-mixed. In the deeper reservoirs, algal growth usually starts month later in the spring (March-April) and lasts for a shorter period (to May) (Steel, 1976, 1978b). This seasonal pattern is illustrated by Steel (1978b: Fig. 1) for the early years (1968–71) of jetting in Queen Elizabeth II Reservoir and in Fig. 2 for the year 1988 for both Queen Elizabeth II and Wraysbury reservoirs (TWA data, unpublished).

Herbivorous zooplankton grazing

The seasonal time course of the chlorophyll *a* concentrations in the River Thames during 1988 are very high during April–June but are not reflected in the reservoirs' biomasses during May and June, despite the continuous input (Fig. 2). In this period, the development of considerable biomasses of zooplankton during May and June imposes another form of biological control, namely by the grazing of the largely herbivorous zooplankton. Figure 2 gives the seasonal time course of the cladoceran biomasses (as dry weight per vertical net haul or approximately equivalent to per m^{-3}) for 1988 for the same reservoirs (TWA data, unpublished). Studies during the last 2 decades of the zooplankton of these reservoirs (Kibby, 1971; Doohan, 1973; Burgis, 1975; Duncan, 1975a,b; Andrew, 1976; Chalk, 1983; Santos, 1989) have recorded five species of clado-

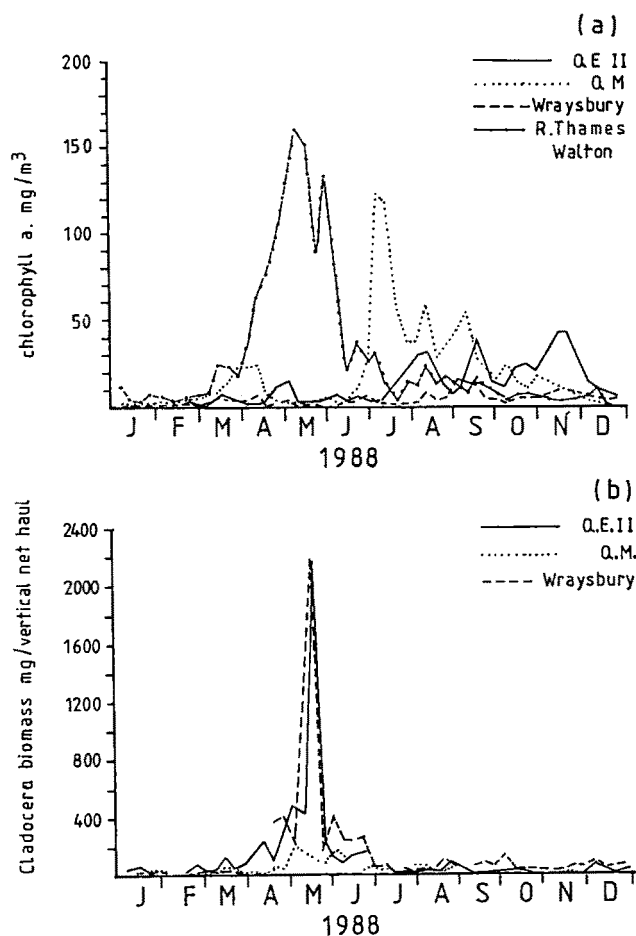


Fig. 2. Seasonal patterns during 1988 of (a) the chlorophyll *a* concentrations in Queen Elizabeth II, Wraysbury and Queen Mary reservoirs and in the River Thames at the intake and (b) the planktonic cladoceran biomass in the same three supply reservoirs of different depths and jetting regimes (data from Thames Water).

cerans including the predatory *Leptodora kindtii*, three species of copepods and seven species of rotifers present in very low densities. Of these, the most abundant were the three species of coexisting *Daphnia* (*magna*, *pulicaria* and *hyalina*) which rarely contributed less than 80% of the total zooplankton biomass, the copepods (*Eudiaptomus gracilis* and two species of cyclopoids forming the remaining biomass. The most striking feature of the zooplankton of Queen Elizabeth II and Wraysbury reservoirs is its large-bodied nature. Not only are *D. magna* (0.78–4.45 mm) and *D. pulicaria* (0.65–3.27 mm) big species but their populations consist of large

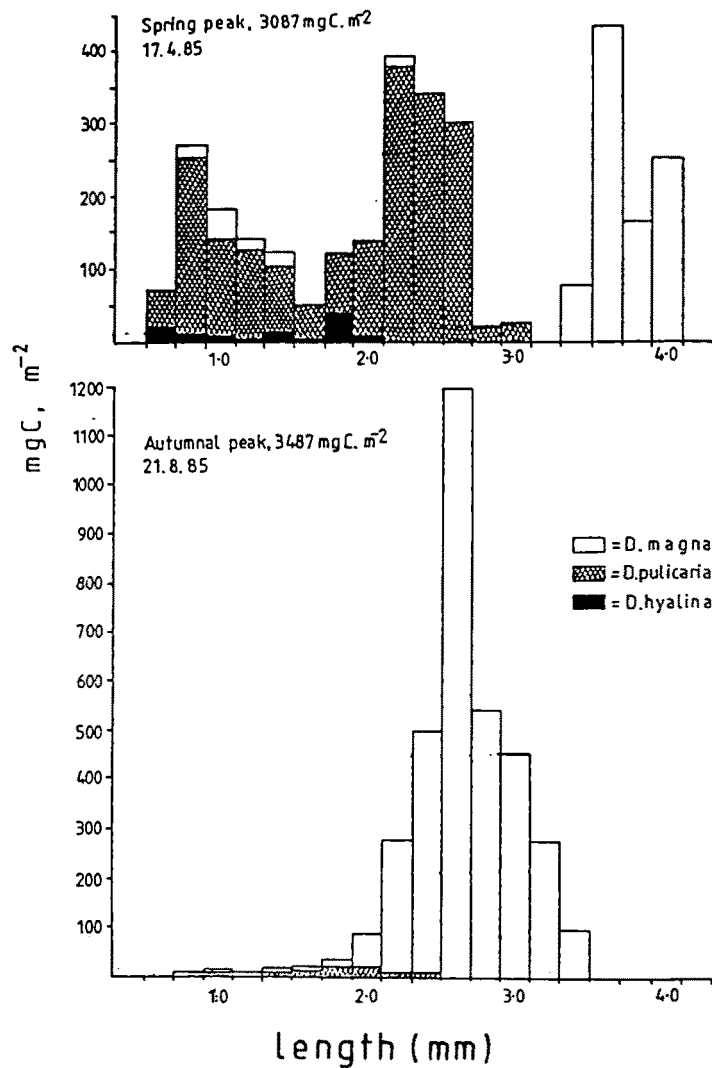


Fig. 3. The size frequency distribution of three co-existing *Daphnia* species during the spring and autumnal biomass peaks in Wraybury Reservoir during 1985 (after Santos, 1989).

individuals. This is illustrated in Fig. 3 from Santos (1989) which shows the length frequency distribution of the three species during the spring and autumnal biomass peaks in Wraybury Reservoir which attained levels of about 3 gC m^{-2} during 1985. All three species were present throughout 1985 varying densities and *D. hyalina* was always the least abundant. Both Duncan (1975a) and Chalk (1981) show a similar situation in Queen Elizabeth II Reservoir for the 1970 decade.

The fish fauna

Systematic investigations of the fish fauna of the deeper flow-through reservoirs has been carried out only for Queen Elizabeth II Reservoir by Hopkins (1975) during 1972–74 and Bubb (pers. comm.) during 1976–78. Sampling the fish fauna is difficult in a reservoir that is 15.3 m deep and has a 1 in 3 littoral slope of concrete slabs. Qualitative gill netting of the littoral region revealed the presence of natural but sparse percid

and cyprinid populations, with ruffe (*Gymnocephalus cernua*) and roach (*Rutilus rutilus*) as the most relatively abundant species, followed by perch (*Perca fluviatilis*), gudgeon (*Gobio gobio*), bleak (*Alburnus alburnus*) and dace (*Leuciscus leuciscus*) in descending order of relative abundance (Hopkins, 1975); their order of abundance in the River Thames differs: roach, bleak, gudgeon, perch, dace, bream and ruffe (Williams, 1967).

From other investigations on the species composition and size structure of freshwater zooplankton during the last decade, the presence of a large-bodied zooplankton such as has just been described implies the existence of a low level of fish predation pressure, although this is rarely quantified. An attempt was made to assess the absolute densities of fish larvae and fry in Queen Elizabeth II Reservoir during 1976–78 by Bubb (1980) by quantitative netting, the only technique then available. It was assumed that knowledge of the maximal observed densities of the O-group cohorts (accompanied by information on their mortality and growth rates) would provide some indirect measure of the existing vertebrate pressure and, also, that most of the young fish in their first year of life inhabited the littoral zone. The latter assumption determined the design of the littoral seine net, with a 3 mm mesh and a buoyant gas-fillable head line, capable of capturing the young fish in 100 m⁻³ or 200 m⁻³ littoral samples (Bubb, 1980). Maximal estimates of densities for ruffe, roach and perch were 7.2, 3.7 and 0.04 ind m⁻² respectively, giving a total maximal density of 10.9 fish m⁻² for littoral belt down to 4 m depth. For the whole reservoir, this density comes to 0.33 fish m⁻² but assumes the absence of any pelagic populations of young fish. These values contrast with the estimate of 81.5 fish m⁻² for the River Thames at Sonning published by Mathews (1971). Further indirect evidence for low fish densities in the reservoirs is provided by the high growth rates recorded by Bubb and Hopkins for both juvenile and adult roach and perch, compared with other British and European populations. During the period 1975–78, 5 year-old roach and 3-year old perch reached mean fork

lengths of 24.5 cm and 21.0 cm, respectively; by the end of August 1978, 100-day old roach and perch fry attained fork lengths of 60 mm and 70 mm, respectively.

Changes in the fish populations: top-down effects

Hopkins (1975) associated by the low densities of coarse fish populations in Queen Elizabeth II Reservoir with the absence of suitable spawning sites, since there are no macrophytic weed beds at the reservoir margins. However, there is some evidence from local angling club records (Hopkins, 1975) that angling was excellent in the London reservoirs during the 1960s. There are also records of large-scale 'fish kills' of mainly large-bodied perch in many of the reservoirs during 1966 and 1967 (Windle-Taylor, 1967, 1969) which coincided with an epidemic spread of a viral infection (ulcerated dermal necrosis) in Great Britain to which perch were particularly vulnerable. This infection appears to be long-lasting in the reservoirs, as perch older than three years have been very rare since that time. A third fish 'event' occurred in the early 1980s when cages of rainbow trout were introduced into Queen Elizabeth II Reservoir, followed by a mass escape of unknown proportions when the cages were damaged during a storm. Thus, the fish situation in Queen Elizabeth II Reservoir can be summarized as three chronological phases:

- 1) 1968–73 – immediately following the loss of larger predatory perch and some roach, with reduced recruitment and with ruffe as the dominant species;
- 2) 1974–81 – with increasing O-group recruitment and increasing proportions of roach in the fish fauna; and
- 3) 1984–88 – immediately following the mass escape of a new predatory fish, the rainbow trout, with potential new impacts upon the coarse fish recruitment.

Associated with these changes in the fish populations from 1968–88, large scale changes occurred in the relationship between the planktonic algae and grazers during the April-May-June

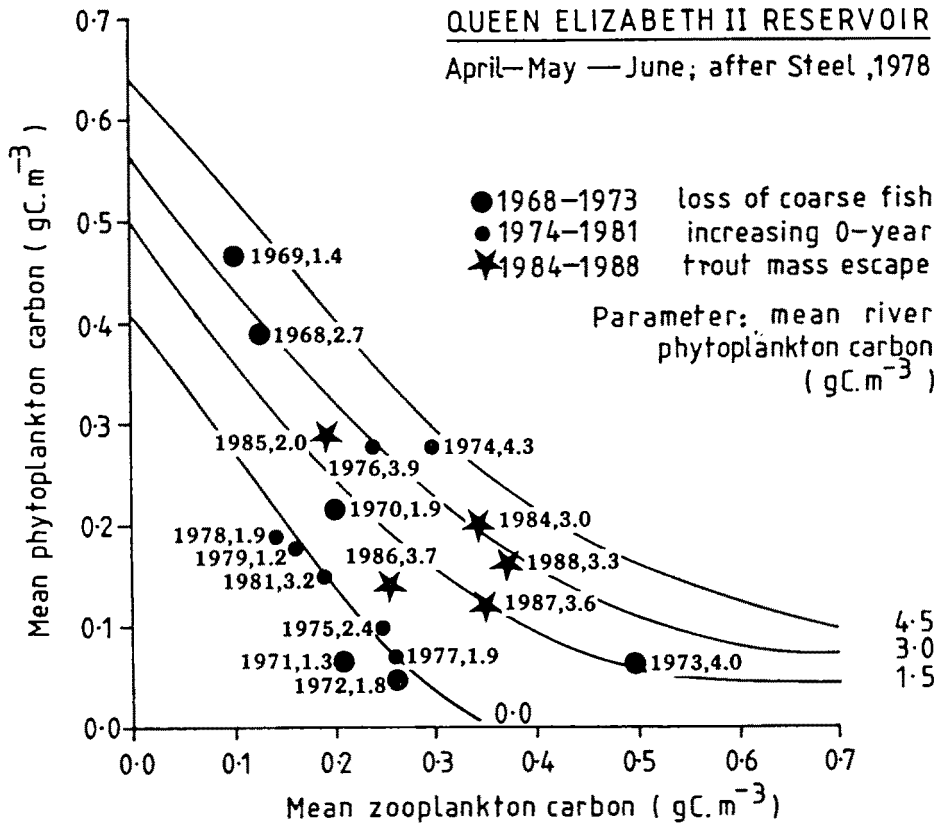


Fig. 4. Changes in the relationship between the mean biomasses of the phytoplankton and zooplankton standing crops of Queen Elizabeth II Reservoir during the spring quarter (April–May–June) for the years 1968–88 and under the impact of changing fish predation pressure and varying levels of river algal crops. The lines represent predictions by the Steel (1972) model of algal biomass at the observed grazer levels (assuming a body size of 1.5 mm) and varying levels of river algae. (After Steel, 1975: Fig. 10; 1978b: Fig. 3; Duncan, 1975; new data from Thames Water).

quarter of the year when the grazers were capable of controlling both the autochthonous spring diatom growth (Duncan, 1975a) and expression of the allochthonous riverine input (Fig. 2). These changes are illustrated in Fig. 4 which updates for the years 1977–88 two earlier versions (Steel, 1975: Fig. 10 for 1968–73; Steel, 1978b: Fig. 3 for 1974–76) and is based upon weekly monitored data by Thames Water Authority for chlorophyll *a*, sestonic particulate organic carbon (POC) and zooplankton dry weight per vertical net haul.

For each year in Fig. 4, the spring quarterly mean values ($n = 13$) for phytoplankton concentration are plotted against the mean values for the crustacean zooplankton, both concentrations expressed as gC m^{-3} . These are based upon a

depth-series of water samples for determination of chlorophyll *a* and sestonic particulate organic carbon and vertical net haul samples ($n = 1-4$) for the zooplankton dry weight biomass, all taken from a single station which provided a representative sample for the reservoir (Steel, 1975; Duncan, 1975a; Bottrell *et al.*, 1976). Chlorophyll *a* biomass (*a*) was converted to algal carbon (*c*) using a conversion ratio of *a* : *c* of 1 : 30 which was derived by linear regression analysis of the paired chlorophyll *a* and POC samples during the spring diatom growth: POC was determined titrimetrically using the COD method in Mackereth & Talling (1978). The zooplankton filtered onto a GFC pad was dried at 60 °C to a constant weight and converted to carbon as 0.44 dry weight

(Duncan, 1975). The lines in Figure 4 represent predictions by the Steel (1972, 1978a) model for a nutrient-unlimited flow-through reservoir like Queen Elizabeth II Reservoir and substituting the particular year's spring quarter conditions of mixed depth, light intensity, optical properties, flow-through regime, concentrations of riverine algal carbon and grazer biomass (assuming a uniform body size of 1.5 mm). Against each yearly point in Fig. 4 is given that year's quarterly mean river phytoplankton carbon; at the end of each predicted line is given the river carbon level used for the prediction; both values are in the same units of carbon, gC m^{-3} , as on the X and Y axes. As a guidance for the interpretation of Fig. 4, Steel (1975, 1978b) predicts from his model that, in the absence of significant grazing, a maximal potential algal concentration of $0.4\text{--}0.5 \text{ gC m}^{-3}$ would be light energy-limited for the operational conditions of Queen Elizabeth II Reservoir with its high nutrient levels.

Considering in Fig. 4 the period 1968–73 (large dots) in the immediate aftermath of the fish-kill of adult piscivorous perch (1966–67), the spring plankton biomass ratios changed from a high phytoplankton: low zooplankton (0.4:0.1) in 1968–69 (with algal biomasses near their predicted maximal energy-limited levels) to almost the reverse condition (0.1:0.5) in 1973, when the level of fish predation would be reduced by decreased recruitment following the fish-kill of adults. Taking into consideration the existing input levels of river carbon, the reservoir algal biomasses in 1971, 1972 and 1973 are all less than predicted and this may be due to the presence of, and greater clearance power of, *Daphnia* spp with a larger mean size than 1.5 mm (Duncan, 1975a; Steel, 1978b: Fig. 4). During the next phase, 1974–81 (small dots), but excepting the transitional years 1974 and 1976, zooplankton biomasses were gradually reduced to less than 0.2 gC m^{-3} and phytoplankton levels both gradually increased up to 0.2 gC m^{-3} and were consistently lower than the predicted levels for the observed river carbon values. This condition of the spring plankton is associated with an increased young fish recruitment during 1976–78

(Bubb, pers. com.) in the absence of large piscivores and with the presence of *Daphnia* spp measuring $> 1.5 \text{ mm}$ in length (Chalk, 1981). The last phase from 1984–88 (stars in Fig. 4) was introduced with the accidental release in 1983 of an exotic predator capable of being a zooplanktivore feeding on the larger daphnid individuals and, probably, on the larval fish in the earlier years and then of being mainly a piscivore on the juvenile fish in general as they became older. In general, the spring phytoplankton attained similar levels as just before (1974–81) but with somewhat higher zooplankton biomasses (starred points mostly fall on the predicted lines for the observed river carbon levels except in 1986 and 1987). This may be due to a return to a smaller body-sized zooplankton (mean size $< 1.5 \text{ mm}$) by predatory selection of the larger daphnid individuals but the size structure of the zooplankton for this phase remains to be investigated. This last phase is not a stable predatory situation, since trout are not being continuously stocked, do not have a natural recruitment and the original escapees are becoming older, larger and sparser. This may account for the cyclical appearance of the 1984–88 chronological changes compared with the unidirectional changes of the 1968–73 and the 1977–81 periods.

Conclusion

The changes described here for the spring quarter are complex ecosystem responses attributed to top-down effects of different regimes of relatively low levels of fish predation upon the large-bodied daphnid zooplankton which is maintained at high biomasses during the spring quarter by a continuous input of high concentrations of riverine algal carbon. The top-down effect passes onto the phytoplankton which, under high grazing pressures of large-bodied daphnid population greater than 0.2 gC m^{-3} , cannot attain its energy-limited and nutrient-unlimited maximal, potential biomass. The levels of fish biomass thought to be responsible for the situation described in 1976–78 were very low; a best estimate is about 0.006 g

DW m⁻² or 0.3 kg WW ha⁻², using Bubb's maximal O-group fish densities, his mean dry weights and a 20% dry weight to wet weight ratio. With the advent of recently developed dual-beam hydro-acoustic techniques for sizing and counting fish *in situ*, it should be possible in future to generate absolute densities simultaneously for all three components of the top-down cascade effect. Over the span of the twenty years of TWA data presented in Fig. 4, there were variations in weather conditions (e.g. 1976 was an exceptionally warm, dry year) which are incorporated as unidentified 'noise' in the figure. However, there is a great deal of dynamic constancy in morphologically simple flow-through ecosystems like the reservoirs and in the River Thames itself, which forms such an important influence on the biology of the reservoirs. It is against the background of this dynamic stability that it is possible to see the effects of the biological interactions associated with changes in the top-down fish predation pressure.

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References

- Andrew, T. E., 1976. The production and respiration ecology of reservoir populations of zooplankton, with special reference to daphnids. PhD Thesis, Royal Holloway College, Univ. London, 296 pp.
- Bottrell, H. H., A. Duncan, Z. M. Gliwicz, E. Grygierek, A. Herzig, A. Hillbricht-Ilkowska, H. Kurasawa, P. Larsson & T. Weglenska, 1976. A review of some problems in zooplankton production studies. *Norw. J. Zool.* 24: 419-456.
- Bubb, M. J., 1980. A large buoyant net designed to catch coarse fish fry quantitatively from shallow weed free water. *Fish Mgmt.* 11: 29-34.
- Burgis, M. J., 1975. The biomass of cycloids in two London reservoirs. *Verh. int. Ver. Limnol.* 19: 1836-40.
- Chalk, E. A., 1981. Cladoceran filter feeding in a Thames Valley reservoir. PhD Thesis, Central London Polytechnic & Thames Water, 266 pp.
- Cooley, P. & S. L. Harris, 1954. The prevention of stratification in reservoirs. *J. instn. Wat. Engrs.* 8: 517-37.
- Doohan, M., 1973. Energetics of planktonic rotifers applied to populations in reservoirs. PhD Thesis, Royan Holloway College, Univ. London, 226 pp.
- Duncan, A., 1975a. The importance of zooplankton in the ecology of reservoirs. Water Research Centre symp. The Effects of Storage on Water Quality. Medmenham, U.K. 247-72.
- Duncan, A. 1975b. Production and biomass of three species of *Daphnia* co-existing in London reservoirs. *Verh. int. Ver. Limnol.* 19: 2858-67.
- Hopkins, D. G., 1975. An ecological study of fish in a Thames Valley storage reservoir. PhD Thesis, Royal Holloway College, Univ. London, 249 pp.
- Kibby, H. V., 1969. Energy transformations by a population of *Diaptomus gracilis*. PhD Thesis, Westfield College, Univ. London, 224 pp.
- Mackereth, F. J. H., J. Heron & J. F. Talling, 1978. Water Analysis: some revised methods for limnologists. *Freshwat. Biol. Ass. Sci. Publ.* 36: 101-106.
- Mathews, C. P., 1971. Contribution of young fish to total production of fish in the River Thames near Reading. *J. Fish. Biol.* 3: 157-80.
- Ridley, J. E., P. Cooley & J. A. Steel, 1966. Control of thermal stratification in Thames Valley reservoirs. *Proc. Soc. Wat. Treat. Exam.* 15: 225-244.
- Ridley, J. E. & J. A. Steel, 1975. Ecological aspects of river impoundments. In B. Whitton (ed.), *River Ecology*. Blackwells Sci. Pub.: 565-588.
- Santos, L. C. dos, 1989. The effects of food limitation on the population dynamics, production and biological interactions of three *Daphnia* species co-existing in a London reservoir. PhD Thesis, Royal Holloway & Bedford New College, Univ. London, 236 pp.
- Steel, J. A., 1972. The application of fundamental limnological research in water supply system design and management. *Symp. zool. Soc. Lond.* 29: 41-67.
- Steel, J. A., 1975. The management of Thames Valley reservoirs. Water Research Centre symp. The Effects of Storage on Water Quality. Medmenham, U.K.: 371-419.
- Steel, J. A., 1976. Eutrophication and the operational management of reservoirs of the Thames Water Authority. *Instn. Publ. Hlth. Engrs. symp. Eutrophication of Lakes and Reservoirs*. Chameleon Press, U.K.: J1-J9.
- Steel, J. A., 1978a. Reservoir algal productivity. In A. James (ed.) *Mathematical Models in Water Pollution Control*. Wiley & Sons: 107-135.
- Steel, J. A., 1978b. The use of simple plankton models in the management of Thames Valley reservoirs. *DVGW-Schriftenreihe, Wasser*, 16: 42-59.
- Vollenweider, R. A., 1968. Scientific fundamentals of the eutrophication of lakes and flowing waters, with particular reference to nitrogen and phosphorus as factors in eutrophication. OECD Directorate for Scientific Affairs, Paris.
- Williams, W. P., 1967. The growth and mortality of four species of fish in the River Thames at Reading. *J. anim. Ecol.* 36: 695-720.
- Windle-Taylor, E., 1967. Forty-third Report of the Metropolitan Water Board: 65-67.
- Windle-Taylor, E., 1969. Forty-fourth Report of the Metropolitan Water Board: 86-88.