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VIRKNINGER av VASSDRAGSREGULERING

En matematisk modell for virkningen av
1. Otta dam utbyggingen på Mjøsas økosystem

Prosjekt for Norges Vassdrags- og Elektrisitetsvesen

Knut L. Seip

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VIRKNINGER AV VASSDRAGSREGULERING

En matematisk modell for virkningene av den
1. Otta damutbyggingen på Mjøsas økosystem,
og på noen økonomiske parametre knyttet til
Mjøsa som naturressurs

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Faggruppe eller felt	Referat Modellberegninger viser at det ikke er noen forskjell mellom planteplanktonbiomasse i Mjøsa før og etter den 1. Otta damutbyggingen ved høy og middels vannføring. Ved lav vann- føring fører utbyggingen ifølge modellen til ca. 10% høyere biomasse. I enkelte år med spesielt tidlig vårflom ser det ut til at en sinking av vårflommen kan være gunstig. De økonomiske parametre er meget lite påvirket av reguleringen	
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FORORD

Det foreliggende prosjekt ble påbegynt i 1980 i samarbeid med Y. Mæhlum og M. Fossdal. Senter for Industrieforskning (SI), fikk dengang i oppdrag å komme frem til en metode for beregning av endringer i innsjøers økologi ved vassdragsutbygging. Etter samtaler med de berørte parter ble man enige om å se konkret på virkningen av den 1. Otta damutbyggingen. De hydrologiske virkninger er tatt opp av Thendrup og medarbeidere ved Norges Hydrodynamiske Laboratorier. Vi har derfor konsentrert oss om de økologiske virkninger, og også inkludert virkninger på rekreasjon, fiske og rensekostnader for drikkevann.

Y. Mæhlum avgikk ved døden under prosjekttiden. Hans entusiasme og villighet til å sette ting i sammenheng var viktig for prosjektet. Vi håper likevel at resultatet av prosjektet kan være til nytte i det videre arbeid med vassdragsreguleringer.

Knut L. Seip

ABSTRACT

A simulation model and several regression models were used to examine the impact of river regulation, especially that caused by the 1. Otta dam construction, on selected parameters of the Lake Mjøsa ecosystem.

A decrease in annual total flow of the main river entering the lake from upper to lower quartile flow increases phytoplankton standing crop with 20% (\pm 8%). Estimates vary with model type. With present day average flows the simulation model, give the lowest estimate. It is suggested that the reason for this is that the 30 years average flow at low flow volumes is shifted towards flow pattern which give relatively lower biomass. The simulation model is the only model which incorporates changes in flow patterns. The 1. Otta dam construction may at low flow give an increase in plankton biomass of about 10%. At median and high flows there is no significant difference between present day and post construction flows.

Unexpectedly, we found that the flow in 1981 gave a significantly higher biomass than the 30 years average flow of the same volume would have given. We therefore believe that the flow pattern that year contributed to the exceptional deviation from a decreasing trend in biomass values in Lake Mjøsa for the years 1976-1983.

The models for fish abundance and economic and social effects of water quality changes are rather speculative, however, effects from the proposed dam construction are probably insignificant.

1. INNLEDNING

Formålet med det foreliggende arbeid er å utvikle en metode for å studere virkningene av vassdragsreguleringer på innsjøers forurensningstilstand. Som et eksempel har vi beregnet virkningene av en foreslått utbygging av Otta-vassdraget på forurensningssituasjonen i Mjøsa. Vi har tatt utgangspunkt i beregnede verdier for vannføringen ved Hunderfossen av et 1. byggetrinn av Otta-utbyggingen. Til beregningene har vi benyttet en "skadeberegningsmodell" for vassdrag utviklet ved Senter for Industrieforskning. (Seip 1981 a,b, Seip 1984). Modellen er sammensatt av flere del-modeller. Del I er en simuleringsmodell for deler av det økologiske systemet i en innsjø. Del II består av en pakke med regresjons- eller erfaringsmodeller som viser sammenhengen mellom kjemiske og biologiske parametre i sjøen. (F.eks.: sammenhengen mellom fosfor og klorofyll-a). Del III er en modell for sosiale og økonomiske skader av forurensning av sjøen.

2. MJØSA OG DETS NEDBØRFELT

Mjøsa (61° N, 11° E) nedbørfelt ligger i deler av Oppland, Hedemark og Akershus fylke. En del karakteristiske trekk ved Mjøsa er stilt sammen i Tabell 1 i Appendix. Mjøsas retensjonstid for vann er ca. 6 år, men siden sjøen er meget dyp, er det rimelig å anta at retensjonstiden for de dypere vannmassene er større og retensjonstiden for de øvre vannmasser tilsvarende lavere. Dette vil bli diskutert nærmere under avsnittet om regresjonsmodeller. Det alt vesentlige av vanntilførselen til Mjøsa, kommer gjennom Lågen. (I 1976 kom 88% av vannføringen på $8 \cdot 10^9$ m³ gjennom denne elven). En rekke forhold som påvirker Mjøsas økosystem er diskutert i rapporter fra NIVA, bl.a. i Kjellberg (1982 a, b). Han fremstiller variasjoner i påvirkning og respons fra 1976 til 1981. I publikasjoner fra SI (Seip 1981 a, b) diskuteres de mulige virkningene av næringstilførsler, innlagringsdyp for tilførselene, virkning av vertikal vannutveksling (indre bølger) etc. Vi skal imidlertid her ta utgangspunkt i den situasjonen som ble observert for Mjøsa i 1981.

I simuleringsforsøkene som følger vil vi i tillegg benytte tre sett med data for vanntilførsel til sjøen. i) Vanntilførselen slik den er observert i 1981. Vanntilførselen dette året hadde et ekstremt tidsforløp og vi skal senere se at dette får innflytelse på planktonproduksjonens forløp. ii) Vanntilførselen beregnet som karakteristiske verdier for 7 døgns middel for perioden 1920-1950. Øvre og nedre kvartil og medianverdi. iii) De beregnede endringer i disse forløp som følge av 1. byggetrinn i Otta-utbyggingen.

3. MODELLENE

Vi vil her kort beskrive de tre sett av modeller som er benyttet i arbeidet med vassdragsvurderinger. En mer utfyllende beskrivelse er gitt i Appendix.

3.1 Simuleringsmodellen

Modellen er en to-lags modell der det ene laget representerer det øvre produktive lag i sjøen (epilimnion) og det andre laget representerer de nedre, ofte næringsrike vannmassene (hypolimnion). Modellen beskriver tidsutviklingen av 10 hovedstørrelser i begge lag; næring, plante-planktongrupper, detritus, bakterier og zooplanktongrupper. Vekst og død av organsimer i planktonsamfunnet reguleres av temperatur, lys, næringsstofftilførsel, synkeegenskaper etc.

3.2 Regresjonsmodellene

Vi har valgt å benytte 5 regresjonsligninger for klorofyll-a som funksjon av næringskonsentrasjon. Modellene baseres dels på OECD-arbeid, dels på arbeider tilsvarende OECD-arbeidene fra innsjøer i USA og dels på norske arbeider. (Referanser er gitt i vedlegget). Modellene er delvis akseptert som et praktisk planleggingsverktøy.

Vi har valgt to ligningssett for dyreplankton (total mengde og fordeling på størrelsesfraksjoner). Modellenes pålitelighet er lite undersøkt.

Vi benytter 4 ligninger for fiskebestand og fiskeavkastning. En av disse gir fordeling av sportsfisk, forfisk og "rough" fisk. Modellene er klart undersøkende og vil bare kunne gi en pekepinn om sjøens teoretiske kapasitet. Sjøens historie og en rekke andre faktorer kan bidra til at de aktuelle forekomster er svært forskjellige fra de predikerte.

De uavhengige variable for regresjonsligningene er i noen tilfeller selv beregnede størrelser. Vi har da brukt ulike alternativ for den uavhengige variable, slik at totalt antall beregninger er noe større enn antall grunnligninger. Forutsetningene for å benytte de ulike ligningene er antydning, f.eks. med å karakterisere datagrunnlaget for beregningen av ligningens koeffisienter. Disse forutsetningene vil vi ta utgangspunkt i når resultatene diskuteres.

3.3 Sosio-økonomiske modeller

De sosio-økonomiske modellene er meget enkle. Vi har beregnet tre størrelser som hver er tenkt å uttrykke egenskaper ved vannkvaliteten av betydning for brukerne av innsjøen. Modellen for kostnader ved å rense drikkevann baserer seg på opplysninger fra lokale vannverk og Statens Institutt for folkehelse (Bergan, 1984. Se litteraturliste i Appendix). Tolkningen av sammenhengen mellom råvannskvalitet og rensebehov er imidlertid delvis vår egen. Kostnadene ved rensing måles i NOK.

Rekreasjon har vi valgt å la være en funksjon av siktedyp og andel alger med blå-grønn algekaraktistikk. Rekreasjon måles langs en skala fra 0.0 til 1.0, der 1.0 er best. Fordelene av fiske måles i NOK. Grunnlaget er estimat av fiskeforekomster, og av forekomstenes rekreasjonsverdi. Det siste estimatet baserer seg på arbeider av Strand (1981-82, se Appendix).

4. KALIBRERING OG TILPASNING

Når resultater fra simuleringsberegninger, regresjonsligninger og observasjoner skal sammenlignes må en ta stilling til en del stochiometriske konstanter, dvs. forholdet mellom ulike kjemiske komponenter i organismene. Vi har valgt følgende verdier (litteraturhenvisninger til Appendix):

- Forholdet mellom forfor og tørrvekt av plankton er satt lik 0.01. Parsons og Takahashi (1973) oppgir verdier mellom 0.5 og 3%, Peters og Rigler (1973) finner 1.8% for naturlig dyreplankton og Lehman (1980, s. 629) finner 1.25%, men vi antar at forholdstallet tenderer mot lave verdier i oligotrofe-mesotrofe sjøer.
- Forholdet mellom fosfor tilgjengelig for algene og totalt fosfor er satt lik 60%, dvs. vi regner med at alt oppløst fosfor (50% av totalt fosfor) + 20% av partikulært fosfor er tilgjengelig. Broberg (1983) indikerer at alt oppløst fosfor (bare oppløst fosfor undersøkes) er tilgjengelig for alger over noen tid i ikke-sure innsjøer. Seip (1983) fant at 60% totalt fosfor ga best overensstemmelse med observasjoner i en simuleringsundersøkelse.
- Forholdet mellom alge tørrvekt og alge våtvekt er satt lik 15%. Denne verdien er beregnet på basis av Stratham₃ (1967) for diatomeer med et gjennomsnittlig volum på $900 \mu^3$ og med et carbon/tørrvektforhold på 0.5.
- Forholdet mellom klorofyll-a og alge tørrvekt er satt lik $2.0 \cdot 10^{-2}$ på vektbasis. Okino (1973) finner $2.0 - 10.0 \cdot 10^{-3}$ for eutrofiske Lake Suwa, Japan (høyest om sommeren). Fra data presentert av Kjellberg (1983) finner vi $(1.9 \pm 0.5) \cdot 10^{-2}$ for maksimumverdier av klorofyll-a og biomasse og $(2.0 \pm 0.2) \cdot 10^{-2}$ for gjennomsnittsverdier. Banse (1982) refererer den samme verdien som Kjellberg; $2.0 \cdot 10^{-2}$ som sommerverdi.

5. RESULTATER

Resultatene av modellberegningene viser at vassdragsreguleringer generelt vil kunne ha betydning for Mjøsas økosystem. Den 1. Otta-utbyggingen er imidlertid liten. Reguleringen har ingen virkning ved høye og middels vannføringer. Ved lav vannføring viser modellen at biomassen av planteplankton kan øke med omkring 10%. Som et uventet resultat fant vi at den spesielle vannføringen i 1981 sannsynligvis hadde betydning for den høye biomassen av planteplankton dette året. Sammenlignet med regresjonsmodeller gir simuleringsmodellen informasjon også om endringer i form på vannføringen gjennom året. Resultatene synes å vise at dette er en viktig parameter, særlig ved studiet av mindre reguleringsinngrep.

De økonomiske og sosiologiske modeller er ganske spekulative og resultatene må støttes på annen måte ved en endelig vurdering. Resultatene synes imidlertid å vise at den 1. Otta damutbyggingen ikke har noen vesentlig betydning for fiske, rekreasjon eller rensekostnader for drikkevann.

Detaljer i resultatene er gitt i Appendix.

APPENDIX

THE IMPACT OF RIVER REGULATION ON LAKE MJØSA. A COMPARISON BETWEEN RESULTS FROM A SIMULATION MODEL AND REGRESSION MODELS.

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THE IMPACT OF RIVER REGULATION ON LAKE MJØSA. A COMPARISON BETWEEN RESULTS FROM A SIMULATION MODEL AND REGRESSION MODELS

1. INTRODUCTION

To what extent does water through-flow have an impact on lake ecosystems? The question is important when nutrient load/lake response functions are studied. In Norway there are 481 hydroelectric power plants greater than 1 MW, and thus river regulation is an important part of lake management practice.

River regulation may impact the ecosystem by changing the nutrient inputs and by diluting or increasing concentrations of nutrient and plankton in the lake. It may also effect the stability of lake watermasses, cause changes in temperature and change the amount of suspended particles in the lake. In northern latitudes ice-cover changes may occur (Thendrup, 1978, Kinnunen et al., 1982). In ecosystem monitoring and management systems effects of water through-flow have to be taken into account in terms of the impacts listed above. Two types of mathematical models are coming increasingly into use for this purpose: simulation models and regression models.

Simulation models usually consist of a set of partial differential equations describing time development of the main variables of the lake ecosystem. They often predict responses for one or several consecutive years, with time resolution of days or shorter and for a wide selection of variables (5-20). Regression models are statistical models which often describe the response in terms of annual averages of one parameter. Accordingly, regression models typically require fewer direct input data with less temporal resolution than simulation models.

In the present work we have compared the result of a particular simulation model, the NORECO model, and results of a series of regression equations for the case of the 1. Otta dam construction project of the Norwegian Water- and Electricity Board (NVE).

The formulas and the database used for the NORECO model were developed initially at the University of Washington (Lazow et al., 1976). They are described in some detail, because we feel that lake ecosystem models too often are presented in a "short form". We hope that the presentation given here is satisfactory for an assessment of the model.

The Mjøsa ecosystem

Lake Mjøsa is a relatively large and deep dimictic lake. A N-S cross section is shown in Figure 1 and some key data are given in Table 1. The lake is susceptible to wind stresses, especially in the NW/SE direction, and large internal waves (including seiches) with periods

of 5-7 days may then dominate the temperature and flow conditions in the lake (Thendrup, 1978).

2. METHODS

The development of the models is presented below. We first present the simulation model and the database used to calibrate the model, then we describe the regression models.

Components and structure of the simulation model

The equations governing the model NORECO are set forth in Table 2 and details of model equations are shown in Tables 3 and 4. A flow diagram of the program is shown in Figure 2.

For each variable in the model a partial differential equation is constructed. Depending upon the species type, special functions can be called upon for the calculation of coefficients. Thus the model allows for a free selection of the number of nutrients, plankton or bacteria species. In the present simulation series there are two nutrients, phosphorous and nitrogen, three species groups of phytoplankton and three species groups of zooplankton. There is also one species of bacteria included. One differential equation represents an organic matter pool. To exchange matter between different compartments, stoichiometric ratios are given as constants.

The set of differential equations are solved by a fourth order Runge-Kutta method.

The database used for determining the parameters of the model are primarily based on literature data from north latitude lakes, some data are also found by observations of Lake Mjøsa plankton. The literature data vary according to experimental conditions, type of species examined, etc. Nevertheless, we have computed average values of data supposed to represent comparable parameters, and investigated differences between these data and data extracted from Lake Mjøsa observations.

Phosphorus is assumed to be the most limiting nutrient for phytoplankton in Lake Mjøsa. To the degree that silica will be limiting, we assume that phosphorus and silica will act in concert. However, the model in its present version also includes nitrogen as a nutrient. Thus, to find the nutrient which actually limits growth the nutrient is chosen which gives the greatest reduction in realized growth rate according to a simple one-compartment Michaelis-Menten form of nutrient limitation (Lehman, 1980). Other growth limitation kinetics (McCarty and Goldman, 1979; Turpin and Harrison, 1979; Lehman and Scavia, 1982) and other ways of combining limitations of phytoplankton growth by two or more nutrients have been considered (Kunikane et al., 1981; Smith, 1980), but we believe that the database required for the implementation of such mechanisms is yet not sufficiently developed. The error introduced by using the simple one-compartment nutrient kinetics will probably be greatest for the results on species succession (cf. Gilbert and Goldman, 1981; Tilman, 1977). The actual values for nutrient limitations are based on data compiled from Tilman and Kilham (1976), Okeda and Sudo (1980), Holm and Armstrong (1981),

Gotham and Rhee (1981a,b), Rhee and Gotham (1981a, b), Tilman et al. (1982), Smith (1982), Källqvist (1982), and Lövstad (1982). The two last authors have used data from Lake Mjøsa.

Bracket values for the references given are shown in Table 5. Generally, data from non-Norwegian lakes show higher half saturation constants for nutrient uptake than the average for the Mjøsa data. However, on the basis of the data presently available it is not possible to separate significantly between algal species groups in terms of this parameter. (For eutrophic lake Suwa, Japan, with another set of dominating algae and to which the model also has been applied, we believe that separation was possible; Seip and Satoh, 1984).

Phytoplankton growth is regulated by light both on a daily and on a seasonal basis. Algae may, however, adapt to changing light intensities by changing for example photosynthetic pigment content or reduce cell volume. Adaption may take time, from a few minutes for marine cyanobacteria (Falkowski, 1980) to several days for many algal species. Correspondingly algae may respond to the instantaneous light intensity or to some time average (cf. discussion by Malone and Neale, 1981, on marine phytoplankton).

A general pattern emerge for both fresh water and marine plankton groups: diatoms always harvest light at maximum capacity, green algae and blue-greens adapt rapidly to changing light intensities.

The response of plankton groups to light intensities is formulated as a stepwise linear approximation to a bell shaped curve, see equation (3) of Table 3. Data on characteristic response parameters are given in Table 5 and are based on data from Rhee and Gotham (1981 b), Perry et al. (1981), Sorokin and Krauss (1957), Falkowski and Owens (1978), Aruga (1965), Steemann-Nielsen and Jørgensen (1968), Okino (1973 a), Krüger and Eloff (1977), Watanabe (1979), Zevenboom et al. (1980), Meyers and Kratz (1955), Beljanin and Trenkusu (1977) and Foy et al. (1976). Data are for marine and fresh water algae, however, when the data are split into freshwater and marine forms, the relative characteristics shown in Table 5 seem to hold. When these data are compared to data for Lake Mjøsa (Källqvist, 1982), the lower limit of the optimum plateau is apparently lower for the Mjøsa data than for the average of the rest of the data (Seip and Satoh, 1984).

We have tried to consider part of the effect of adaption by a) making the algae respond to running averages over past light intensities, b) let the biomass/chlorophyll-a ratio be a function of the average light intensity, and c) make the growth rate a function of chl-a. Preliminary simulations indicated that model results were relatively insensitive to reasonable variations in parameters chosen for these functions. We therefore decided to use one day averages for light, a fixed biomass/chl-a ratio of 50 and fixed maximum growth rates (the last parameter values are given in Table 5).

Temperature impacts both growth rate, respiration and mortality. In many species the general form of a growth modifying temperature function is bell shaped, but with the optimal temperature - the top of the bell - displaced towards an upper limiting temperature. As with light, adaption occur, but with longer time lags (3-6 days). The growth/temperature response is given on the format of eq. (3), Table 3. Data or characteristic response-parameters are given in Table 5 and are based on data from Rhee and Gotham (1981a), Malone and Neale (1981), Foy et al. (1976), Aruga (1965), Källqvist (1982), and Lövstad (1982,

1983).

When these data for non-Norwegian lakes are compared to data for Lake Mjøsa, Källqvist (1982) it is seen that diatoms have the lowest optimum temperature in both sets (cf. Seip and Satoh, 1984).

Both data for light and temperature seem to show a response pattern which separates between the three main species groups: diatom, greens, and blue-greens. However, single species within each group may fit another group better. Thus the partition is "fussy".

Temperature also affects zooplankton growth. Work by Meijering and Jacobi (1981) and Orcutt and Porter (1983) shows that life processes tend to be lower below about 10C. This temperature is also supported by observations by Kjellberg for Mjøsa (personal communication).

Temperature affects respiration and mortality of plankton. We use the form of eq. (9) and eq. (10) in Table 3. In eq. (9), individual body weight is the independent parameter. We have used characteristic weights for mature populations of bacteria ($5 \cdot 10^{-8}$ g), diatoms ($9 \cdot 10^{-5}$ g) and green and blue-green algae ($1.4 \cdot 10^{-5}$ g) as well as for zooplankton ($2 \cdot 10^{-2}$ to 2. g). The choice of weight and values for respiration are based on Dumont et al. (1975) and others listed below.

It is not possible to adopt the same set of coefficients in eq. (9), Table 3 for bacteria, phytoplankton and zooplankton, therefore values have been calculated for bacteria from Curds (1971), Williams (1982) and Banse (1976, 1982), for phytoplankton from Banse (1976), Eppley and Sloan (1965) and Laws (1975), and for zooplankton from Ikeda (1970), Ikeda and Motoda (1978) and Dewey (1976). If parameters are not given as functions of temperature, we assume that it is possible to interpolate linearly between the quoted values at the temperature given (or inferred) and an assumed low respiration rate at 4C. We have computed the resulting respiration rates in percent of biomass and given the results in Table 5 for phytoplankton. For zooplankton the values range between 8%, for large zooplankton at 10C to 60%, for small zooplankton at 20C. For both phytoplankton and zooplankton we have calculated a general mortality term which is linearly dependent on temperature (Ikeda and Motoda, 1978).

The growth reducing factors can be combined in several ways. Nutrients limitation and light and nutrient limitation is discussed by Rhee and Gotham (1981a and b). They conclude that the simultaneous limitations of light and nutrients and of suboptimal temperatures and nutrients are greater than the sum of the individual effects, i.e. a cell ceases to grow before an additive model for interaction would predict zero growth. The authors also conclude that multiplicative models are in error. Kiefer and Mitchell (1983) adopts the most limiting approach between light and nutrients. In an ecosystem model the exact response of plankton to external forces when the growth rate is lower than the sum of respiration and mortality is probably not very important. However, mechanisms compensating for apparent growth reduction by single factors (Rhee and Gotham 1981b, p. 655) may be potentially important at high growth rate. Parabolic terms for the relationship between nutrient uptake and light intensity have been proposed by McIsac and Dugdale (1972) and Reshkin and Knauer (1979) with half saturation values in the range 1-20% of surface light intensity. In assessing the probable error in combining both nutrients, light and temperature we found that the form given in eq. (7) of Table 3 will

produce the least error for medium and fast growth situations (preliminary simulations not reported).

Settling rates for phytoplankton vary with species, growth condition, nutrient status, season, time of day and relative brightness as the probably most important factors (cf. Reynolds et al., 1982). In Table 5 we have reported on settling velocities for species grouped into diatoms, greens and blue-greens, and distributed on growth status. The values are representative for the actual species represented in each group, and the results coincide with qualitative statements on the sinking characteristics of the three groups.

The diatoms tend to sink out fast of the water column at the end of their growth period (Smayda, 1974; Davies, 1982). Thus, in enclosure experiments artificial mixing has been used (Grice et al., 1980). It is probable that diatoms, because of the silicification, can withstand dissolution and breakage during sinking (and also during zooplankton ingestion) more than other algae, thus their removal from the aquatic system (and associated nutrient depletion of the water) may be very effective (cf. Smayda, 1971).

Some species of blue-green algae can move actively in vertical direction so that their sedimentation rate in periods may be zero or negative (Burns and Rosa, 1980). They often decompose extensively during sedimentation, 60 to 90% is reported to decompose in Lake Mendota, Wisconsin, by Fallon and Brock (1980).

Green algae seem to behave intermediate between diatoms and blue-green algae with respect to sedimentation rates and also with respect to decomposition.

The sinking velocities reported are probably characteristic for real waters with little mixing.

However, the effects of mixing are disputed. Burns and Rosa (1980) hold that the effect of turbulence hardly effects settling in most lakes and oceans, whereas Therriault et al. (1978), Smayda (1974), Fallon and Brock (1980), Scavia and Bennet (1980) and Griece et al. (1980) in different ways show that turbulence (on various scales) has a significant impact on net depletion rate of living and nonliving material from the water column. Vertical movement in the water column may give a net benefit for algae, depending on the relation between sinking rate, nutrient availability and other growth resources (Titman and Kilham, 1976; Okeda et al., 1981). In the model sinking rates have been made a function of growth rate or, alternatively, of nutrient availability, as in eq. (2) of Table 4. We will later report on simulations with different modes of sinking.

The model includes a description of three zooplankton species. The grazing process is assumed to be approximated empirically by a hyperbolic model with density of prey as the independent variable, and with a low level threshold concentration as shown in eq. (4) of Table 3. Such grazing modes have been shown to give adequate descriptions for several species (Mullin et al., 1975). The model requires 3 parameters to be determined; saturating ingestion rate, a half saturating constant for ingestion and a threshold value below which no grazing occur. Values for these parameters are given in Table 6 together with values for g , the fraction of phytoplankton grazed by zooplankton and used for zooplankton growth. The values are obtained from Lam and Frost (1976), Frost (1972), Banse (1982), Carothers and Grant (1983),

Lehninger (1980), and Fenchel (1980). However, often prey densities are given in cell number, and we have to infer cell size from prey species characteristics.

Zooplankton mortality and respiration are formulated as for phytoplankton (eq. (8)-(10) in Table 3). Constants in the equations are derived from Ikeda and Motoda (1978, p. 360) using 1ml O_2 per 1 mg dw respired, and give respiration values at 10C, as shown in Table 6. The value corresponds with data used by Borgman et al. (1980) for natural assemblages of copepods.

Mortality is also made a function of temperature as shown in equation (10) of Table 3. Temperature dependence was derived from Ikeda and Motoda (1978, Table 4). Here we also included an additive constant term which represents the grazing pressure on zooplankton from species not included in the model.

Zooplankton can graze on selected preys by assigning appropriate values in a matrix relating any two species. The grazing formulation follows basically the method described by Scavia and Eadie (1976). The formulation is of the type shown in eq. (5) in Table 3, but with a half saturation constant relative to the total biomass available. Selected data for half-saturation constants and refuge biomass are given in Table 6. In the present model small zooplankton, including ciliates, graze on bacteria. Medium zooplankton graze on diatoms and green algae with no differences in selection between the two species. There is no grazing on blue-green algae in the model, although such grazing is reported to occur on small individuals (Holm et al., 1983) and single cells. Large zooplankton graze on small and medium size zooplankton, but this grazing pressure is adjusted to give a relative small contribution to the mortality of the former zooplankton species.

Nutrients are regenerated to pools of dissolved or particulate material as a result of excretion or of break-down of incompletely digested remains of egested algal cells. Matter from this pool is probably directly or after a short time available for uptake by phytoplankton (Peters and Lean, 1973). Thus it is estimated that 40% of the nutrient required for growth after the vernal bloom period comes from recirculation through a zooplankton pathway (Lehman, 1980; Lehman and Scavia, 1982). We have therefore assumed that a high fraction, 0.4 day^{-1} , of this excretion and break-down pool is transformed into available nutrients. However, settling velocity for non-living organic material may be high, depending upon size and condition. Burns and Rosa (1980) quote values from 0.24 m.day^{-1} to 2.32 m.day^{-1} for fractions ranging from 10μ to 64μ , whereas Smayda (1971) and Small et al. (1979) quote values as high as $60\text{-}200 \text{ m.day}^{-1}$. For the assemblage of algae used in the model we have chosen a value of 1.5 m.day^{-1} . This is also in the range of sinking rates for plankton at decreasing growth rate and can be compared to the value of 2.0% of epilimnetic phosphorus sedimenting out per day found by Prepas and Rigler (1980) for a medium size (6 ha), shallow deep Canadian lake.

Interchanges between epilimnion and hypolimnion occurs via functions for exchange of watermasses. The thermocline downward migration and a superimposed apparent diffusion between the two layers are modelled in this way. The effect of seiches would cause periodic variation in epilimnion thickness, and thus in light penetration, but this mechanism is not used in the present simulations (Seip, 1981). Inflow and outflow are assumed to occur to and out of epilimnion.

Some conversion ratios

When results from simulation studies, regression equations and observations are to be compared, the weight ratios of some chemical species to algae biomass have to be determined. These ratios may change with time and with the depth at which the organisms are found. We here summarize our choices of ratios:

- The ratio between phosphorus and dry weight of phytoplankton is set to 0.01. Parsons and Takahashi (1973) quote values between 0.5 and 3%. Peters and Rigler (1973) find 1.8% for a natural zooplankton assemblage and Lehman (1980) finds 1.25% for moderately large freshwater algae. We will assume that the ratio tends to low values in oligotroph/mesotroph lakes like the Mjøsa because the algae will tend to utilize the available phosphorus efficiently.
- The ratio between available phosphorus and total phosphorus is set equal to 60%, i.e. we assume that all soluble phosphorus is available and 20% of the particulate phosphorus. (SRP is about 50% of TP).
- The ratio between algal dry weight and algal wet weight is set equal to 15%. This value is calculated from Strathmann (1967) for diatoms, assuming an average cell volume of $900 \mu^3$ and a carbon/dry weight ratio of 0.5
- The ratio between chl-a and algal dry weight is set equal to $2.0 \cdot 10^{-2}$ (weight). Okino (1973 a) finds $(2.0-10.0) \cdot 10^{-3}$ for eutrophic lake Suwa, Japan with highest value during summer. Kjellberg (1983) finds $(1.9 \pm 0.5) \cdot 10^{-2}$ for ratios between summer maximums and nearly the same value $(2.0 \pm 0.2) \cdot 10^{-2}$ for average values. Scavia and Chapra (1977) in their comparison of simulation model for Lake Ontario and two regression models use C:P \approx 41:1 and C: chl-a = 50 which corresponds well with our choice.

3. REGRESSION EQUATIONS

The ecological model NORECO will be compared below with regression models. Five models are for chl-a as a function of nutrient load or in-lake nutrient concentration, 2 for zooplankton biomass as a function of nutrient or chl-a concentration, and 3 models for fish biomass as a function of nutrient concentration. In this type of regression models, the input data are often from literature sources, so that observations of lake parameters are not always made on a uniform format. In Table 4 we have listed the regression equations and we have indicated what type of data the regressions is based upon. Unfortunately, sampling frequency, season, depth etc. are only fragmentarily reported. However, all of the regression equations have a typical domain of validity corresponding to the characteristics of the lakes on which each equation was constructed. By comparing those to the characteristics of Lake Mjøsa we can make an assessment of the results each model gives compared to the observations.

Socio-economic impacts

Eutrophication of lakes causes unwanted effects. We have chosen to emphasize decreased utility for swimming and recreation, increased cost for drinking-water purification and changes in fishing utility. Large uncertainties are associated with the assessment of such damages, however, we felt it could be useful to develop a first numerical approximation to "educated guesses". We have used estimates of utility fairly directly related to ecological lake parameters: the attribute "swimming" which also includes boating and aesthetic values of a clear lake (willingness to pay for swimming, boating and aesthetic values was shown to have the ratio 1:3:1 in a Swedish study (Hjalte et al., 1982) is related to water transparency and percentage of nuisance algae as described by eq. (2) of Table 8. About 200.000 people get their drinking water from Lake Mjøsa or downstream waters, and bad water quality has been reported during blue-green algal blooms. We have made drinking water purification costs a function of the annual average plankton biomass and of the fraction of nuisance algae as shown in eq. (3) of Table 8. Our third attribute, the utility of recreational fishing, is based on data for numbers of people fishing, fish quantity and fish quality, and the value of recreational fishing which also include the optional value of this activity (eq. (11) and (12) of Table 7 and eq. (3) of Table 8).

4. RESULTS

Simulation model.

The main features of the time sequence of phytoplankton blooms in northern-temperate lakes are described and explained in about the same manner by most authors (e.g. Wetzel 1975). Many of the mechanisms involved, like increasing temperature and light in the early spring, stratification, increased predator pressure and then renewed nutrient availability are represented by equations in the model and thus the model allows for a close biological interpretation of the simulation results.

In the first of the simulation series we examine the impact of changing the waterflow through the lake. We use three sets of waterflow data; the flow observed in 1981 and also displaced in time relative to the actual observations. The average flow during the years 1920 to 1950 (NVE) and the anticipated waterflow that would result from the construction and operation of the 1. Otta dam project (NVE). Graphs showing the waterflow as a function of time are given in Figure 3.

The results of the simulations for the year 1981 are compared to observations in Figure 4. In that year the lake plankton was dominated by diatoms, and this is also the dominating algae in the simulations (Peak ratios for diatoms, greens and blue-greens are 1:0.002:0.005 (model) and 1:0.007:0.0006 (observed)). The first pronounced nutrient peak load occurs in May and concurrently with a peak in the flow, but plankton blooming does not begin before stratification occurs in late June. The observed spring bloom has a pronounced "knee" in June not seen in the simulation. More important, the observed plankton biomass decreases to about half the peak value in August, whereas the simulation shows a nearly complete disappearance of phytoplankton in September. The small, observed second peak in September may correspond to the predicted reappearance of plankton in October-November.

Comparisons of simulated and observed values for available phosphorus in epilimnion is shown in Figure 5. The observed values are for the upper 10 m only, whereas the simulated values are for the total epilimnion, i.e. depths varying from 10 to 40 m. It is seen that there is a fair correspondence between the pattern of variation between the observed and simulated results, but the simulated values are probably too high, even if we correct for differences in depths of the upper layer.

In the first simulation series we used the time series for water flow under present and post construction conditions as shown in Figure 3. The results showed that the changes in water flow (less than 10% changes in peak flow) could induce up to 14% changes in peak biomass response. However, when parameters of the model was changed during a sensitivity analysis, the responses to the two different water flow regimes was only significantly different at very low flows (lower quartile flow). (Cf. also discussion below)

We also examined the impact of shifts in peak flow time. This was done by displacing to flow at certain time intervals before and after the actually observed dates. Since we only displaced waterflow, an error is introduced because nutrient inputs are partially correlated with flow. (The river is usually lower in nutrient concentrations than the average for the lake). However, a satisfactory theoretical calculation of nutrient flow to the lake is not yet available. The results depicted in Figure 6 show that a shift in the water flow of about one month before or after the observed date may increase or decrease the plankton biomass with about 6%.

In the simulations explained above, the water volume was constant. In the next set of simulations we used the flow-patterns corresponding to upper and lower quartile flow and median flow for the years 1920-1950. The results are shown in Figure 7 for chl-a summer averages as a function of flow volume.

The flow in 1981 had an annual flow volume close to the upper quartile flow of Figure 3 b and the simulation result for this year is included in Figure 7, together with the observation for that year. It is seen that both simulation result and observation have higher values than those corresponding to the average flow pattern with the same volume.

Regression models

On the same figure is also shown results from the regression equations of Table 5. Generally, increasing water through-flow decreases the concentration of chl-a for all types of calculations. The lowest and highest chl-a estimates differ with a factor of three.

The regression equation for zooplankton shown in Figure 8 gives 1.5 to 2 times higher values than those obtained with the NORECO model. Observations are only available as number of individuals per square meter during a few months period around August from 0 to 50 m depth (Kjellberg, 1981). If we assume an average nominal zooplankton diameter of 1.000 μm (biomass $\approx 10 \mu\text{g dw}$) we find a peak value of 120 mg.dw.m^{-3} . This is only about half the peak value simulated by the NORECO model.

Predictions of fish densities are only made with regression equations

and results for standing stock are shown in Figure 9. The equations reproduce the overall trends in the characteristics of fish densities in lakes of different eutrophy degree (cf. Colby et al., 1972; Welch, 1981), but confidence limits are large. (r^2 -values are in the range 0.5-0.8). The results from the two regression equations differ with a factor of about two and observations in Lake Mjøsa lie within regression limits. Observations of fish yield (4-7 kg.h year⁻¹) in Lake Mjøsa also lie within yield calculations based on equations given by Jones and Lee (1982), Adams et al. (1983) and Hanson and Legget (1982) (equations and results are given by Seip 1985).

There is not significant differences in fish density before or after dam construction.

In Figure 10 we have shown the results for economic and recreational impacts of river regulation. Water purification costs increases slightly with decreasing river flow. The differences between current and regulated flows are insignificant. It should be noted that increasing costs would occur stepwise, i.e. when new facilities must be constructed, and that the slight cost incurred rather should be interpreted as compensation for possible decreasing drinking water quality (Seip, 1985).

There is no change from an optimum value in recreational utility (fishing not included). Fishing value, however, decreases with increasing flow and there is a slight decrease (\approx 10%) in value with river regulations at low flow. Part of the change is caused by a low value on, and an increase in the proportion of, roughfish.

5. SENSITIVITY ANALYSIS

The confirmation of water quality models is difficult, because they are often complex and non-linear, and the systems studied often exhibit an apparent high noise to signal ratio. In the present effort we have compared the results of several models, one simulation model and several regression models. Thoman (1977, 1978) has shown that under certain conditions the two types of models can be put on the same mathematical form. In the present study we a) did simulations with several sets of parameter values, b) closely monitored plankton characteristics (eg. growth rate) and nutrient fluxes as the simulation proceeded, c) compared the results to regression equations and observations, and d) adopted two statistical measures, i.e. the relative error and t-statistics for comparison of simulated and observed results.

The sensitivity analysis were performed by substituting 7 of the parameters which describe algal growth with values 10% below or above the "best" value. It should be noted that 10% change have different effects on different parameters. During the simulation runs it was apparent that among the parameters chosen, changes in temperature optimum gave the greatest response. However, a 10% change in this parameter also gave a value outside of the reasonable range for expected values of this parameter. For each of the waterflow regimes before and after the 1. Otta dam construction we run simulations with 10 different parameter sets. The average total biomass varied with about 30% for each single waterflow regime. However, the difference in total biomass for present day and post construction regimes run with

the same parameter sets differed on the average only 3% (0-7%) for median and high flow and about 10% for low flow. This procedure is not statistically valid, but it is reasonable to conclude that the two flow regimes do not cause significantly different responses, except at low flow. Since our first choice of a 10% variation in parameter values caused some parameters to be outside a reasonable range, we decided to limit changes in parameter values describing temperature and light optimum and settling velocity to 5%. This procedure has been used to establish the "responseband" of Figure 6. It is seen that shifts in the timing of waterflow has an impact on the total biomass produced in the lake.

Monitoring of detailed processes like the modifications of growth and mortality by light, temperature and nutrient deficit showed a general agreement between anticipated and simulated results. Some of the processes were examined in more detail, and we here give as an example the simulation series for the study of diatom sinking rates. We know that sinking rate depends upon the growth condition of the algae. This dependence is formulated in eq. (2) of Table 4. By increasing the exponent S_{exp} the algae becomes increasingly susceptible to low growth rates (sinking rate increases). In Figure 11 is shown yearly average phytoplankton biomass as a function of the exponent S_{exp} for two different flow regimes. All curves show a strong increase in biomass when the sinking rate increases less than linearly with decreasing growth rate (For values $S_{exp} < 1.0$). However, the enhanced plankton values associated with the exceptional waterflow in 1981 prevail for all values of S_{exp} .

The simulation model NORECO and the regression equations give approximately the same relative increase in chl-a values with decreasing waterflow, although the absolute values for a given flow volume varies by a factor of 2-3. The regression models do not separate between different seasonal patterns of waterflow. Thus it is not possible to corroborate the simulation results for the particular flow pattern of 1981.

The two statistical measures used were not very successful. The relative error was quite insensitive to the different flows. The t-test gave percentage points of the t-distribution ranging from 0.2 (low flow volume, current condition) to 7.2 (high flow volume, current condition), but this information was clearly inferior in assessing goodness of fit compared to visual inspection of peak positions, relative heights of peaks, etc.

6. DISCUSSION AND CONCLUSION

Some of the discrepancies between observation results and observations will here be discussed in more detail. The simulation results for phytoplankton were compared to observations in Figure 4. The simulation results showed a nearly complete disappearance of plankton in September. This is in contrast to observations which only showed a decrease to about half the spring bloom value. The mechanisms governing plankton growth at that time were therefore examined in detail. Sinking of diatoms showed no sharp time gradients, but growth reduction caused by nutrient depletion and a concurrent increase in grazing pressure seemed to be responsible for the sharp decrease in simulated phytoplankton biomass. The reason why these factors tend to

dominate in the model more than in the lake may be that our description of the diatom functional group is not characteristic for the post bloom species. Those species tend to be more slow growing, require less nutrients and be more resistant to grazing because of larger size than the bloom species (Davies, 1982). However, we do not yet know enough about algal characteristics of Lake Mjøsa to warrant the inclusion of a new functional group of plankton.

The late start of the spring bloom may be caused by low initial concentration of nutrients in the upper layer. Unfortunately, we do not have measurements of phosphorus at simulation start, but have used best estimates.

The model predicts dominance of diatoms consistent with observations. However, since green and blue-green algae were nearly absent in the 1981 simulation and observation, we have here not got an adequate test of the model's ability to predict species succession. The application of the model to a Japanese lake indicated, however, that it would do so. (Seip and Satoh, 1984).

The simulation results for present day and post construction waterflows were different only at low flow conditions. Then the total biomass was $(10 \pm 0.4) \%$, ($n = 10$) higher than with present day flow conditions. It seems reasonable that differences in flow regimes are most pronounced when production is high, however, the basic shape of the flow curves are also different between low and high flow conditions as shown in Figure 3a.

Concurrent with the low level of phytoplankton we also get a low level of zooplankton biomass in September and also for the whole year average. The values are lower than those predicted by the regression equations and probably also lower than observations. We believe that this is because the simulated low phytoplankton values with much less than optimum growth can not support an adequate zooplankton biomass. (However, the specific grazing pressure on phytoplankton was still high).

The flow in 1981 (as was shown in Figure 3 a) had an annual flow volume close to the upper quartile flow of Figure 3 b. Normally such a high snow melt flow during spring will tend to dilute the nutrient and plankton content of the Lake Mjøsa waters and thus depress the spring phytoplankton blooming. However, in the year 1981 the spring flow came well in advance of stratification and thus did not contribute to the dilution and "wash out" of the spring bloom. This corresponds well with the observed bloom in 1981 which had a high peak value. It dramatically intercepted a decreasing trend in plankton peak values (max. values 1976 to 1983 were 3.3, 3.4, 2.5, 2.8, 1.7, 3.7, 2.4 and 1.4).

The 1981 simulation showed that the through-flow patterns this year gave higher total phytoplankton biomass than if the "average" flow pattern had occurred (cf. Figure 7). If dam construction can delay an early flow, this may in some instances prove to be advantageous.

Like the simulation results, the regression equations also give an increase in chl-a values with decreasing waterflow.

The increase is, however, lower for the simulation model than for the regression models (present day through-flow patterns). In contrast to the regression models which only use total volume of waterflow as

independent parameter, the simulation model also reflects flow patterns. The difference between the two results may therefore partly be explained by the shift in peak flow from June to July as flow volume decreases.

For a given flow volume the highest estimate is given by the Smith regression (4) and the lowest is given by the NORDIC regression (2). The difference between the estimates can often be "explained" by invoking common limnological parameters. For example, shallow lakes typically have additional inputs of nutrients from the sediments and thus support a proportionally higher crop than comparable deeper lakes. However, we do not yet know why the Holtan et al. (1979) regression give so much higher values than the NORDIC regression.

Regression equations for fish gave no significant changes in fish abundance, but a tendency towards less sports fish, and a lower value on recreational fishing with regulation of the river. The results for drinking water costs and recreational value of the lake did not change when the river was regulated.

The application of regression equations to zooplankton and fish is at the present rather speculative, as are the formulations for economic and social impacts. However, the equations are easily interpreted and the results can be compared to more qualitative assessments.

The reliability of the assessment of river regulation impact on chl-a concentrations in Lake Mjøsa is supported by the similarity of the results obtained for changes in annual average phytoplankton values with river flow volume and by the results for the 1981 simulation. It would, however, have been desirable to have a better correspondence between simulated and observed time series for the nutrients.

We have in the discussion above assumed that we can represent low and high flow conditions by average flows. The flow of 1981 showed that this in certain instances can be misleading. In future applications it may be a better approach to construct considerably more than three scenarios for flow-patterns following river regulation, assess their probability of occurrence, and then calculate the effect on lake parameters.

From the present simulation study we will conclude that regulation of the main river entering Lake Mjøsa potentially may have an impact on the lake ecosystem. However, the 1. Otta dam construction will only cause an increase in plankton at low flows. It may also have a slight favourable effect in particular years by delaying a very early spring flow.

TABLES

1. Key data for Lake Mjøsa
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TABLE 1.

Key data for Lake Mjøsa

Geographic position 61° N, 11° E	Theoretical retention time: approx. 6 years
Area 365.10^6 m^2	
Volume 56.10^9 m^3	Phosphorus load 1976: 393.10^3 kg or 1 g P/m^2
Max depth : 445m	Phosphorus concentration 19/5 1976: 5.10^{-6} OP/m^3
Mean depth: 153m	Mean water flow: $320^3 / \text{s}$
Length/width ratio: approx. 20	Max total biomass 1976: 4.10^{-3} kg/m^3
Average epilimnion depth: 30m	Stratified period: approx. June - November

TABLE 2.

Equations and parameters, general forms for nutrients and species

(1) Nutrients:

$$\dot{N} = -G_p \cdot P - G_B \cdot B + C \cdot OM$$

(2) Organic Matter:

$$\dot{OM} = D_p \cdot P + D_B \cdot B + [(1-g) \cdot G_z + D_z] \cdot Z - C \cdot OM + S_{OM}^+ - S_{OM}^-$$

(3) Phytoplankton:

$$\dot{P} = [G_p - D_p] \cdot P - G_z \cdot Z + S_p^+ - S_p^- - S_p^-$$

(4) Bacteria:

$$\dot{B} = [G_B - D_B] \cdot B - G_z \cdot Z + S_B^+ - S_B^-$$

(5) Zooplankton

$$\dot{Z} = [gG_z - D_z] \cdot Z + S_z^+ - S_z^-$$

Where N is nutrients: nitrogen and phosphorus available to plankton and bacteria

P is phytoplankton biomass, dry weight

B is bacteria biomass, dry weight

OM is organic matter, dry weight

(cont.)

- Z is zooplankton biomass, dry weight
- G_P, G_B are growth rates for phytoplankton and bacteria
- G_Z is grazing rate for zooplankton
- D_P, D_B, D_Z are mortality and respiration for phytoplankton, bacteria and zooplankton, respectively.
- S^+, S^- are terms for sources and sinks of nutrients and species in the water segment considered.
- g is the fraction of phytoplankton or bacteria biomass grazed by zooplankton, and used for growth

TABLE 3.

Details of model equations

Functions for phytoplankton growth and mortality:

$$(1) \quad G_p = r_0 \cdot R(g_1, g_2, \dots, g_n)$$

$$(2) \quad D_p = d_1 + d_2 + \dots + d_0$$

Modification of growth rate by abiotic factors

$$(3) \quad g_i = L[A_c, T_{i,1}, T_{i,2}, O_{i,1}, O_{i,2}]$$

Modification of growth rate by nutrient limitation

$$(4) \quad g_n = MM(N)$$

$$(5) \quad MM = \text{Michaelis-Menten form } (N - N_0) / (N_{MM} + (N - N_0))$$

$$(6) \quad LI = \text{Linear interpolation}$$

$$(7) \quad R = \min(g_i) \cdot \frac{1}{J-1} \sum_{i \neq i'}^J g_i \quad (i' \text{ corresponds to } \min(g_i), J = \text{no. of modifying factors})$$

$$(8) \quad d_i = \text{res}_i + \text{mort}_i$$

$$(9) \quad \text{res}_i = (k_1 \cdot T + k_2) \cdot W^{(k_3 \cdot T - k_4)}$$

$$(10) \quad \text{mort}_i = \frac{k_5}{5} T + \frac{k_6}{6}$$

(cont.)

where

r_0 is maximum growth rate

g_i are factors modifying growth rate

d_0 is a basic mortality rate, comparable to senescence

A_c is current value of abiotic factor

$T_{i,1}, T_{i,2}$ are threshold values of abiotic factor below and above which no growth occurs

$O_{i,1}, O_{i,2}$ are lower and upper bound for optimal growth

N is nutrient for species on next higher trophic level, eq. phosphorus for phytoplankton

N_0 is minimum threshold level below which no nutrient uptake occurs

N_{MM} is half saturation coefficient for growth

res_i are respiration rates

$mort_i$ are mortality rates

T is temperature

k_i are constants

TABLE 4.

Nutrients and phytoplankton input

$$(1) \quad S^+ = \sum_{i=1}^5 S_i^+$$

S_1^+ = e.N is input from external sources, like river inflow. Data are given as a time dependent rate. e is fraction of flow to upper and lower water segment, respectively

S_2^+ = N_{ex} is input from neighbouring water segments and is associated with an apparent diffusion or with horizontal water flows. The input parameters are computed from expressions for the effect of an eroding thermocline or for internal waves.

S_3^+ = N_{sett}/z input from water segment above. z is segment thickness.

S_4^+ = N_{rel} is input from sediments (nutrients only). It is either given as input or computed as a function of nutrient concentration in sediments and oxygen level

$$(2) \quad S_5^+ = - (S_{max} - S_{min}) \cdot R^{S_{exp}} + S_{max}$$

S_{min} , S_{max} is maximum and minimum sinking velocity, respectively

S_{exp} is an exponent

R is relative growth rate, or relative nutrient availability (relative to maximum values).

TABLE 5.

Values for selected phytoplankton parameters.
The value chosen depends upon an assessment of the values given
within the bracket values.

Parameter	Diatom	Greens	Blue-greens	Comments and references
Maximum				References, see text
growth rate				
- Bracket values (day ⁻¹)	0.5-2.0	1.3,3.0	0.25,1.3	
- value chosen (day ⁻¹)	0.9	2.5	0.7	
Half saturation constant for uptake of nutri- ents as a func- tion of external concentrations				Titman and Kilham (1976) Okeda and Sudo (1980) Holm and Armstrong (1981 a.b) and others, see text.
- bracket values (μ MP)	0.6-1.0	0.6-1.2	0.6-1.2	
- value chosen	0.8	0.9	0.9 ¹⁾	

Table 5 continued.

(cont.)

Parameter	Diatom	Greens	Blue-greens	Comments and references
Light response				
- low ($\mu\text{Em}^{-2}\text{s}^{-1}$)	0	0	0	Number of samples 4-6
value chosen	0	0	0	
- optimum plateau low limit				references, see text
($\mu\text{Em}^{-2}\text{s}^{-1}$)	87 ± 72	114 ± 42	78 ± 46	
value chosen	90	120	80	
optimum plateau - high limit				
($\mu\text{Em}^{-2}\text{s}^{-1}$)	395 ± 368	323 ± 74	67 ± 58	
value chosen	400	320	70	
- high threshold				
($\mu\text{Em}^{-2}\text{s}^{-1}$)	476 ± 487	>1280	266 ± 127	
value chosen	480	1300	270	
Temperature response				
- low ($^{\circ}\text{C}$)	$<6.9\pm 2.9$	4.3 ± 1.2	4.0 ± 1.0	number of samples 4-7
value chosen	7.0	5.0	3.0	
($^{\circ}\text{C}$)				references, see text
- optimum plateau low limit ($^{\circ}\text{C}$)	17.6 ± 4.6	24.8 ± 4.6	22.8 ± 3.5	
value chosen	18.0	25.0	23.0	
- optimum plateau high limit ($^{\circ}\text{C}$)	20.0 ± 4.1	27.4 ± 2.5	24.2 ± 3.8	
value chosen	22.0	28.0	24.0	
- high ($^{\circ}\text{C}$)	25.0 ± 4.0	29.7 ± 4.0	31.4 ± 2.3	
value chosen	25.0	30.0	32.0	

Table 5 continued.

(cont.)

Parameter	Diatom	Greens	Blue-greens	Comments and references
Respiration rate (% of individual biomass at 10 °C and 20 °C)	10-25	10-30	10-30	Ikeda and Motoda (1977) and others, see text
Mortality (% of individual biomass at 10 °C and 20 °C)	2-5	2-5	2-5	Ikeda and Motoda (1978) and others, see text
Sinking rates bracket values for growth phase (m.day ⁻¹)	0.08-0.67	-0.1-0.02	-0.1-0.0	Burnes and Rosa, (1980) Reynolds et al. (1976) Smayda, (1971, 1974), Tilman (1977)
values chosen	0.30	0.18	0.0	Fallon and Brock, (1980) De Pinto et al (1976)
Bracket values for no growth phase (m.day ⁻¹) bracket values (m.day ⁻¹) values chosen	0.24-1.87	0.2-0.9	0.3-0.4	
Overall net sinking rate for total P m-day ⁻¹	1.05	0.9	0.4	0.1, Thoman (1977) on esti- mated coefficient for Lake Ontario. 0.04, Scavia and Chapra (1977) for Lake Ontario

1) During some simulations, a half saturation constant of 0.45 was used to mimic a possible ability for the algae to move to nutrient rich water segments (Okeda et al 1981).

TABLE 6.

Values for selected parameters for zooplankton

Parameter	Small	Medium	Large	Comments
Size (gdw)	$2 \cdot 10^{-7}$ - $2 \cdot 10^{-6}$	$2 \cdot 10^{-6}$ - $2 \cdot 10^{-5}$	$>2 \cdot 10^{-5}$	Small zooplankton: rotifers, protozoans medium zooplankton: daphnia pulex, large zooplankton: post- naupliar copepods
spp no. (m^{-3}) (initial value)	800	80	8	
growth rate max (day^{-1})	1.0	0.6	≈ 0.3	12 h daily
grazing rate (day^{-1})	3.0	1.0	≈ 0.3	Based on Banse (1982) Carothers and Grant (1983) (large spp)
growth/ ingestion ratio %	30	30	30	1.3-4.0, Frost (1972)
Half-saturat- ion constant (gdw/m^3)	≈ 7	3	0.15	Fenchel 1980 (small spp) Lam and Frost (1966)
			0.15-0.30	Scavia and Eadie
			0.2-30	(1976) (large spp)

Table 6 continued.

(cont.)

Parameter	Small	Medium	Large	Comments
Threshold-value below which zooplankton ceases to graze (gdw/m ³)	0.2-7.0	0.2	0.08 0.03-0.38	Fenchel 1980 Scavia and Eadie (1976) (small spp)
Respiration-rate, % of individual biomass at 10 °C and 20 °C	20-60	12-44 ≈20	8-20	Ikeda and Motoda (1978) Borgman et al (1980)
Mortality rate, % of individual biomass at 10 °C and 30 °C		1-6		Ikeda and Motoda (1978)

* Carbon/biomass ratio ≈ 0.5

TABLE 7

Selected regression equations for ecological and chemical variables of lakes.

Equation	r	Independent variable X_i	Dependent variable Y	Type source data	Reference
$Y = \frac{X}{(1+\sqrt{\tau})}$		Annual average throughflow	average annual inlake TP		τ is eciptrocal of flushing rate OECD 1982
OECD-data (1) $Y=0.28.X^{0.96}$	0.88	annual average inlake TP mg.m^{-3}	annual average chlorophyll mg.m^{-3}	data exclude re-servoirs and nitrogen li-mited lakes, 77 lakes TP-8, 300 mg.m^{-3}	OECD 1982
Nordic-data (2) $Y=0.08.X^{1.27}$	0.93	annual average inlake TP mg.m^{-3}	annual average chlorophyll mg.m^{-3}	data exclude reservoirs and nitrogen limited lakes, 14 lakes TP-8, 160 mg.m^{-3}	OECD 1982
Shallow lakes and reservoirs (3) $Y = 0.52.X^{0.81}$	0.90	annual average inlake TP mg.m^{-3}	annual average chlorphyll mg.m^{-3}	20 lakes TP-5-290 mg.m^{-3}	OECD 1982

Equation	r	Independent variable X_i	Dependent variable y	Type source data	Reference
Phosphorus nitrogen data					
(4) $\log Y = 0.653 \log X_1 + 0.548 \log X_2 + 1.517$	0.76	growing season mean of $X_1 = TP$ $X = TN_2$ $mg.m^{-3}$	growing season average of chl a $mg.m^{-3}$	228 north latitude lakes ("all lakes") TP: 2, 1000	Smith (1982)
Norwegian lakes					
(5) $Y = 0.42.X-93$	0.94	annual average inlake TP	summer-half year chl a in epilimnion ⁽¹⁾	20 relatively large, deep east-norwegian lakes TP 4-11 $mg.m^{-3}$	Holtan et al (1979)
• zooplankton					
(6) $\log Y = 0.719 \log X + 1.01$	0.86	phyto-plankton biomass, dry weight, calculated values (eg from chl-a) $mg.m^{-3}$	crustacean zooplankton dry weight $mg.m^{-3}$	litterature data x- (300-60.10 ³ $mg.m^{-3}$) depth not given	McCauley and Kalff (1981)

Equation	r	Independent variable x_i	Dependent variable y	Type source data	Reference
(7) $\ln(\bar{y}+1) = 0.048.X + 2.003$	0.66	Carlsons trophic state index ⁽²⁾	zooplank- ton crust- acean rotifers ciliated protozoans, dry weight mg.m^{-3}	39 Florida lakes $1-120 \text{ mg.m}^{-3}$ annual mean chl a . $1-20\text{m}$ dephts	Bays and Crisman (1983)
Fish					
(8) $\ln(y) = 0.0425.x + 2.452$	0.42	Carlsons trophic state index (2) based om eq (1)	total fish kg.ha^{-1}	30 Florida lakes	Bays and Chrisman (1983)
(9) As above, but changes in X		Carlsons trophic state index (2) based on NORECO simulation result			
(10) $\log X = 0.708 \log X + 0.774$	0.75	average (year?) total phos- phorus epilimnetic value (mg.m^{-3})	total fish kg.ha^{-1}	14 lakes and ponds TP $10-500$ mg.m^{-3}	Hanson and Legget (1982)
(11) $\ln Y = 1.37.X + 131.3$	0.50	Carlsons trophic state index as in (8) above	% sport fish		Bays and Crisman (1983)

- (1) We assume that chl-a values are average for values over epilimnion, however, only in few cases is this stated explicitly. For Mjøsa the values are vertical averages over the upper 10 meters.
- (2) Carlsons trophic state index is calculated as $\log \text{TSI} = 6. - 3.32 \cdot \log(64.9/\text{TP})$ or $\log \text{TSI} = 6. - 332 \cdot \log(7.7/\text{chl a}^{0.68})$,
TP = total phosphorus.

TABLE 8.

Selected sociological and economic effects of lake eutrophication.

Equation	Independent variable	Dependent variable	Type source data	References
Secci disc depth (m) (1) $Y = 2.3 / (0.2 + 0.07 \cdot x)$	chl-a concentration in $\text{mg} \cdot \text{m}^{-3}$	secci-dic depth in m	Mjøsa data Literature data	Holtan et al (1980) Megaard et al 1980
Swimming (2) $Y = \text{LI}(X_1) \cdot \text{LI}(X_2)$	Linear inter- polation in graphs for x_1 : secci disc depth and x_2 : % blue- green-algae	Relative reduction in utility	Health authority regulations	
Drinking water purification (3) $Y = (k_1 \cdot \text{TSI} + k_2 \cdot \text{BGR} + 2.0) \cdot P$	TSI in Carlsons trophic state index, see note 2 of table 4 BGR is percen- tage blue-green alge, P is water use in person equi- valents $k_1 = 0.14$ $k_2 = 7.0$	Cost of water purification in NOK	Health authority regula- tions	Sleire (1980) Bergan personal communication

(cont)

Equation	Independent variable	Dependent variable	Type source data	References
Recreational fishing (4) $Y = \frac{FY.A.\sum k_i F_i}{\sum F_i}$	FY is fish yield; A is lake area; F_i is proportion of fish type i $k_1=100$ sports fish, $k_2=15-40$ for other fish	Value of recreational fishing	Fish yield estimates; Fish value estimates	Bays and Crisman (1983), Strand (1980)

FIGURES

- Fig. 1 Lake Mjøsa
- Fig. 2 Flow diagram for Lake Mjøsa ecosystem model.
- Fig. 3 Flow through river Lågen. a) Average flow 1920-1950. Median lower and upper quartile flow. Dashed lines indicate flow after completion of the 1. Otta dam construction project. b) Approximation to observations of flow used in the model. Shaded curve show the flow in 1981. Arrows indicate peak nutrient inputs.
- Fig. 4 Phytoplankton (dry weight) as a function of time in Lake Mjøsa 1981. Full line shows simulation results, broken line shows observations.
- Fig. 5 Available phosphorus as a function of time. Full lines show simulation results for concentrations in epilimnion and hypolimnion. Broken line shows observed concentration in upper 10 meter layer.
- Fig. 6 Phytoplankton (average dry weight) as a function of displacement (in days) of the 1981 water through-flow. Nutrient inputs, stratification and other external driving functions as in 1981. Shaded area corresponds to results after sensitivity analysis. (See text).
- Fig. 7 Phytoplankton (average summer chl.a) as a function of river flow volume. Results from five regression equations as given in Table 4 and from the simulation model NORECO.
Observed 1981
Simulated 1981
- Fig. 8 Zooplankton (average dry weight) as a function of river flow volume. Results from two regression equations as given in Table 4 and from the simulation model NORECO.
Observed 1981 (recalculated from observations of number of individuals).
Simulated 1981.
- Fig. 9 Fish (kg/ha) as a function of river flow volume.
Observed 1981.
Simulated 1981.
- Fig. 10 Recreation, water purifying costs and fish value as a function of river flow volume.
- Fig. 11 Phytoplankton (average summer dry weight values) as a function of sinking rate coefficient.

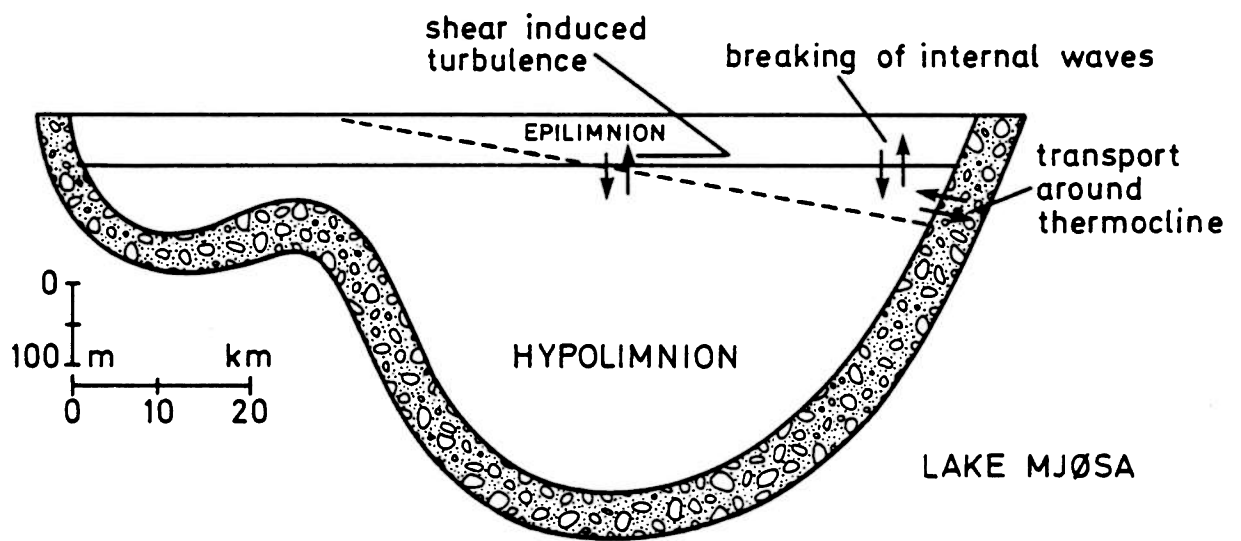


Fig 1

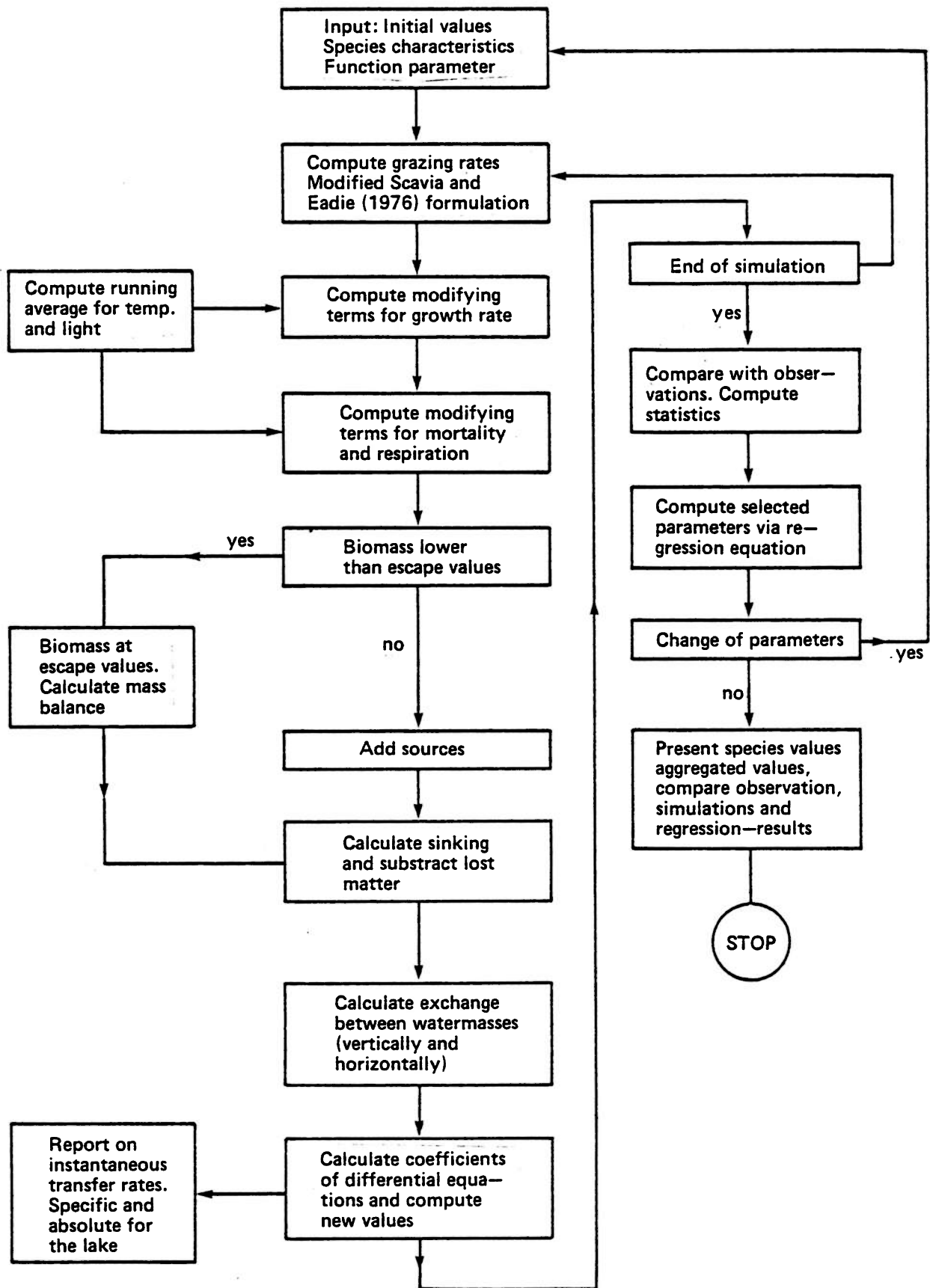


Fig 2

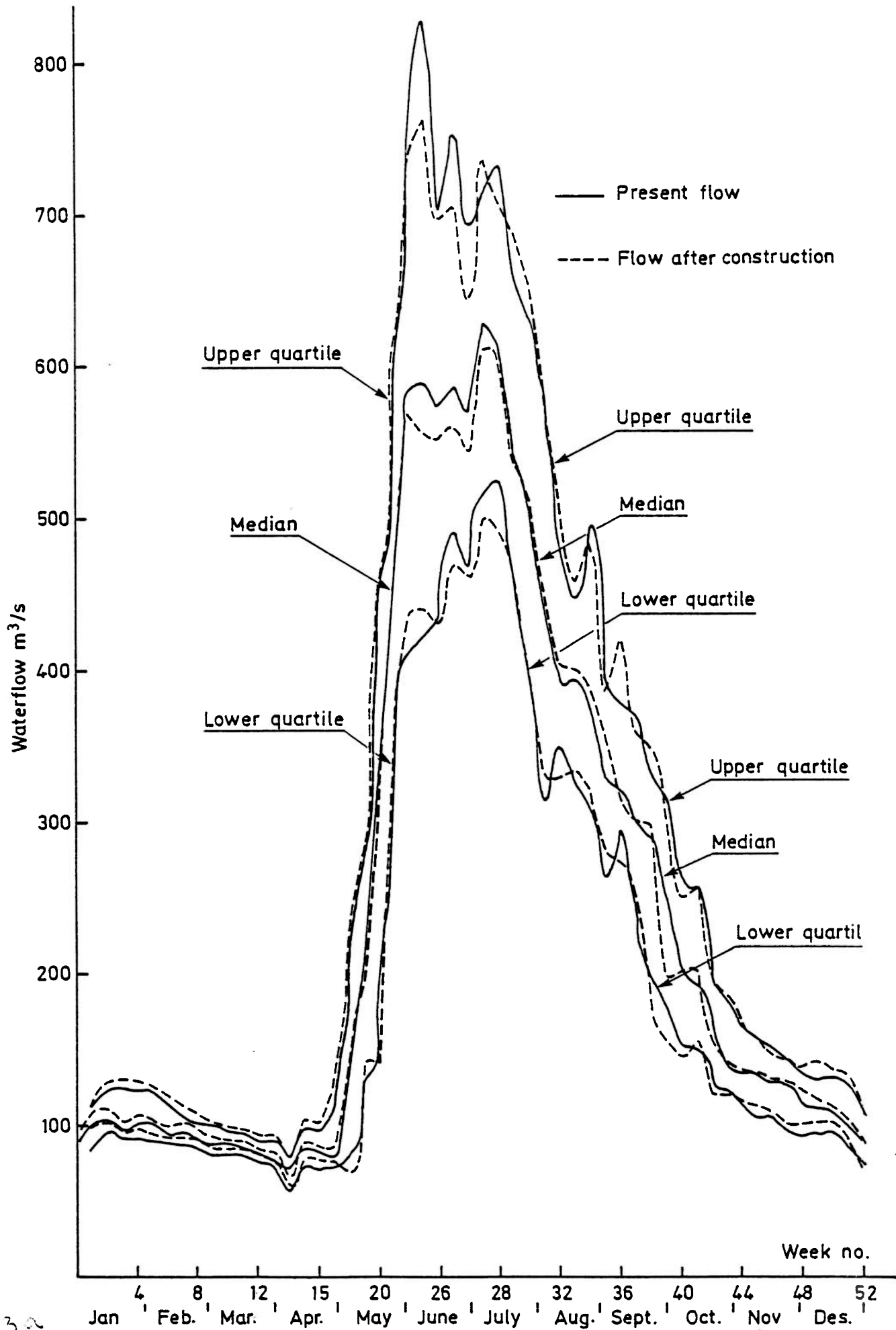
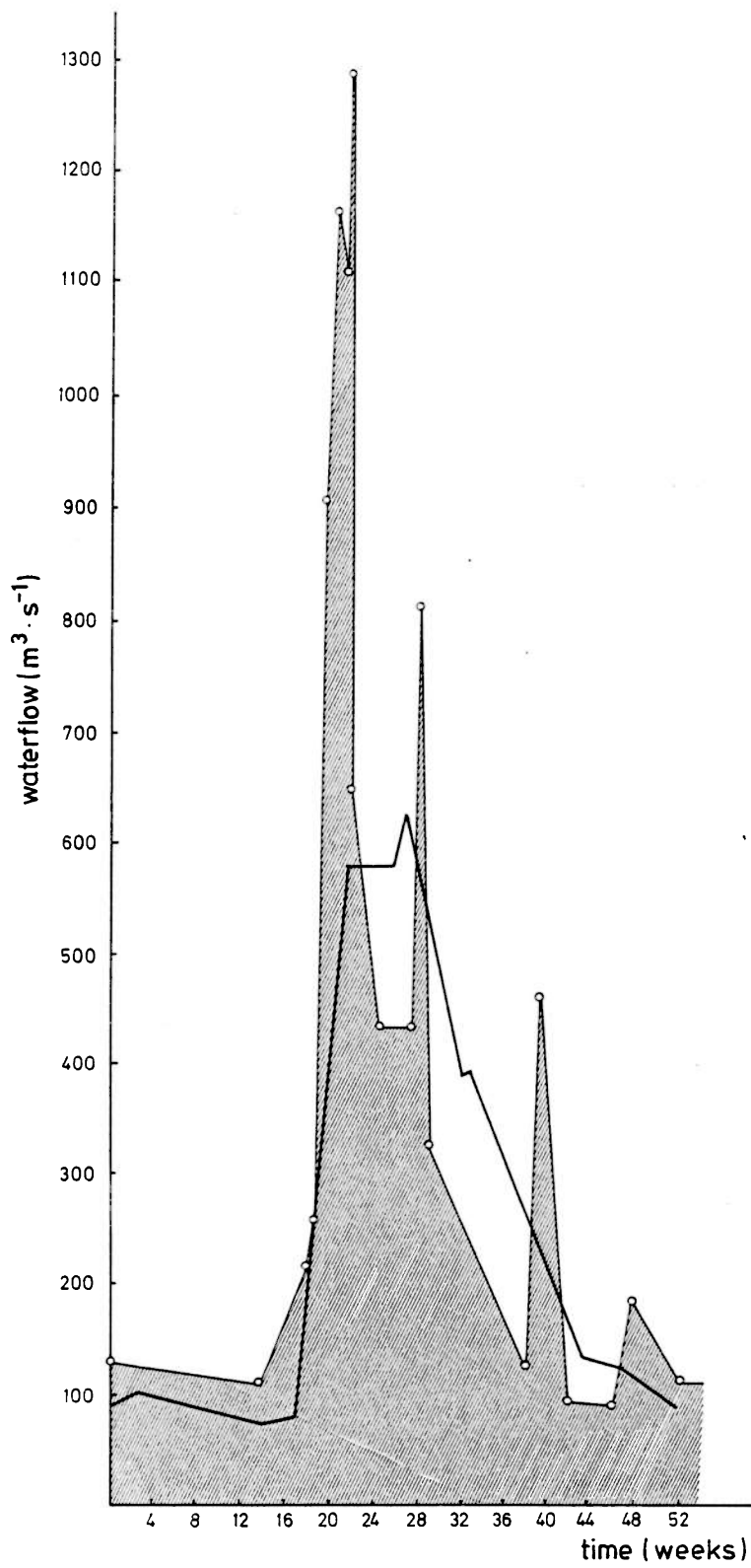


Fig 3 a



51-26

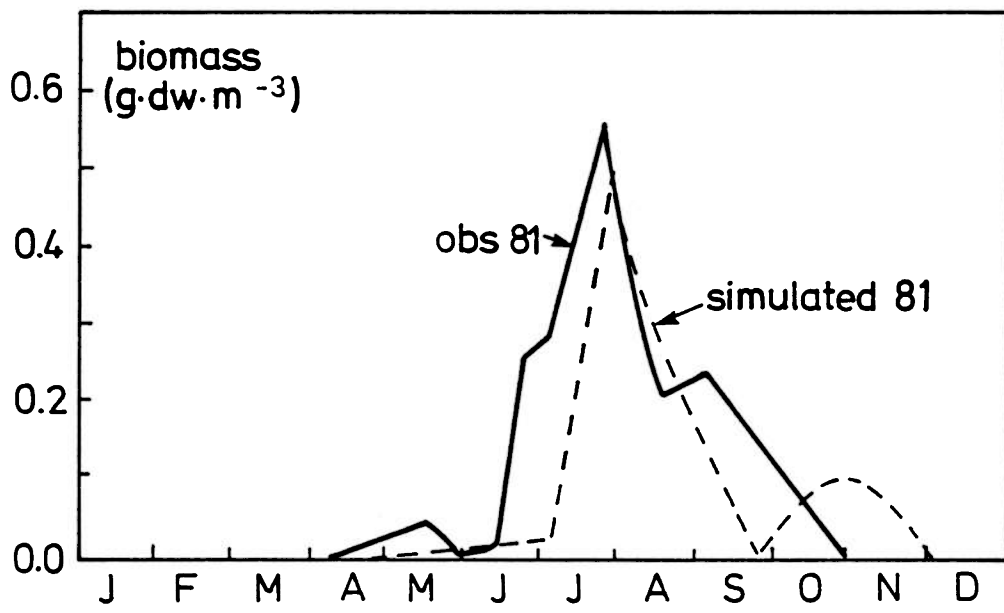


Fig 4

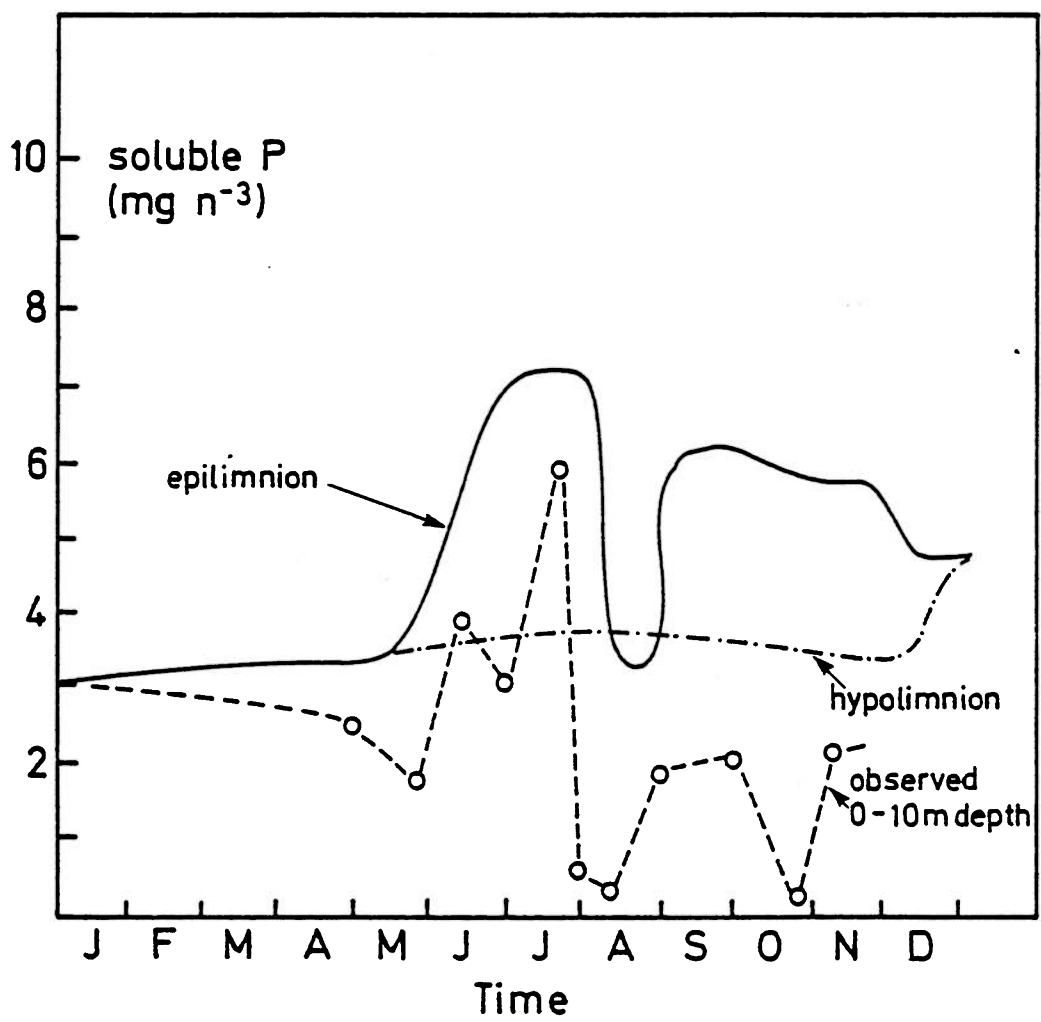


Fig 5

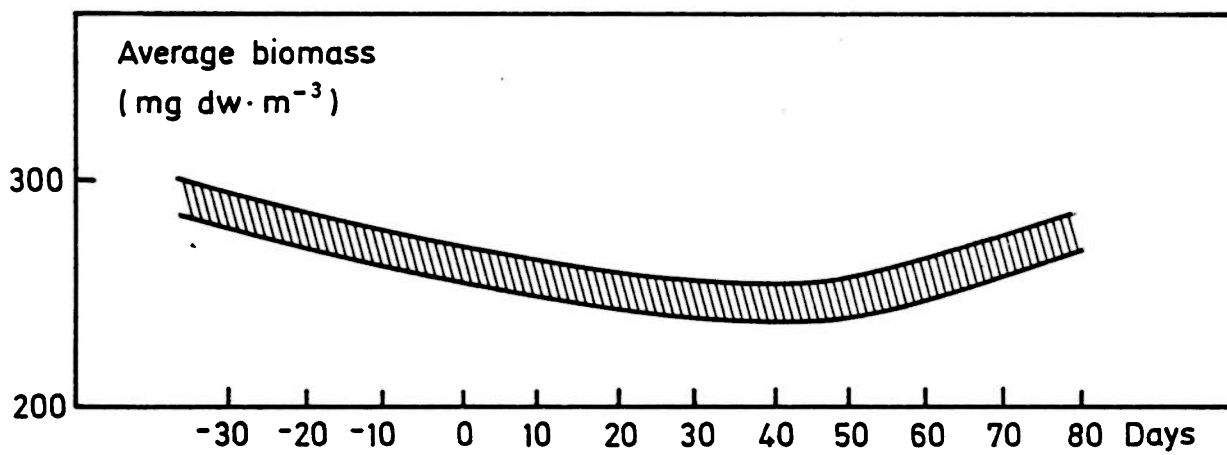


Fig 6

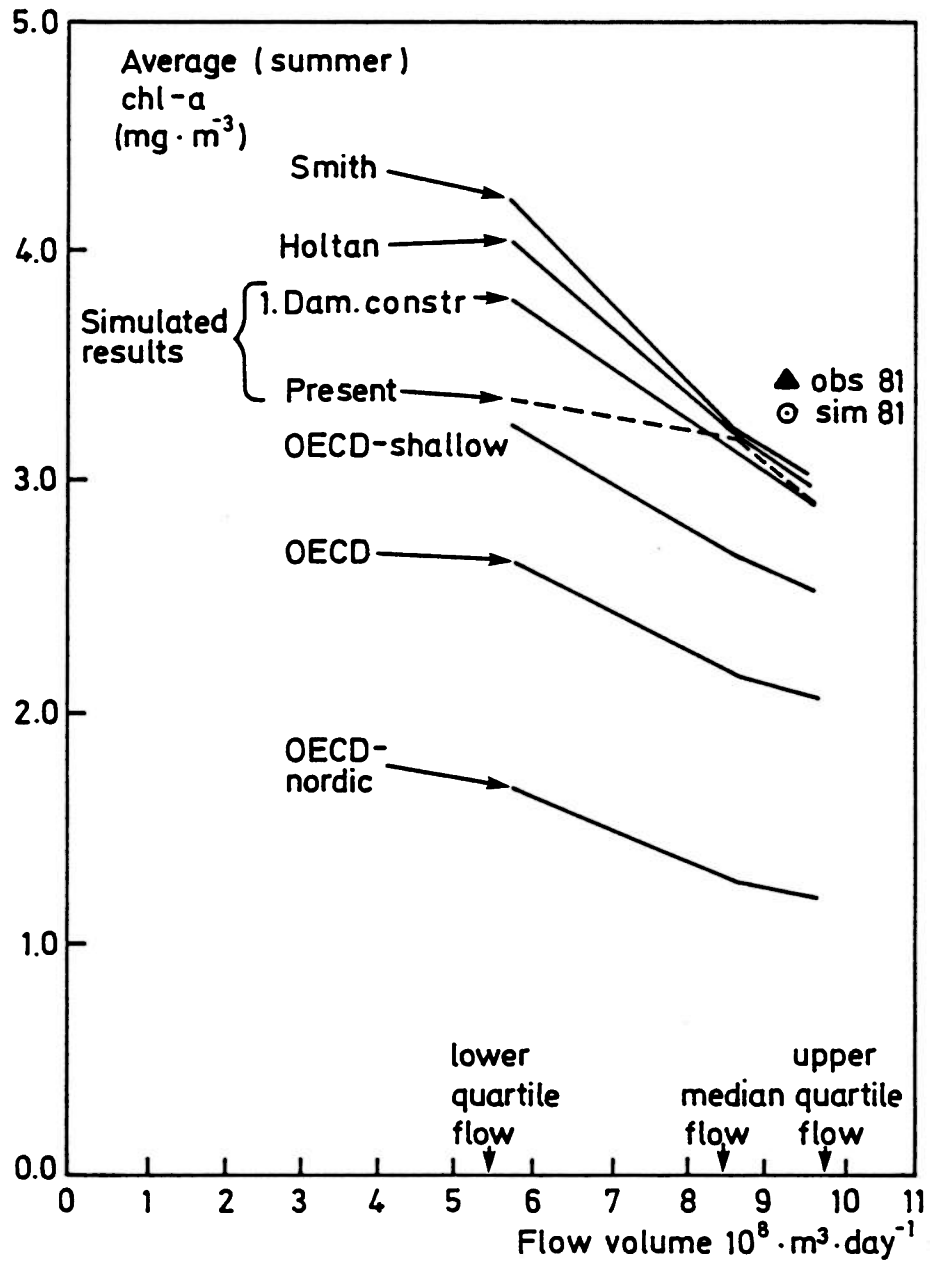


Fig 7

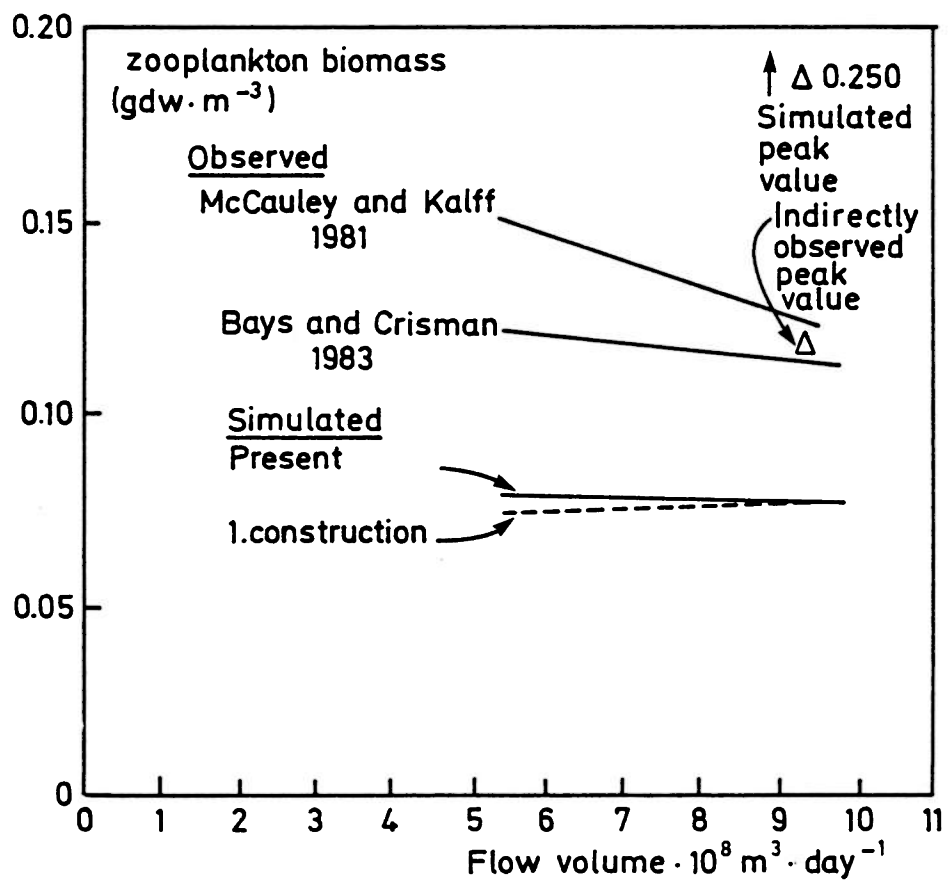


Fig 8

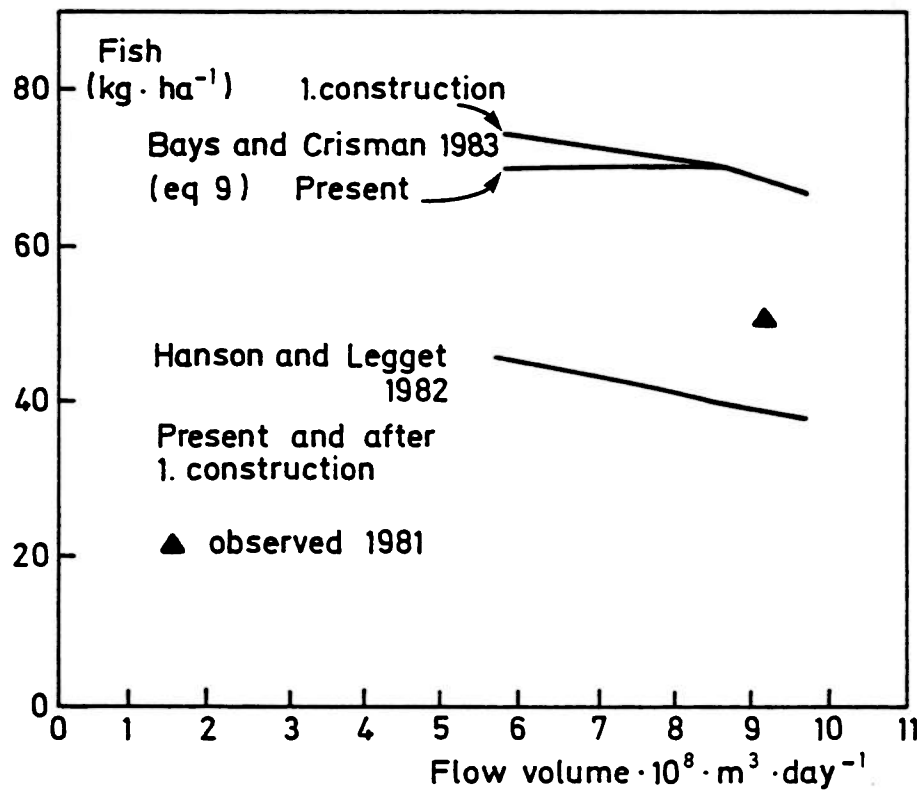


Fig 9

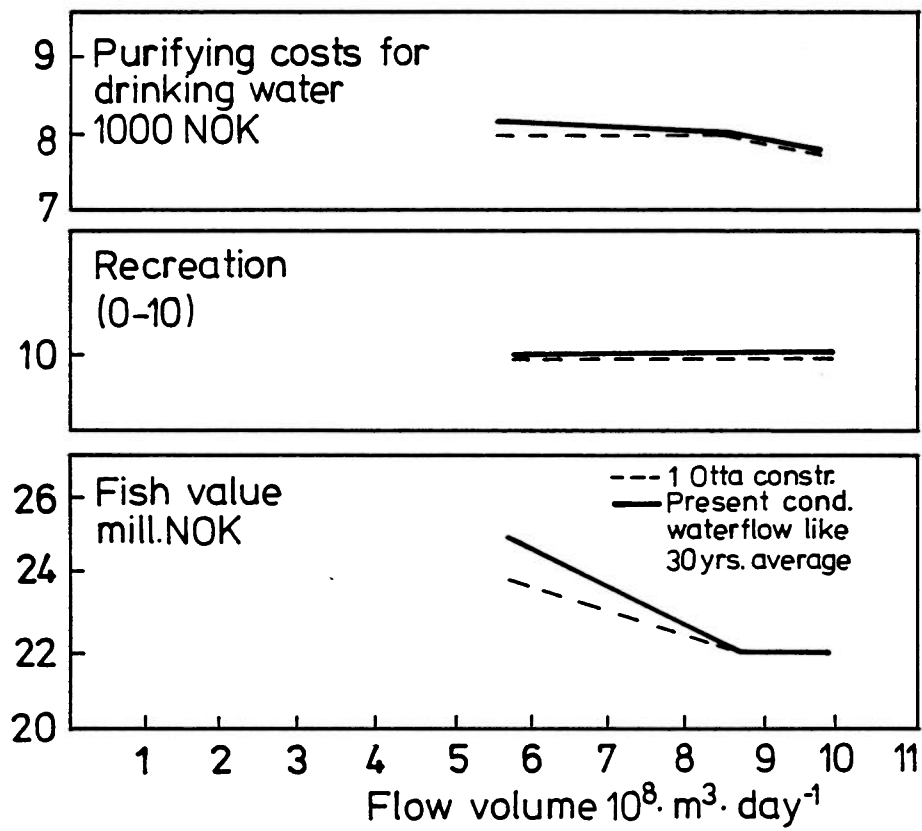


Fig 10

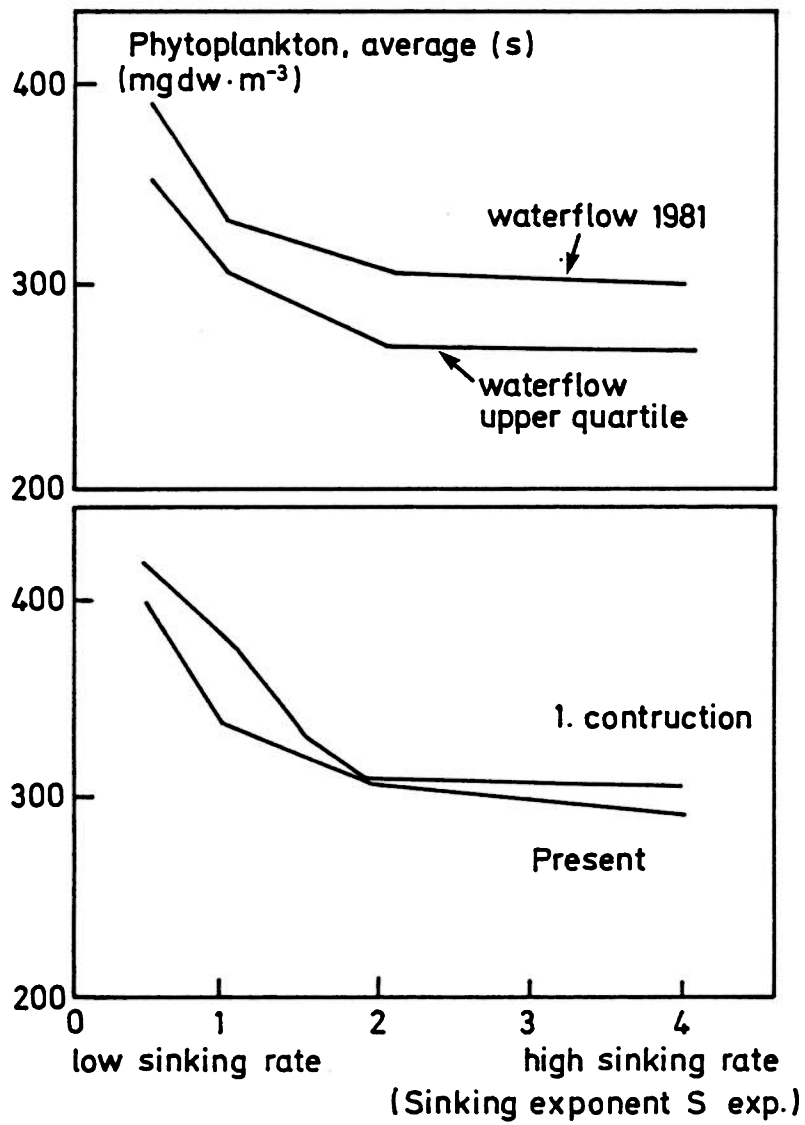


Fig 11

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