

LETTERS

Light limitation of nutrient-poor lake ecosystems

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Productivity denotes the rate of biomass synthesis in ecosystems and is a fundamental characteristic that frames ecosystem function and management. Limitation of productivity by nutrient availability is an established paradigm for lake ecosystems^{1–3}. Here, we assess the relevance of this paradigm for a majority of the world's small, nutrient-poor lakes, with different concentrations of coloured organic matter^{4,5}. By comparing small unproductive lakes along a water colour gradient, we show that coloured terrestrial organic matter controls the key process for new biomass synthesis (the benthic primary production) through its effects on light attenuation. We also show that this translates into effects on production and biomass of higher trophic levels (benthic invertebrates and fish). These results are inconsistent with the idea that nutrient supply primarily controls lake productivity, and we propose that a large share of the world's unproductive lakes, within natural variations of organic carbon and nutrient input, are limited by light and not by nutrients. We anticipate that our result will have implications for understanding lake ecosystem function and responses to environmental change. Catchment export of coloured organic matter is sensitive to short-term natural variability and long-term, large-scale changes, driven by climate and different anthropogenic influences^{6,7}. Consequently, changes in terrestrial carbon cycling will have pronounced effects on most lake ecosystems by mediating changes in light climate and productivity of lakes.

Nutrient limitation of productivity has been a cornerstone for the understanding of lake ecosystems. This paradigm predicts that increased input of nutrients increases production at the basic trophic level (phytoplankton), with concomitant effects on higher trophic levels. Accordingly, comparative data from oligotrophic to hyper-eutrophic lakes show an increase not only in phytoplankton production⁸ but also in top consumer (fish) biomass and yield with increasing total phosphorus^{9,10} (Fig. 1a).

The nutrient limitation paradigm is mainly based on studies of the pelagic habitat, not accounting for the fact that a substantial part of the resources supporting top consumers can be generated in the benthic habitat^{11,12}. Benthic algae, limited primarily by light availability, dominate whole-lake primary production in clear-water and shallow lakes⁸. Increased nutrient supply in such lakes increases phytoplankton biomass at the expense of benthic primary production⁸. Light penetration is controlled by phytoplankton light absorption, so an increase in pelagic production may compensate for loss of benthic production, and nutrients thus become a good predictor of whole-lake productivity. However, most natural lakes worldwide have low nutrient concentrations (Fig. 1a and Supplementary Table 3) and low phytoplankton biomass, and the variation in light penetration to the benthic habitat is mainly controlled by variation in input of coloured terrestrial organic matter¹³. There are no studies on the extent to which light absorption by terrestrial organic matter causes loss of benthic algal production or how this affects total lake productivity. For example, increased nutrient input associated with

terrestrial organic matter¹⁴ can stimulate phytoplankton production and compensate for losses in benthic primary production, although it has been suggested that light absorption by coloured organic matter may even depress pelagic primary production^{13,15}. Thus, it is not known to what extent variation in productivity at different trophic levels depends on nutrient availability or light availability in lake ecosystems with low input of nutrients.

As a first test of the applicability of the nutrient limitation concept on small unproductive lakes, we compiled literature data on the relationship between fish biomass and total phosphorus in oligotrophic and mesotrophic (total phosphorus, 0–30 $\mu\text{g l}^{-1}$) lakes in Finland, New Zealand and Sweden. In contrast to the situation in

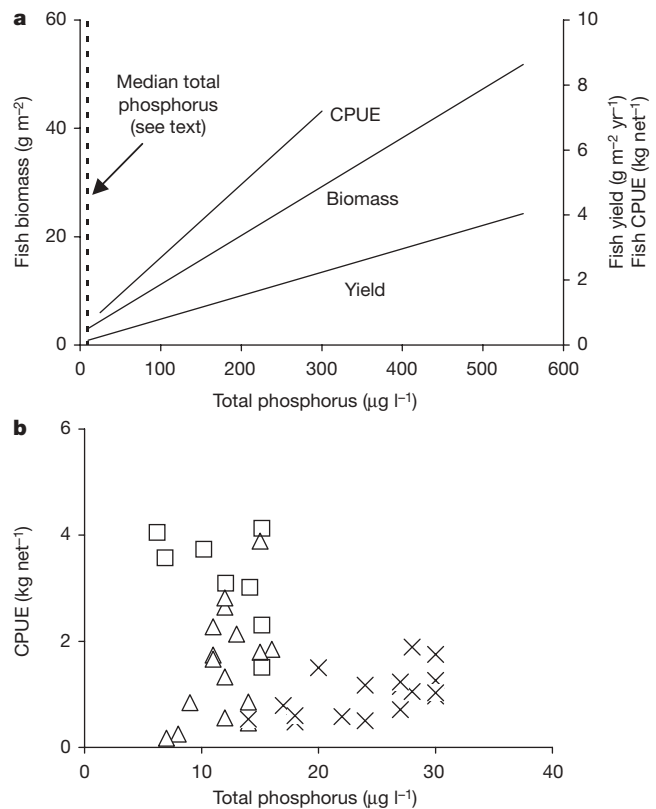


Figure 1 | Fish biomass and yield in temperate lakes. **a**, Published relationships ($r^2 = 0.75\text{--}0.84$) between fish biomass⁹, yield⁹ and catch per unit effort (CPUE)¹⁰. The vertical dashed line shows the average (12 $\mu\text{g l}^{-1}$) of reported median total phosphorus concentration in Norway (2 $\mu\text{g l}^{-1}$, $n = 1,006$), Finland (13 $\mu\text{g l}^{-1}$, $n = 873$), Sweden (8 $\mu\text{g l}^{-1}$, $n = 3,025$) and Wisconsin (United States) (12 $\mu\text{g l}^{-1}$, $n = 168$). **b**, Fish CPUE in oligotrophic and mesotrophic lakes (0–30 $\mu\text{g l}^{-1}$) from Finland (crosses), Sweden (triangles) and New Zealand (squares) as a function of total phosphorus. See Supplementary Tables 3 and 4.

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more nutrient-rich lakes (Fig. 1a), we found no relationship between fish biomass and total phosphorus (Fig. 1b), suggesting that factors other than nutrients determine the development of fish biomass in these ecosystems. To elucidate the roles of nutrients and light as limiting factors for the productivity of naturally nutrient-poor lakes in detail, we then carried out a detailed study in 12 lake ecosystems where we measured production of algae and bacteria, the biomass of intermediate consumers, and the biomass and production of top consumers (fish). On a global scale, the selection of lakes represents the most common lake types^{4,5} in terms of small size (area, 0.02–0.17 km²; mean depth, 2.6–6.0 m), low nutrient concentrations (total phosphorus, 4.1–24.0 µg l⁻¹; total nitrogen, 89–483 µg l⁻¹) and range in dissolved organic carbon (DOC) concentrations (2.4–16.8 mg l⁻¹) (Supplementary Table 1). The DOC concentration, representing conditions for lakes in a clear- to brown-water gradient, was strongly related to lake water colour ($r^2 = 0.96$, $P < 0.001$) and to the vertical light attenuation of photosynthetically active radiation (PAR; $r^2 = 0.97$, $P < 0.001$). Terrestrial organic matter, which dominated the DOC pool in these lakes¹⁶, thus had a strong negative influence on light penetration, and mean light irradiance of the whole-lake volumes (I_m), expressed as a fraction of surface light, varied between 0.05 and 0.57.

We measured the basal production of algae and bacteria (primary production and heterotrophic bacterial production based on terrestrial organic carbon) in benthic and pelagic habitats¹⁷. These processes represent mobilization of energy in the lake from external sources and form a base for production at all trophic levels^{13,18,19}. The production (mean \pm 1 s.d.) of benthic algae (86 ± 66 mg C m⁻² d⁻¹ (mg carbon per square metre per day)) showed high values and spanned a larger range between lakes compared to the production of phytoplankton (11 ± 8 mg C m⁻² d⁻¹) and heterotrophic bacteria based on terrestrial organic carbon in pelagic (23 ± 19 mg C m⁻² d⁻¹) and benthic (14 ± 14 mg C m⁻² d⁻¹) habitats in the lakes. The biomass of zoobenthos varied between 0.01 and 1.16 g m⁻² and was positively related ($r^2 = 0.49$, $P = 0.012$) to the benthic basal production. The biomass of zooplankton varied between 0.02 and 1.23 g m⁻² and was not related to pelagic basal production. All lakes had allopatric fish populations of either Arctic char (*Salvelinus alpinus*) or Eurasian perch (*Perca fluviatilis*), two of the most common top consumers in Arctic and boreal regions²⁰. From lake-specific, size-dependent growth functions and the size structure of the fish populations, we calculated the relative biomass production of fish to be between 30 and 565 g net⁻¹ yr⁻¹ in the lakes.

The whole-lake primary production ($r^2 = 0.81$, $P < 0.001$), basal production by algae and bacteria ($r^2 = 0.65$, $P = 0.001$) and production of top consumers ($r^2 = 0.59$, $P = 0.004$) was negatively related to total phosphorus in the lake water (Fig. 2). Therefore, factors other than nutrient supply controlled the biomass production in these lakes. The decrease in whole-lake basal production (from 234.8 down to 24.1 mg C m⁻² d⁻¹) with increasing nutrient content was related to the decrease in benthic primary production (from 195.8 down to 0.1 mg C m⁻² d⁻¹) along the gradient. Epipelagic algae, which dominate the basal production in clear lakes¹⁷, retrieve nutrients from the sediments, and their exploitation of these nutrients is mainly regulated by the light penetration to the sediment surface²¹. Accordingly, light attenuation and mean depth of the lakes explained 73% ($P < 0.001$) of the variability in whole-lake benthic primary production among the lakes. Increased production of phytoplankton and heterotrophic bacteria did not compensate for the loss of benthic primary production with decreasing light penetration, despite higher nutrient content in the more coloured lakes.

Analyses of stable carbon isotopes ($\delta^{13}\text{C}$) showed that the decrease in light and the consequent loss of benthic primary production also decreased the importance of this energy pathway for fish. The mean $\delta^{13}\text{C}$ of fish in the lakes ranged between -22.9% and -31.4% with higher values, similar to those of surface sediment and zoobenthos, in clear-water lakes and with lower values, more similar to those of

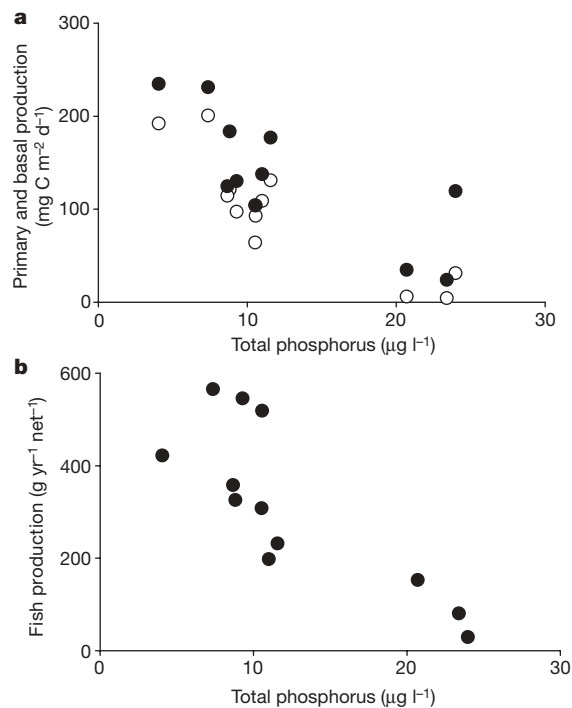


Figure 2 | Production as a function of nutrients. **a**, Whole-lake (benthic + pelagic) primary production (open circles) and basal production (filled circles, primary production plus bacterial production based on allochthonous organic carbon) as a function of total phosphorus. **b**, Whole-lake fish production as a function of total phosphorus. Solid line, error bars.

zooplankton, in humic lakes (Fig. 3a). The contribution of benthic algal carbon to fish biomass (F_{bent}) was estimated using a two-source mixing model, including the $\delta^{13}\text{C}$ of benthic (littoral zoobenthos) and pelagic (cladoceran zooplankton) energy sources, and showed that F_{bent} varied between 14% and 98% and was positively related ($r^2 = 0.86$, $P < 0.001$) to the mean light irradiance in the lakes (Fig. 3b).

The change in basal resource use by fish from benthic dominance in clear-water lakes to pelagic dominance in coloured humic lakes also affected the biomass production of fish. Fish production was positively related to benthic primary production ($r^2 = 0.49$, $P = 0.012$) and zoobenthos biomass ($r^2 = 0.45$, $P = 0.018$) in the lakes. Basal production by phytoplankton and heterotrophic bacteria did not correlate to fish production and did not significantly add to the explanation of fish production in the regression analysis (Supplementary Table 2). Furthermore, fish production was negatively related ($r^2 = 0.44$, $P = 0.019$) to zooplankton biomass in the lakes. Thus, an increase in fish resource use and growth on organic carbon generated in the pelagic habitat did not compensate for the loss of fish resource use and growth on autochthonous organic carbon generated in the benthic habitat. Consequently, we found that fish production was positively related ($r^2 = 0.63$, $P = 0.002$) to the annual light irradiance in the lakes (Fig. 4a), suggesting that light availability ultimately controlled fish production by its impact on benthic algal primary production.

We extended our analysis to include a larger data set (33 lakes in Sweden and Finland, Supplementary Table 4) to test the generality of our findings concerning the relationship between light irradiance and fish production. This analysis confirmed the fundamental light–fish relationship using annual light irradiance and fish biomass (Fig. 4b, all lakes: $r^2 = 0.52$, $P < 0.001$). Our results stress the crucial role of light availability in controlling not only basal but also top consumer production and biomass. Furthermore, our results show how interactions across ecosystem boundaries (that is, terrestrial organic matter controls lake productivity) and habitat boundaries (that is, exploitation of benthic and pelagic resources by top consumers) determine the

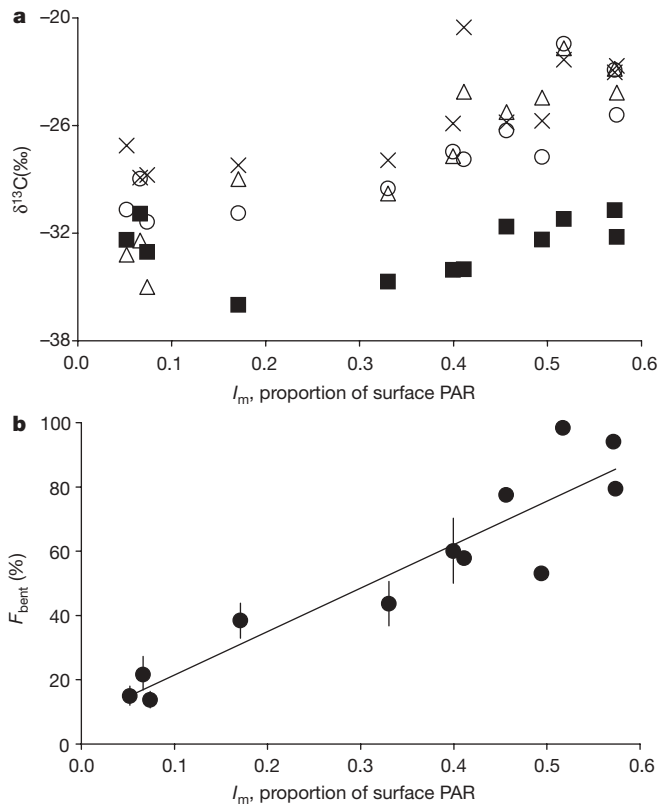


Figure 3 | Fish resource use. **a**, The mean $\delta^{13}\text{C}$ of fish (circles), shallow surface sediment (crosses), cladocerans zooplankton (squares) and chironomid zoobenthos (triangles) as a function of the mean light irradiance (I_m) in the lakes. **b**, Benthic contributions to fish body carbon (F_{bent}) as a function of I_m . The solid line describes the linear relationship between F_{bent} and I_m ($r^2 = 0.86$, $P < 0.001$). Error bars (s.d.) in the six lakes where littoral zoobenthos samples were not available for isotope analysis represent the uncertainty introduced by calculating F_{bent} using the range in $\delta^{13}\text{C}$ of littoral zoobenthos from other lakes.

production of lake ecosystems. The negative effect on lake productivity by terrestrial carbon also indicates that this carbon represents a repression of lake productivity rather than a subsidy.

We question the general value of the nutrient limitation paradigm for explaining and predicting the productivity of unproductive lake ecosystems. Undoubtedly, input of nutrients resulting, for example, from cultural eutrophication can stimulate pelagic biomass production of nutrient-poor lakes³. However, we show that changes in nutrient input do not necessarily result in increased total ecosystem productivity. Nutrients input in unproductive lakes is normally associated with terrestrial organic matter¹⁴, and the effects of terrestrial organic matter on light penetration and benthic (light-limited) photosynthesis override possible positive effects of nutrients on pelagic (nutrient-limited) production. We suggest that nutrient availability is a major controlling factor of lake productivity mainly in systems that are dominated by pelagic production (for example, eutrophic lakes or very deep oligotrophic lakes), whereas light availability determines the productivity in a majority of the world's unproductive lakes within natural variations of organic matter and nutrient input. The light climate of most unproductive lakes is a function of lake depth and, more importantly, of coloured organic matter input from the catchment. Catchment export of organic matter and related lake DOC concentrations in northern (temperate, boreal and subarctic) areas where most of the world's unproductive lakes are located varies within one to two orders of magnitude²². This variation is largely related to differences in catchment vegetation, air temperature and runoff²³. Consequently, spatial and temporal variation in lake productivity determined by light absorption of organic material, as

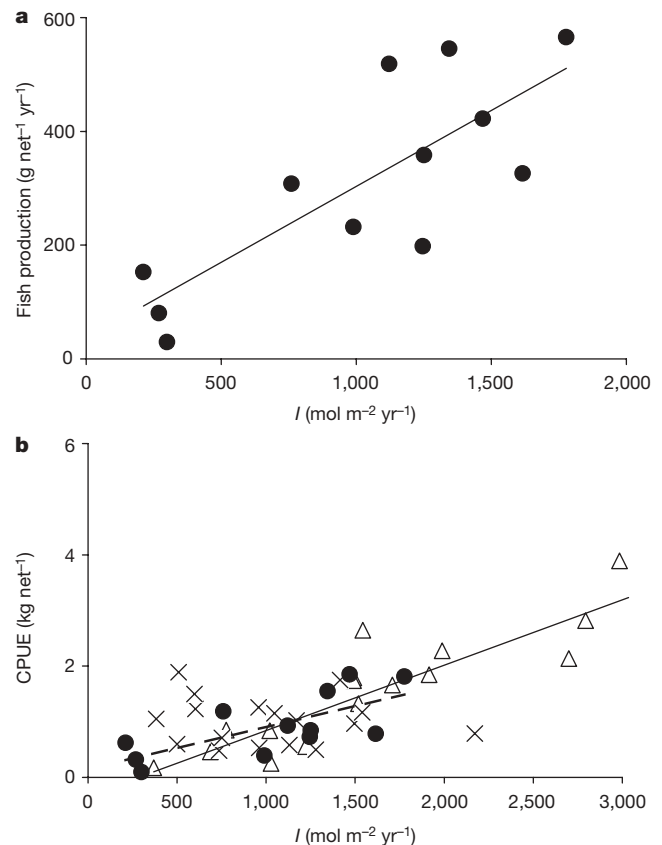


Figure 4 | Fish production and biomass as a function of light. **a**, Fish production as a function of the annual light climate (I , representing the mean PAR in the whole-lake volume during the ice-free period) in the 12 lakes ($r^2 = 0.63$, $P = 0.002$). **b**, Fish CPUE as a function of I in the 12 study lakes (circles, $r^2 = 0.50$, $P = 0.010$, dashed line) and in 33 additional lakes ($r^2 = 0.50$, $P < 0.001$, solid line) from Finland (crosses) and Sweden (triangles). There was no difference ($P = 0.76$) in the slope between the two regression lines. For references see Supplementary Table 4.

shown in this study, should be pronounced (Fig. 4) and also susceptible to changes in catchment carbon cycling induced by, for example, climate and land use change.

METHODS SUMMARY

We sampled 12 lakes in northern Sweden (64–68° N, 18–19° E) in midsummer. A composite water sample was collected and analysed for DOC, total nitrogen, total phosphorus and absorbance (440 nm)¹⁷. The vertical attenuation coefficient (K_d) was calculated from the slope of the linear regression of the natural logarithm of PAR versus depth. The mean light irradiance (I_m) in the lakes was calculated as the integrated light of the whole-lake volume, and expressed as a fraction of surface light (PAR at depth 0). Annual light irradiance in the lakes was calculated by multiplying I_m with surface PAR during the ice-free period.

Pelagic primary production was measured (five to eight depths, one occasion) using the ¹⁴C method. Benthic primary production was obtained (one occasion) from changes in dissolved inorganic carbon in water overlying sediment cores (six depths) or stones (one depth)¹⁷. Bacterial production was measured on composite water (pelagic) and sediment (benthic) samples, using the [³H]leucine method^{17,24}. Fish were sampled with multi-mesh gillnets in benthic and pelagic habitats (two to four per habitat). From length–age and weight–length relationships we derived size-dependent yearly growth rate functions for each lake. The fish production per net was calculated as the sum of individual yearly growth of all captured fish divided by number of gillnets used. Zooplankton was sampled (two to four occasions, three locations) using a plankton net, zoobenthos was sampled (one occasion, three locations) using an Ekman dredge, and the biomass was calculated using length–weight regressions^{25,26}. All data were converted to integrated whole-lake values using bathymetric data of the lakes¹⁷. We measured $\delta^{13}\text{C}$ of chironomids (two to five samples per lake), cladocerans (two to five samples per lake), surface sediment (five to eight samples per lake) and fish dorsal muscle (25–30 samples per lake) at the Department of Geology and Geochemistry, Stockholm University.

Full Methods and any associated references are available in the online version of the paper at www.nature.com/nature.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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METHODS

Calculations. Water colour was calculated from absorbance at 440 nm (ref. 27). The mean light irradiance of the whole-lake volume (I_m), that is, a dimensionless estimate that expresses the variation in light climate between lakes, was calculated as:

$$I_m = (1 - e^{-K_d \times Z_m}) / (K_d \times Z_m)$$

where K_d is the vertical attenuation coefficient and Z_m the mean depth of the lakes. The annual light irradiance (I) in the lakes was calculated as the product of I_m and the surface PAR during the ice-free period.

The contribution of benthic algae to fish (F_{bent}) was estimated using a two-source mixing model including the stable carbon isotopic signature of benthic ($\delta^{13}\text{C}_{\text{bent}}$) and pelagic ($\delta^{13}\text{C}_{\text{pel}}$) energy sources and a trophic fractionation factor (F) of 0.4‰ as:

$$F_{\text{bent}} = (\delta^{13}\text{C}_{\text{fish}} - F - \delta^{13}\text{C}_{\text{pel}}) / (\delta^{13}\text{C}_{\text{bent}} - \delta^{13}\text{C}_{\text{pel}})$$

Cladoceran zooplankton was used as the pelagic end-member¹⁶, and littoral zoobenthos (chironomids) was used as the benthic end-member¹². The model assumes that cladocerans and chironomid zooplankton are consumed directly by fish.

The littoral sediments were defined as the benthic habitat where primary production exceeded respiration (that is, net autotrophic with negligible respiration of external organic carbon). Littoral zoobenthos were obtained from six lakes and in the other lakes F_{bent} was calculated using the mean $\delta^{13}\text{C}$ of littoral zoobenthos from the other lakes (Supplementary Fig. 1). This introduced an uncertainty in calculated F_{bent} . The effect of variation in the $\delta^{13}\text{C}$ of the benthic end-member in these six lakes was tested by calculating F_{bent} using the range of $\delta^{13}\text{C}$ of the benthic end-member. The $\delta^{13}\text{C}$ are calculated as:

$$\delta^{13}\text{C} = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1,000$$

where $R = {}^{13}\text{C}/{}^{12}\text{C}$.

We calculated total new basal biomass production in both pelagic and benthic habitats as the sum of measured autotrophic production and calculated

heterotrophic bacterial production based on allochthonous organic carbon¹⁷. Bacterial production based on autochthonous organic carbon represents recycling of material and was not included in the measure of new basal biomass production. Total basal biomass production for the whole lake was obtained as the sum of benthic and pelagic production.

Literature data. Published relationships between total phosphorus and fish CPUE, biomass and yield were obtained from the literature. A summary of the literature data is given in Supplementary Table 3.

We also collected literature data on fish CPUE, total phosphorus and I . A selection of lakes was based on total phosphorus ($0\text{--}30\ \mu\text{g l}^{-1}$), standardized sampling of fish (multi-mesh nets) and data for calculating I . A summary of the literature data are given in Supplementary Table 4. CPUE was standardized based on net area and reported as kilograms per net ($30 \times 1.5\ \text{m}$) per night. The annual light irradiance in the lakes was calculated as above when possible. When not directly measured, K_d was estimated from data on lake water colour or Secchi depth using relationships between K_d and colour (this study) and between colour and Secchi depth²⁸. Surface PAR data for the published lakes were obtained from the STRÅNG model for solar radiation, derived from the Swedish Meteorological and Hydrological Institute, and were produced with support from the Swedish Radiation Protection Authority and the Swedish Environmental Agency. The length of the ice-free season, when not stated, was obtained from the literature²⁹.

Statistical analysis. Variables were log transformed to obtain normality. The data ($n = 12$) were analysed using least-squares linear regression, partial correlation (Pearson) and Akaike's information criterion corrected for small sample sizes³⁰. Slopes of linear regressions on the lakes from this study ($n = 12$) and from the literature ($n = 33$) in Fig. 4b were compared using a two-tailed t -test.

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