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Terrestrial organic matter input suppresses biomass production in lake ecosystems

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Abstract

Terrestrial ecosystems export large amounts of organic carbon (t-OC) but the net effect of this OC on the productivity of recipient aquatic ecosystems is largely unknown. In this study of boreal lakes we show that the relative contribution of t-OC to individual top consumer (fish) biomass production, and to most of their potential prey organisms, increased with the concentration of dissolved organic carbon (DOC; dominated by t-OC sources) in water. However, the biomass and production of top consumers decreased with increasing concentration of DOC, despite their substantial use (up to 60%) of t-OC. Thus, the results suggest that although t-OC supports individual consumer growth in lakes to a large extent, t-OC input suppresses rather than subsidizes population biomass production.

Keywords: Allochthonous organic matter, lake ecosystem, productivity, subsidy

Introduction

In most ecosystems the organic carbon (OC) supporting the production and biomass of consumers is traditionally assumed to be mainly generated via photosynthesis within the ecosystem's boundaries (i.e. autochthonous OC). However, many ecosystems receive considerable amount of allochthonous OC generated in adjacent ecosystems. There are many examples of consumers using OC from external ecosystems (Bartels et al. 2012) and this is typically viewed as a subsidy supporting higher consumer biomass than could be supported by autochthonous OC (Polis et al. 1997). Yet, OC input can have negative direct and/or indirect effects on local production, and the net effect on consumer populations (i.e. biomass production) has rarely been addressed for whole ecosystems (Marczak et al. 2007). Therefore, a central question is to establish the extent to which external OC acts as a true subsidy, increasing the productivity of recipient consumer populations (Polis et al. 1997).

In lake ecosystems, the amount of terrestrial OC (t-OC) imported from surrounding catchments (allochthonous OC) may be several orders of magnitude higher than the amount of autochthonous OC that is generated inside the lake (Algesten et al. 2004, Jansson et al. 2008). The potential of t-OC to support aquatic consumer growth was recognized early (Nauwerck 1963), but only recently have we started to understand and quantify its actual contribution to lake productivity (Jansson et al. 2007). Terrestrial OC clearly alters lake metabolism by supporting heterotrophic respiration, thus inducing net heterotrophic conditions (del Giorgio and Peters 1994). Moreover, a significant part of consumer biomass can be based on t-OC (Grey et al. 2001, Cole et al. 2011). Still, most studies of consumer growth supported by t-OC consider relative (allochthony, i.e. % contribution of t-OC sources) rather than absolute effects (i.e. productivity). Hence, the extent to which t-OC subsidizes population growth and overall biomass production in recipient lake ecosystems is still poorly understood.

Although input of t-OC introduces an extra energy source to be used by heterotrophs, several lines of data suggest that t-OC still does not act as a true subsidy for lake ecosystems (Karlsson et al. 2009, Jones et al. 2012, Kelly et al. 2014). First, available data suggests that t-OC decreases whole lake primary production by decreasing the availability of light and nutrients (Jones 1992, Carpenter et al. 1998, Ask et al. 2009, Thrane et al. 2014). In lakes with high input of t-OC a large part of the basal production consists of heterotrophic bacteria growing on the t-OC (Ask et al. 2009), but this may not compensate for the loss of autochthonous production in pelagic and benthic habitats (Jansson et al. 2003, Ask et al. 2009, Gudasz et al. 2012). Second, t-OC is a poor food resource for consumers at higher trophic levels due to its low quality and high respiratory losses during its transfer through the food chain (Hessen 1998, Berglund et al. 2007, Wenzel et al. 2012). Third, effects of t-OC on physical (e.g. light and temperature regimes) and chemical (e.g. oxygen) lake characteristics may have direct negative effects on consumer growth and their performance (Stasko et al.

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2012). For these reasons, increased use of t-OC resources by consumers may not fully compensate for the potential loss of autochthonous OC resources as a result of t-OC input to lakes.

In this paper, we present results from a comparative study of boreal lake ecosystems along a gradient in dissolved organic carbon (DOC) concentrations. Given the large dominance of allochthonous over autochthonous OC sources in the lake DOC pool of the study region (Karlsson 2007, Karlsson et al. 2012), we assume the DOC gradient represents a gradient in t-OC potentially available for consumers. To assess the net effect of t-OC on terrestrial resource use and biomass production of top consumers, we analyzed the stable isotopic composition of invertebrates in benthic and pelagic habitats and estimated biomass production of fish. We found that consumers used t-OC for growth, and that the relative contribution of t-OC to consumer growth generally increased with increasing DOC concentration in lakes. However, the net effect of t-OC was an inhibition rather than stimulation of top consumer biomass production.

Methods

Sampling and chemical analysis

We studied 13 boreal lakes located close to Umeå (63°49′32″N, 20°15′49″E) in northern Sweden. The lakes are in close proximity to one another (total area of approx. 200 km^2), implying that the lakes have more similar climatic conditions (e.g. insolation, air temperature and ice cover) compared to previous comparative studies of fish production in Sweden (Karlsson et al. 2009). The lakes are small (area: 1-5 ha, mean depth: 2.0-6.0 m) with catchments dominated by coniferous forest and mires. In ten of the lakes the fish community consisted of a single species, Eurasian perch (*Perca fluviatilis*), and in one lake perch coexisted with pike (*Esox lucius*). Perch was absent from the remaining two lakes that

contained a few individuals of brown trout (*Salmo trutta*). The lakes were sampled and analysed for: physical characteristics, water chemistry, stable isotopes of all relevant food web components, fish biomass (catch per unit effort (CPUE) in kg net^{-1}), and fish production (kg year^{-1} net^{-1}). Fish production estimates were only applied to lakes with allopatric perch populations. Similar to many other fish top consumers in fresh water lakes, perch are an ontogenetic omnivore feeding on zooplankton when small and thereafter shift to feed on benthic macroinvertebrates and prey fish as adults (Persson 1988). We therefore regard perch to be a representative model species to investigate general patterns in fish resource use and growth across lakes. Still, we acknowledge that results and conclusions may not be directly transferred to fish species restricted to more specialized habitats and diets such as obligate planktivores. The following stable isotopes were analysed: stable hydrogen isotopes (δ^2H) of end-members (aquatic, terrestrial and water), δ^2H and stable nitrogen isotopes (δ^{15}N) of pelagic (crustacean zooplankton) and benthic (macroinvertebrates) intermediate consumers, and δ^2H and δ^{15}N of perch. We used previously published data (Karlsson et al. 2009) on four lakes from which we did not have stable isotopic data of end-members or intermediate consumers. We used stored fish samples from these four lakes to obtain δ^2H of fish (not analyzed in Karlsson et al. 2009).

Water samples were collected from mid- epilimnion and hypolimnion in the middle of the lakes using a Ruttner sampler. Samples were taken every 2nd week during open water season (9 lakes) or once in mid-summer (4 lakes). Water samples were analysed for DOC, total phosphorus (TP) and total nitrogen (TN) concentration. Water was passed through a pre-ignited (400°C, 3 h) Whatman GF/F filter for determination of DOC. The filtrate was acidified and stored cold. DOC and TN were analyzed with an IL550 TOC/TN analyzer (Hach-Lange GmbH, Dusseldorf, Germany). TP was analyzed with the molybdenum blue method (Murphy and Riley 1962) using a JASCO V- 560 spectrophotometer (Easton, MD,

U.S.A.) after autoclaving the samples with potassium persulphate. Photosynthetically active radiation (PAR) was measured at every 0.5 m in the water column using a LI-193 Spherical Quantum Sensor (LI-COR Biosciences, Lincoln, U.S.A.). The vertical attenuation coefficient (K_d) was calculated from the slope of the linear regression of the natural logarithm of PAR versus depth. Bathymetric maps and estimates of maximum (Z_{max}) and mean (Z_{mean}) depths were determined from integrated GPS and echo sounding depth measurements (m52i, Lowrance, Tulsa, U.S.A.).

We sampled OC from the soil humus layer (3 replicates) of the dominant vegetation types (pine, spruce and/or mixed forest of deciduous and evergreen trees, mire) in the lake catchments to analyze δ^2H of allochthonous OC and collected periphyton from shallow water (0-0.5m, 3-6 occasions during the summer) to analyze δ^2H of the autochthonous OC. We did not collect phytoplankton for isotopic analysis due to the difficulty of physically separating phytoplankton from the particulate organic matter pool in these lakes (Karlsson et al. 2007). Periphyton are a suitable autochthonous δ^2H end-member (Karlsson et al. 2012) and the photosynthetic fractionation factor for periphyton in this study (159.8 ± 11.9‰; mean ± 1SD) is very similar to published fractionation factors for phytoplankton (160.9 ± 17.0‰, Wilkinson et al. 2013; 162.8 ± 26.1‰, Berggren et al. 2014). Crustacean zooplankton were sampled monthly (5 occasions) by vertically hauling a plankton net through the water column. The zooplankton were then stored in filtered lake water for gut evacuation for 12-24 h before separation of calanoid copepods (*Eudiaptomus* sp.) and cladocerans (*Cerodaphnia* sp*., Daphnia* sp., *Bosmina* sp.). Common zoobenthos (chironomids, trichoptera) were collected at three locations (1-2 m deep) on 3 occasions (early, mid and late summer) and were separated and washed with distilled water. Fish were sampled in August or September with standard survey multi-mesh gillnets (Nordic 12, 30 × 1.5 m, mesh sizes 5, 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43, 55 mm) in the littoral (1-3 m depth), profundal (5-8 m) and pelagic (surface)

habitats. In five lakes, 4 littoral, 4 profundal and 2 pelagic nets were set over night. In the

other six lakes, one or in some cases two multi-mesh survey nets were set in each habitat

(these lakes are subjected to long term studies on fish dynamics with restricted gillnetting

efforts every second year*)*. A potential problem with using CPUE data from gill nets as

measures of abundance is that catchability of fish may vary in time and across different

systems (Appelberg et al. 1995). To minimize this variation we focused on single species

system of perch, which have relative high catchabilities in gill nets, and on lakes of small size

and relatively similar morphometrics which at least minimize the risk that our results are

biased due to lake-specific and day-specific variation in catchability. Weight and length of all

captured fish were recorded and from a subsample of perch the operculum bones were

removed for age determination. Part of the dorsal muscle of fish representing a range of size

classes from 5 to 25 cm was used for isotopic analysis (n = 8-15 per lake). Water for δ^2H

analysis was filtered (0.2 μm) and stored in air-tight glass bottles without air bubbles until

analysis. Solid material for isotopic analysis was freeze dried or dried at 65ºC, homogenized

when necessary, and stored frozen until analysis.

   Analyses of δ^{15}N were carried out at University of California, Davis Stable Isotope

Facility, California, by measuring on a continuous-flow isotope ratio mass spectrometer (PDZ

Europa 20-20). Analyses of the δ^2H of non-exchangeable H were carried out at the Colorado

Plateau Stable Isotope Laboratory, Northern Arizona University. Organic matter samples and

standards were equilibrated with local water vapor to correct for exchangeable H. Analysis of

solid samples were carried out by pyrolysis and measurement of isotopic composition of H_2

gas using isotope ratio mass spectrometry. The δ^2H of water samples was analyzed by

headspace equilibration with H_2 gas and a platinum catalyst using isotope ratio mass

spectrometry. The data are expressed in per mil (‰) notation relative to Vienna Standard

Mean Ocean Water (VSMOW) for δ^2H and atmospheric nitrogen for δ^{15}N.

Calculations

Based on the standardized multi-mesh gill netting we estimated whole lake fish production
(kg yr^{-1} net^{-1}) and CPUE by weight (kg net^{-1}) for lakes with allopatric populations of perch
(i.e. we excluded 3 lakes). For each lake with we fitted a length at age function as:

$$\text{length} = a \times \text{age}^b \tag{1}$$

to obtained length at age data, where a and b are lake specific constants. From lake specific
weight-length relationships (based on all captured perch) and the length at age function, we
derived a weight dependent yearly specific growth rate function of perch for each lake as:

$$\text{specific growth rate (yr}^{-1}) = a \times e^{(-bw)} \tag{2}$$

where a and b are lake specific constants and w is the weight of an individual perch. Estimates
per net of fish production were then obtained as the sum of estimated individual yearly growth
in wet weight of all captured fish divided by number of gillnets used. Both production and
CPUE by weight of fish for the whole lake were estimated by accounting for the relative
volume of water for each habitat where netting was carried out. The profundal nets were
assumed to represent the total hypolimnetic volume and the pelagic nets were assumed to
represent the volume above the hypolimnion. The volume represented by the littoral nets was
calculated by subtracting the volume of the pelagic and profundal habitats from the total lake
volume. We compared the data on allochthony and production of perch with the concentration
of DOC. The concentrations of DOC, TP and TN are given as whole-lake, volume-weighted

values based on their respective concentrations in the epilimnion and hypolimnion and the associated water volumes of each.

We calculated the relative contribution of t-OC to consumer biomass (i.e. allochthony) using a mixing model including the δ^2H values of consumers ($\delta^2H_{consumer}$), allochthonous organic matter (δ^2H_{allo}), autochthonous organic matter (δ^2H_{auto}) and water (δ^2H_{water}) as:

$$\text{Allochthony} = 100 \times ((\delta^2H_{consumer} - \omega_{tot} \times \delta^2H_{water}) / (1-\omega_{tot}) - \delta^2H_{auto}) / (\delta^2H_{allo} - \delta^2H_{auto}) \quad (3)$$

The ω_{tot} is the total contribution of dietary water to consumer H and was calculated for each trophic level from the trophic level of the consumer (t) above that of primary producers and the dietary contribution (ω) to consumer H (0.173, Solomon et al. 2009) as:

$$\omega_{tot} = 1 - (1-\omega)^t \quad (4)$$

We assumed that cladocerans and zoobenthos occupy trophic position 2 (Karlsson et al. 2004, Karlsson and Byström 2005) and estimated the trophic position of other consumers (see Appendix A) as the difference in $\delta^{15}N$ with a trophic fractionation (ΔN) of 2.98‰ (Vanderklift and Ponsard 2003). We found no difference (p = 0.804) in δ^2H between soils of different vegetation types and therefore used a mean value (-142.7 ± 8.9‰, n = 45) of t-OC in all calculations of allochthony. For the 4 lakes where we did not have lake-specific data on δ^2H_{auto} and δ^2H_{water} we used a Monte-Carlo procedure (10,000 permutations) where we simulated random numbers of δ^2H_{auto} and δ^2H_{water} from a normal distribution of respective end-members from the other lakes. Based on all simulated end-members, we determined fish allochthony and report the mean and standard deviation for each lake. A few samples of calanoid zooplankton had allochthony <0% and these were set to 0%. We estimated the

uncertainty introduced by assumptions in the calculation of allochthony by varying ΔN (2.8-3.2, Vanderklift and Ponsard 2003) and ω (0.10-0.22, Cole et al. 2011) for consumers in all lakes (see Appendix A). All data are presented as seasonal mean values.

Results

The concentration of DOC varied from 7 to 22 mg L^{-1}, TP from 4 to 36 µg L^{-1} and TN from 277 to 499 µg L^{-1} among the studied lakes (Table 1). The K_d varied from 1.0 to 4.2 m^{-1} and was positively correlated ($r = 0.952$, $p < 0.001$) with the DOC concentration. There was a clear separation in δ^2H between allochthonous and autochthonous organic matter across lakes, where δ^2H of soil (-142.7 ± 8.9‰, mean ± 1 SD) was on average 99‰ higher compared to δ^2H of periphyton (-241.8 ± 11.6‰) (Appendix A). The δ^2H of water showed relatively small variation (-82.0 ± 5.1‰) between lakes. The δ^2H of consumers (Appendix A) was -201.3 ± 9.7‰ in calanoid zooplankton, -180.7 ± 10.1‰ in cladoceran zooplankton, -164.0 ± 11.4‰ in chironomids, -163.3 ± -9.8‰ in trichopterans and -153.0 ± 10.5‰ in fish (perch).

Allochthony in fish (perch) varied between 26 and 57% across lakes (Fig. 1A) and covered a similar (cladoceran zooplankton: 25 to 56%) or slightly lower (chironomids: 36 to 81%; trichopterans: 36 to 79%) range of allochthony as in intermediate consumers. In contrast, allochthony of calanoid copepods was low (0 to 15%) in all lakes. The allochthony of fish was positively related to K_d ($R^2 = 0.88$, $p < 0.001$) and DOC concentration ($R^2 = 0.86$, $p < 0.001$) but not related to Z_{mean} ($p = 0.119$). Absolute values of allochthony should be treated with caution due to assumptions in the calculations of diet water contribution (ω_{tot}) to consumer H. Although the uncertainty in allochthony is rather low for cladoceran zooplankton and zoobenthos, it is relatively high for consumers at higher trophic positions, and especially for fish top consumers (Appendix A). Negative values for allochthony when increasing ω_{tot}

suggest that such high ω_{tot} are unrealistic and that it is likely that the allochthony of

consumers are at least not large overestimates due to using low estimates of ω_{tot}.

Fish biomass production varied considerably between lakes (Fig. 1B) and was negatively

related to K_d ($R^2 = 0.77$, $p < 0.001$) and DOC concentration ($R^2 = 0.54$, $p < 0.05$) but not

related to Z_{mean} ($p = 0.134$). Notably, fish production was also negatively related to TP ($R^2 =$

0.59, $p < 0.01$) and TN ($R^2 = 0.73$, $p < 0.01$) concentrations (i.e. common predictors for lake

productivity). Fish CPUE was also negatively related to DOC ($R^2 = 0.57$, $p < 0.05$). These

results suggest that light conditions, largely determined by DOC mediated light attenuation,

are important for consumer biomass production. Clearly, the data show a contrasting pattern

in terrestrial resource use and biomass production of fish with changes in DOC and light, with

low allochthony and high production in clear, low-DOC lakes and high allochthony and low

production in dark, high-DOC lakes. Accordingly, there was a negative relationship ($R^2 =$

0.74, $p < 0.01$) between production and allochthony of fish top consumers across lakes (Fig.

1C). The relationship persisted ($p < 0.05$) when including a range of uncertainties ($\pm$ 1 SD

from Monte-Carlo simulations) in allochthony for the lakes with unknown end-member δ^2H

values. The combined data on both production and allochthony allowed us to also estimate

fish production based on t-OC only by multiplying allochthony with CPUE. The production

based on t-OC showed small differences between lakes (Fig. 1B), although this pattern should

be interpreted with caution due to uncertainty in allochthony of consumers.

Discussion

Fish top consumers used t-OC for biomass production and this use, in relation to individual

use of autochthonous OC, increased with lake DOC concentrations (dominated by t-OC

sources). Importantly, both fish standing stock (biomass) and production decreased with

increasing t-OC content in the lake water despite the use of t-OC by individual fish top

consumers and their invertebrate prey. Thus, increasing supply of an external OC resource does not necessarily result in an increased (i.e. subsidized) biomass production of top consumer communities, despite the extensive use of this resource by the consumers. These results emphasize the need to combine relative and absolute estimates of resource use and production to understand and predict the effects of external OC resources for overall lake production and their food webs.

The results further suggest that light absorption by colored organic matter is a major controlling factor for fish resource use and biomass production among the lakes. A previous comparative study along a latitudinal gradient showed major control of fish population biomass production by annual whole lake light conditions, which are a function of K_d, lake depth and the length of the ice-free season (Karlsson et al. 2009). By comparing lakes of similar morphometry in a single region, thereby largely excluding variation in ice cover duration and incoming solar radiation, this study shows the particular importance of K_d which alone explained most of the variability in fish production and allochthony across lakes. A previous comparative study of 4 temperate lakes also found increased allochthony of consumers with K_d in lakes (Solomon et al. 2011), but ours is the first study to combine data on terrestrial resource use and biomass production of fish top consumers. Our results reveal contrasting patterns across lakes with high allochthony and low fish CPUE and production in high DOC lakes and low allochthony and high CPUE and fish production in low DOC lakes.

A plausible explanation for this pattern may be lower resource production of autochthonous OC in high DOC lakes with poor light conditions. Theoretical, experimental and comparative studies suggest that increasing t-OC input (and thus decreasing light penetration) results in the loss of first benthic and then pelagic autotrophic production (Diehl et al. 2005, Ask et al. 2009, Jager and Diehl 2014, Thrane et al. 2014), and that eventually most of the basal production is instead carried out by heterotrophic bacterioplankton growing

on t-OC (Ask et al. 2009). This switch from autotrophic to heterotrophic dominance is important since it may actually result in both lower total basal production (Jansson et al. 2003, Gudasz et al. 2012) and lower transfer efficiency through the food web from basal trophic levels to top consumers (Hessen 1998, Berglund et al. 2007). Thus, a negative correlation between biomass production and allochthony and between biomass production and DOC appears logical.

However, the results also point to other factors not directly related to the absolute OC resource supply that may cause low fish biomass in lakes with high concentration of t-OC. Interestingly, the total fish production based on t-OC was similar or even higher in low vs. high DOC lakes (Fig. 1B). Further, although allochthony in individual fish generally increased with DOC, it never reached values more than around 60% despite very high DOC concentrations. Based on the comparative study of lakes we could only speculate on the mechanistic underpinning of these patterns. It is likely that autochthonous resources cannot be completely substituted by terrestrial based resources and that there is a maximum level of allochthony, as previously suggested (Karlsson et al. 2012) based on comparison of carbon fluxes and resource use in one of the high DOC lakes included in this study (Övre Björntjärn; DOC 21 mg L^{-1}). The reason may be that terrestrial particulate organic matter and heterotrophic bacteria, which channel t-OC to higher trophic levels, lack essential compounds that only could be supplied by an algae based diet (Volkman 2003, Wenzel et al. 2012). As a result, consumers in humic lakes may only be able to exploit a relatively small share of the t-OC resources, and consequently not grow well in comparison to consumers in clearer lakes where consumers potentially could use, not only the relatively high supply of autochthonous OC, but also a relatively large share of allochthonous OC resources. Another explanation is that effects of t-OC on fish performance decrease individual growth and population biomass via, for example, lower feeding efficiency in low light or restricted habitat use due to

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hypolimnetic anoxia (Stasko et al. 2012). Restricted use by fish of the hypolimnetic habitat during part of the summer period implies that fish do not have access to potential food resources in that habitat or to a lower temperature environment that could reduce metabolic costs and be beneficial during periods of strong resource limitation (Persson et al. 1996). Correspondingly, the lakes with high DOC concentrations in our study had no or very low CPUE of fish in the profundal zone (Appendix A). Irrespective of the underlying mechanisms, and their relative contribution to the patterns observed, the results suggest that DOC input constrains population biomass and production because a major part of total carbon resource could not be efficiently used for biomass production.

The results highlight the dual effects of t-OC input for consumer growth and biomass. On the one hand, use of t-OC in a specific lake is positive as it results in higher consumer biomass than would have been the case if growth was based on autochthonous OC only. This could be important not only in humic lakes but also in other lakes during occasions when autochthonous production is low, e.g. under ice or in spring (Grey et al. 2001). On the other hand, fish biomass based on both allochthonous and autochthonous OC is lower in humic lakes than in clear lakes where biomass production is based mainly on autochthonous OC. It should also be noted that, although we included a large range of DOC concentrations (7 to 22 mg L^{-1}), our study did not include extreme clear-water systems where it is likely that the effect of a moderate t-OC input on biomass production is less pronounced or even reversed (Finstad et al. 2014, Tanentzap et al. 2014, Seekell et al. 2015). Especially in shallow clear-water lakes, a moderate increase in t-OC may stimulate biomass production because the negative effects of lower light on primary production and fish performance can be small compared to the positive effects of more nutrients and OC resources.

Our results have large implications for the basic understanding of lake ecosystems and how these ecosystems respond to changes in t-OC input. We show that, with increasing DOC

concentration, the production of fish biomass decreases despite increased reliance of fish on t-OC. We suggest that input of t-OC does not subsidize, but rather decreases consumer population production across a large range of lake conditions, as has previously been suggested based on modelling habitat-specific production of intermediate consumers (Jones et al. 2012) and observed patterns in zooplankton (Kelly et al. 2014) and fish (Karlsson et al. 2009) production across lakes. Thus, changes in t-OC export in response to changes in climate and land use (Laudon et al. 2011, Schelker et al. 2012) are expected to have major effects on fish biomass and production in recipient lake ecosystems.

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Ecological Archives material

Habitat specific CPUE of perch, stable isotopic data of end-members and consumers, and uncertainty in calculations of allochthony of consumers.

Table 1. Physical, chemical and biological characteristics of the lakes including: lake mean depth (Z_{mean}), light attenuation (K_d), dissolved organic carbon (DOC), total phosphorus (TP), total nitrogen (TN), and fish species present. Where applicable, values are expressed as summer means (1 SD).

Lake	Z_{mean} (m)	K_d (m^{-1})	DOC (mg L^{-1})	TP ($\mu g\ L^{-1}$)	TN ($\mu g\ L^{-1}$)	Fish
Lake 6	2.0	1.0 (0.1)	7.0 (0.6)	9.6 (1.4)	302 (81)	Trout
Lake 5	3.7	1.3 (0.2)	7.5 (0.4)	16.7 (3.7)	384 (93	Trout
Rengårdstjärnen	2.6	1.1	8.0	4.1	277	Perch
Holmtjärn	3.1	1.9	9.5	10.5	354	Perch
Snottertjärn	2.0	1.1	10.1	7.4	336	Perch
Lake 4	4.5	2.5 (0.5)	10.8 (0.7)	36.1 (22.8)	387 (57)	Perch
Lake 3	2.2	2.2 (0.5)	11.7 (0.7)	13.0 (3.0)	395 (79)	Perch
Lilla Björntjärn	4.6	3	15.9	24.0	483	Perch
Lillsjöliden	2.8	3.2 (0.5)	17.0 (3.1)	26.3 (7.2)	469 (91)	Perch
Nedre Björntjärn	6.0	3.8 (0.4)	19.5 (1.8)	27.2 (2.9)	499 (110)	Perch
Övre Björntjärn	4.0	3.5 (0.5)	21.1 (4.2)	29.3 (9.9)	494 (103)	Perch
Stortjärn	2.7	4.2 (0.9)	21.9 (5.4)	18.8 (4.5)	484 (126)	Perch
Struptjärn	3.5	3.6 (0.7)	22.1 (3.9)	27.5 (5.9)	488 (73)	Perch, Pike

Figure legends

Figure 1. (A) Allochthony of consumers as a function of the DOC concentration in the lakes. (B) Fish catch per unit effort (CPUE, dotted line), fish biomass production (solid line) and fish biomass production based on allochthonous OC only (Prod-allo), as a function of the DOC concentration in the lakes. (C) Fish biomass production as a function of allochthony of the fish in the lakes. The error bars show the variability (± 1SD) in allochthony for the 4 lakes with missing end-members (see methods). Fish biomass and production are volume weighted (see methods).