

Can feeding of fish on terrestrial insects subsidize the nutrient pool of lakes?

Thomas Mehner,¹ Jan Ihlau,² Hendrik Dörner,³ and Franz Hölker

Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Department of Biology and Ecology of Fishes, Müggelseedamm 310, P.O. Box 850 119, D-12561 Berlin, Germany

Abstract

We estimated consumption and excretion rates of terrestrial-borne phosphorus by a population of the insect-feeding fish species bleak (*Alburnus alburnus*) in a 0.12-km² mesotrophic lake of the German lowlands. Fish abundance, growth rates, and diet composition were determined, and consumption and nutrient metabolism were calculated by a bioenergetics model. Mean bleak abundance was about 77,000 ind. km⁻². About 84% of bleak consumption consisted of terrestrial insects. Annual consumption of lake-external phosphorus (P) by bleak was 432 g, representing ~2.1% of the lake internal P-pool. Annual excretion of terrestrial-derived phosphorus by bleak was equivalent to ~11% of the mean epilimnetic SRP concentration. A substantial subsidy of lake nutrient pools by insectivorous fish is more likely in lakes <0.03 km² owing to the increasing perimeter-to-area ratio between donor and recipient habitats. Terrestrial nutrient subsidy by fish feeding may be important only in small oligotrophic lakes in forested areas.

It has only recently been acknowledged that aquatic habitats are tightly coupled, despite their rather isolated consideration in freshwater science (Schindler and Scheuerell 2002). Habitat coupling may occur by both passive transport processes and active habitat shifts of animals. Examples include longitudinal drift of fish prey in streams or migrations of fish between pelagic and littoral or benthic lake sites. Whereas in the first case, the recipient stream stretches are passively subsidized by their upstream parts (Wipfli and Gregovich 2002), in the latter case, active swimming of fish between the differing feeding and excretion habitats couple nutrient cycles in near- and off-shore sites (Brabrand et al. 1990; Vanni et al. 1997).

Habitat coupling may occur even across the system borders (Polis et al. 1997). Marine-derived nutrients from salmonid carcasses were found to subsidize the forests adjacent to the spawning rivers (Willson et al. 1998). Waterfowl transport nutrients from agricultural fields into roosting wetlands during diel feeding migrations (Kitchell et al. 1999). Terrestrial carbon in form of dissolved organic matter (DOM) subsidizes bacterioplankton and the upper trophic levels in small lakes (Pace et al. 2004). Another example for terrestrial-aquatic coupling is the direct subsidy of in-stream production by terrestrial-derived matter and nutrients in form of litterfall or insects living on plants (Gregory et al. 1991). Wipfli (1997) found that terrestrial insects were important

prey for juvenile salmonids and that a riparian overstory may increase salmonid abundance in Alaska streams. Nakano and Murakami (2001) described reciprocal prey fluxes between a stream and the adjacent forest, subsidizing both forest birds and stream fishes. Riparian lizards fed on terrestrial stages of aquatic insects (Sabo and Power 2002), and predatory spiders on river shores were subsidized by emerging aquatic insects (Henschel et al. 2001; Sanzone et al. 2003). However, except for an early study describing that massive swarms of ants may alter the ammonium concentration in a subalpine lake (Carlton and Goldman 1984), no study has dealt with the question whether a strong nutrient subsidy of aquatic food webs from invertebrates living in shoreline terrestrial habitats occurs also in lakes.

In the present study, we focused on a small mesotrophic lake (Großer Vätersee) in the German lowlands. The lake is situated in a rather remote area and is largely surrounded by mixed forest, which makes it comparable to those stream sites in which terrestrial subsidy of fish feeding was described. The dominant fish species in the lake are the zooplanktivorous roach (*Rutilus rutilus* (L.)) and small perch (*Perca fluviatilis* L.) (Kasprzak et al. 2000). A species that contributes less to total fish biomass is the small-sized bleak (*Alburnus alburnus* (L.)), a cyprinid fish frequently occurring in lowland European lakes (Mehner et al. 2005). Bleak lives in shoals close to the water surface and feed mainly on zooplankton (Chappaz et al. 1998) and also frequently take insects from the surface (Biro and Musko 1995). This particular insect-feeding behavior is relatively unique among those fish species that live in central Europe. However, there is only limited information available on bleak population densities and ecology in lakes.

By determining fish abundances and diet composition in Lake Großer Vätersee, we estimated the population size of bleak relative to those of the other species, and evaluated the contribution of terrestrial prey to the diet of the dominant fish species. Furthermore, annual consumption rates of the fish populations were calculated. Because fish excrete phosphorus in a form readily available to phytoplankton (Brabrand et al. 1990), phosphorus balances for consumption and

¹ Corresponding author (mehner@igb-berlin.de).

² Present address: Institut für systematische Zoologie, Museum für Naturkunde, Humboldt-Universität, Invalidenstraße 43, D-10115 Berlin, Germany.

³ Present address: European Commission, Joint Research Centre, IPSC-AGRIFISH Unit, TP 266 I-21020, Ispra, Italy.

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excretion were estimated. Potential subsidy of terrestrial invertebrates to the lake was modeled by an exponential decay equation based on published insect flux and decay rates. We aimed to explore (1) whether the phosphorus supplied by terrestrial production and the excreted part of it after fish digestion can make up a substantial contribution to the lake's nutrient pool, (2) how the terrestrial subsidy might change the ecological interactions between the fishes, and (3) how the lake size and trophic state influence the maximum population size of bleak supported by the terrestrial subsidy.

Material and methods

The study was conducted in the mesotrophic Lake Großer Vätersee (0.121 km²; maximum depth, 11.5 m; mean depth, 5.2 m; volume, 633,000 m³) (for more details, see Kasprzak et al. 2000), situated in the Baltic lake region of northeast Germany, ~80 km north of Berlin. The lake is of glacial origin, has no surface in- or outflows, and is mainly surrounded by mixed or coniferous forest. The littoral zone is partly covered with macrophytes.

Fish community composition was analyzed by gill netting in both littoral and pelagic habitats during both day and night in approximately monthly intervals between April and October 2001 and 2002. Six mesh sizes (8, 10, 12, 14, 16, and 18 mm knot to knot) were used, which caught fish between 5.7 and 20.2 cm total length (TL; thus excluding the 0+ age groups). In total, fish catches from 28 fleets of gill nets were standardized (catch per unit effort [CPUE] number of fish per 100 m² net per hour) and averaged to derive relative numerical species proportions in the lake. Areal bleak density was calculated from the CPUE proportions in the gill nets in comparison to the lakewide abundance estimate of the roach population obtained by a multiple mark-recapture experiment in 2002 (216,100 ± 60,300 [95% confidence intervals, 95% CI] roach km⁻²) (H. Dörner unpubl. data).

In addition, bleak abundance was directly determined by 18 nightly hauls with a pelagic purse seine (length, 50 m; depth, 5 m; mesh size, 6 mm; area covered, 198 m²) between August and October 2002. Age group-specific bleak abundances and 95% CIs were calculated. Because the juvenile age groups 0+ and 1+ of bleak were not retained by the purse seine, an estimate of the juvenile fish abundance was obtained by extrapolating the annual mortality of the older age groups toward the juveniles (i.e., by calculating a negative linear regression between the logarithmic abundances and age).

Diet composition of fish was based on the catches with the gill nets. After measuring TL (nearest 1 mm) and fresh weight (fwt; 0.1 g) of all fish caught, digestive tracts were dissected and stored on ice immediately (2002) or preserved in 4% formaldehyde solution (2001). In the laboratory, diet components were counted and measured in six categories, namely, cladocerans (*Daphnia* spp., *Bosmina* spp.), copepods (*Cyclops* spp., *Eudiaptomus graciloides*), *Leptodora kindtii*, benthic diet (mainly chironomid larvae and pupae), fish, and terrestrial winged insects. Zooplankton biomass was reconstructed by length-weight regressions (Mehner et al. 1995). Chironomids were assumed to weigh 0.1117 mg

fwt per individual (Smit et al. 1993) because accurate length measurements were impossible owing to strong destruction of chironomids by the pharyngeal bones of the cyprinids. The same problem occurred with most of the terrestrial insects, such that only a few undestroyed winged insects could be measured. All of them were clearly identified as originating from the terrestrial environment (Lepidoptera, Coleoptera, Hymenoptera). Their average length was ~5 mm, which was converted into ~3.3 mg fwt per insect by general length-weight regressions for terrestrial insects (Sample et al. 1993).

Calculation of fish consumption and phosphorus metabolism followed the general bioenergetics model provided in computerized form by Hanson et al. (1997). Because a data set parameterized for bleak was not yet available, singular literature data for bleak were converted into the required physiological parameter design for consumption, respiration, egestion, and excretion (Table 1). The only nonbleak parameter that had to be taken from a study on the closely related roach was the increase of maximum consumption over temperature (*CQ*) (Hölker and Haertel 2004). Because bleak consumption estimates never exceeded 26.5% of the maximum rate, there was a low influence of this parameter on consumption estimates, that is, a 10% deviation in *CQ* caused only a negligible change in consumption (<0.1%) (F. Hölker unpubl. data). Variables for phosphorus metabolism followed the standard recommendations of Hanson et al. (1997) (Table 1).

Energetic densities of prey were taken from published studies with 2,650 J g fwt⁻¹ in zooplankton, 3,500 J g fwt⁻¹ for benthic diet, and 3,180 J g fwt⁻¹ for insects (Cummins and Wuycheck 1971). The average energy content used for bleak (6,510 J g fwt⁻¹) was based on 310 fish from four different waters in the same geographical area (Schreckenbach et al. 2001). Phosphorus concentrations used were 0.68% fwt for bleak, 0.20% fwt for chironomids, and 0.15% fwt for zooplankton (Hanson et al. 1997; Schreckenbach et al. 2001), whereas 0.30% fwt was calculated for terrestrial insects based on a water content in fwt of 65% and the average phosphorus content in dry weight (0.857%) provided for 27 terrestrial insect species by Elser et al. (2000, supplementary material). Water temperatures were obtained by fortnightly measurements in 1-m-depth intervals in the lake over the entire years 2001 and 2002. Water samples to determine nutrient concentrations were taken with a vertical tube integrated sampler (1-m length, 4-liter volume) in 1-m steps from the surface to the bottom simultaneously to the temperature measurements. Water samples were transported in cool environment and nutrients determination started 2 h after sampling at the latest. Dissolved substances were analyzed in subsamples filtered through 0.45- μ m membrane filters. Soluble reactive phosphorus (SRP) and total phosphorus (TP, disintegrated with H₂O₂ and H₂SO₄ at 150°C for 10 h) were spectrophotometrically determined with molybdate sulfuric acid and ascorbic acid at 680 nm (Varian Cary 1E).

Because the bioenergetics model requires annual fish growth rates as input, age-specific length data were obtained by scale readings on 90 fish. Lengths per age group at the end of the season were also used as start lengths of the next

Table 1. Symbols (following method of Fish bioenergetics 3.0), parameter values, and literature sources of parameters for the bioenergetics model used to calculate bleak consumption and excretion. Equation number 2 means an exponential term with optimum function.

	Symbol	Parameter	Source
Consumption			
Equation number		2	
Optimum temperature (°C)	<i>CTO</i>	20	Coutant (1977)
Maximum temperature (°C)	<i>CTM</i>	37.7	Horoszewicz (1973)
Increase over low temperatures	<i>CQ</i>	3.8	Hölker and Haertel (2004)
Intercept of allometric weight function	<i>CA</i>	0.33	Keckeis and Schiemer (1990)
Slope of allometric weight function	<i>CB</i>	-0.22	Keckeis and Schiemer (1990)
Respiration			
Equation number		2	
Optimum temperature (°C)	<i>RTO</i>	20	Coutant (1977)
Maximum temperature (°C)	<i>RTM</i>	37.7	Horoszewicz (1973)
Increase over low temperatures	<i>RQ</i>	3.0	Mann (1965)
Intercept of allometric weight function	<i>RA</i>	0.00535	Keckeis and Schiemer (1990)
Slope of allometric weight function	<i>RB</i>	-0.31	Keckeis and Schiemer (1990)
Activity	<i>ACT</i>	2	Winberg (1956)
Specific dynamic action	<i>SDA</i>	0.147	Ware (1975)
Egestion/excretion			
Specific rate of egestion	<i>EA</i>	0.13	Ware (1975)
Specific rate of excretion	<i>UA</i>	0.02	Ware (1975)
Phosphorus metabolism			
Assimilation efficiency	<i>AEP</i>	0.72	Nakashima and Leggett (1980)

higher age group at the beginning of the next season. Lengths were converted into fwt by a regression obtained from the sampled fish ($\text{fwt [g]} = 0.0055 \times \text{TL}^{3.105} \text{ [cm]}$; $F_{1,998} = 27.1$, $p < 0.0001$; for age-length-weight key, see Table 2). Consumption and excretion were modeled for a seasonal duration of 180 d with water temperatures $>10^\circ\text{C}$ (days of the year, 133–312), by using the age group-specific growth rates, the average abundances per age group, and the age group-specific diet compositions, averaged per sampling month over the years 2001 and 2002. Because diet composition for juvenile bleak was not available, the diet of 2+ bleak was assumed to reflect also the diet of the 0+ and 1+ groups. Annual consumption of phosphorus included in terrestrial insects by fish was compared with mean volumetric TP concentrations in Lake Großer Vätersee (average from epilimnetic and hypolimnetic layers of 21 samplings in 2001 and 2002: $32.6 \mu\text{g L}^{-1}$, minimum epilimnetic concentration was $8 \mu\text{g L}^{-1}$ in August 2002; maximum hypolimnetic concentration was $61 \mu\text{g L}^{-1}$ in July 2002) (data not shown). Because phosphorus excreted by fish is directly usable by phytoplankton, phosphorus excretion by bleak from terres-

trial origin was compared with mean annual SRP concentration in the epilimnetic layer of the lake (average of 21 samplings in 2001 and 2002, $3.06 \mu\text{g L}^{-1}$; minimum was $<2 \mu\text{g L}^{-1}$ in April, June, and July 2002; maximum was $14 \mu\text{g L}^{-1}$ in January 2002) (data not shown).

To elucidate how lake size influences the areal density of fish that can be subsidized by terrestrial insects, an exponential decay model

$$BM = ae^{-bD}$$

was calculated with *BM* as insect biomass (mg m^{-2}) and *D* as distance to the donor habitat (in meters). The exponent *b* (0.0853) was calculated from biomass estimates of terrestrial stages of aquatic insects with increasing distance to the donor desert stream (see fig. 1b in Sanzone et al. 2003). Although the habitat in which these values were obtained is not fully comparable to the lake of the present study, other insect decay rates were, to the best of our knowledge, not available in literature. The daily rate of terrestrial-derived insect fall-down per meter of lake shoreline (coefficient *a*) was assumed to be $50.4 \text{ mg dry weight m}^{-2} \text{ d}^{-1}$, the median seasonal flux from the nine studies on streams in forested areas (data for lakes were not available) summarized by Baxter et al. (2005). The studies included data from both deciduous and coniferous forests from Alaska, Virginia, Scotland, Japan, and New Zealand, and thus, the average fall-down from these studies was used as a baseline for the modeling approach. For comparative purposes, both the maximum ($11,000 \text{ mg dry weight m}^{-2} \text{ yr}^{-1}$) and minimum ($624 \text{ mg dry weight m}^{-2} \text{ yr}^{-1}$) annual fluxes cited by Baxter et al. (2005) were used as high versus low scenarios for the coefficient *a*; and the exponent *b* was either reduced to 50% (0.04625, low scenario) or increased to 150% (0.12795, high scenario) of the original value. The low and high scenarios were used in

Table 2. Key for total length and fresh weight of bleak age groups at the end of the season in Lake Großer Vätersee.

Age	Total length (cm)	Fresh weight (g)
0+	4.9	0.76
1+	7.0	2.3
2+	9.8	6.6
3+	11.6	11.2
4+	13.3	17.1
5+	15.3	26.4
6+	16.4	32.5
7+	17.6	40.5

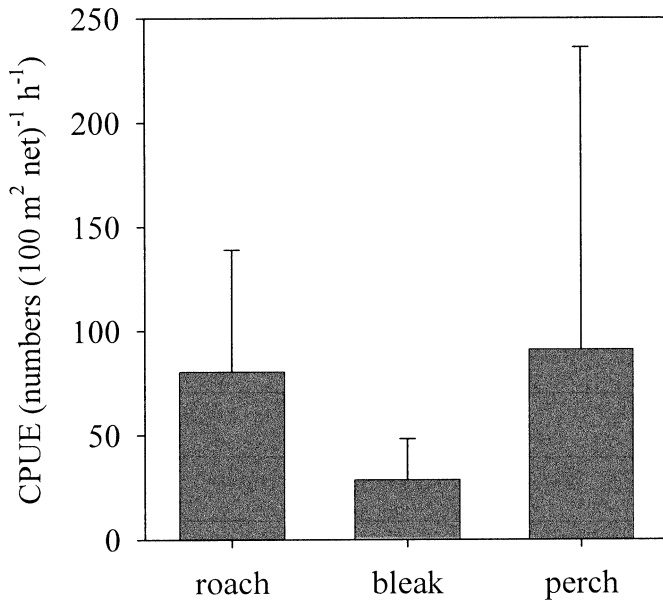


Fig. 1. CPUE (ind. (100 m² net)⁻¹ h⁻¹, arithmetic mean + 95% CI) of the main fish species in Lake Großer Vätersee in 28 fleets of gill nets set between April and October in both 2001 and 2002.

all four possible combinations. For all scenarios, the sum of insect biomass along a perpendicular transect from the shore to the lake center, representing the half-diameter of a circle-shaped lake, was multiplied with the periphery (shoreline) length of that lake to obtain daily lakewide subsidy rates. Based on the season length of 180 d, it was estimated how many bleak with similar age and diet compositions as found in Lake Großer Vätersee were subsidized by these annual fall-down rates of terrestrial insects.

Furthermore, the impact of the periphery length to lake area ratio (shoreline development factor) was modeled by holding the annual insect flux (coefficient *a*) at the medium level, varying *b* (decay rate) from low to high values as above, and increasing the shoreline development factor to 1.5 or 2.0. These scenarios allow calculating whether a deviation from the perfect circle in lake shape (equivalent to a shoreline development factor of 1.0) had a greater impact on insect fluxes than did the variability in the decay rates.

Results

Average fish catches in the gill nets were dominated by perch, followed by roach and bleak (Fig. 1). The CPUE of roach was 2.76 times higher than that of bleak, thus translating into an areal bleak density of 78,300 ind. km⁻² if the previously estimated roach density of 216,100 ind. km⁻² was used as a comparative baseline (see Materials and Methods).

Catches of bleak in the purse seine were variable and comprised age groups 2+–7+, whereas juveniles (i.e., 0+ and 1+ age groups) were not caught. Highest abundances averaged over the 18 hauls were found for 3+ bleak (6,700 ind. km⁻²) and 2+ bleak (5,600 ind. km⁻²; Fig. 2). Total abundance of adult bleak was 15,100 ind. km⁻² (95% CI 8,300–21,700 ind. km⁻²). By assuming a constant annual mortality rate between the age groups (linear regression between log

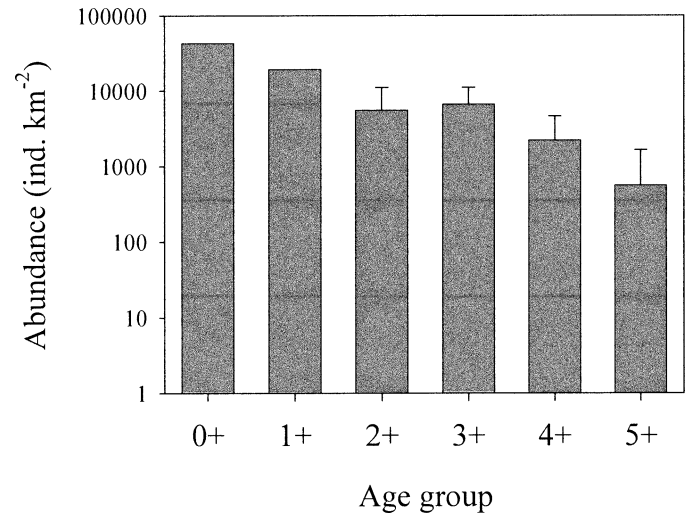


Fig. 2. Mean abundance (individuals km⁻² ± 95% CI) of the four bleak age groups 2+–5+ in Lake Großer Vätersee, calculated from 18 purse seine hauls in 2002. The abundances of the 0+ and 1+ age groups were predicted from a linear regression between abundance and age of the older age groups.

abundance per age group and age, $R^2 = 0.83$, $F_{1,3} = 9.65$, $p = 0.09$), the predicted densities of 0+ and 1+ bleak were 42,900 and 19,200 ind. km⁻², respectively (Fig. 2). The total bleak abundance was thus estimated with 77,200 ind. km⁻² (95% CI 34,500–111,700 ind. km⁻², if CI from adult bleak catches was applied; abundance equivalent to 211 kg fwt km⁻²), a value close to the estimate based on the gill net catches.

Diet of bleak (total $n = 229$) was composed of terrestrial insects (73.3% biomass) and zooplankton, whereas benthic prey comprised only a minor part of the diet (Fig. 3). In contrast, the diet of roach was dominated by zooplankton and benthos; the diet of perch, by fish, zooplankton, and benthos (Fig. 3). Consequently, for the calculation of terrestrial subsidy rates, only bleak were considered in the further analyses.

Terrestrial insects dominated the prey biomass at almost all sampling occasions and in all four bleak age groups (Fig. 4). There was a slightly rising proportion of zooplankton in prey biomass of the age groups 3+–5+ from June–October, but zooplankton proportion never exceeded 49% of total prey biomass except for the 3+ bleak in September (Fig. 4).

Lakewide prey consumption by the bleak population was 172.66 kg fwt over the season. Relative biomass proportions of terrestrial insects, zooplankton, and benthos of total consumption were 83.8%, 15.5%, and 0.7%, respectively. Lakewide TP consumption of bleak population ranged between 1,449 and 3,610 mg d⁻¹ (Fig. 5). This results in a total consumption rate of 476.6 g phosphorus over the season. If only the lake-external phosphorus included in terrestrial insects was considered, the annual consumption rate was 431.6 g phosphorus, equivalent to 0.688 μg phosphorus L⁻¹. In comparison to the average annual TP concentration of 32.6 μg L⁻¹ in Lake Großer Vätersee, phosphorus subsidy by feeding on terrestrial insects was thus 2.11% (Table 3). Phosphorus excretion originated from terrestrial insects ranged between

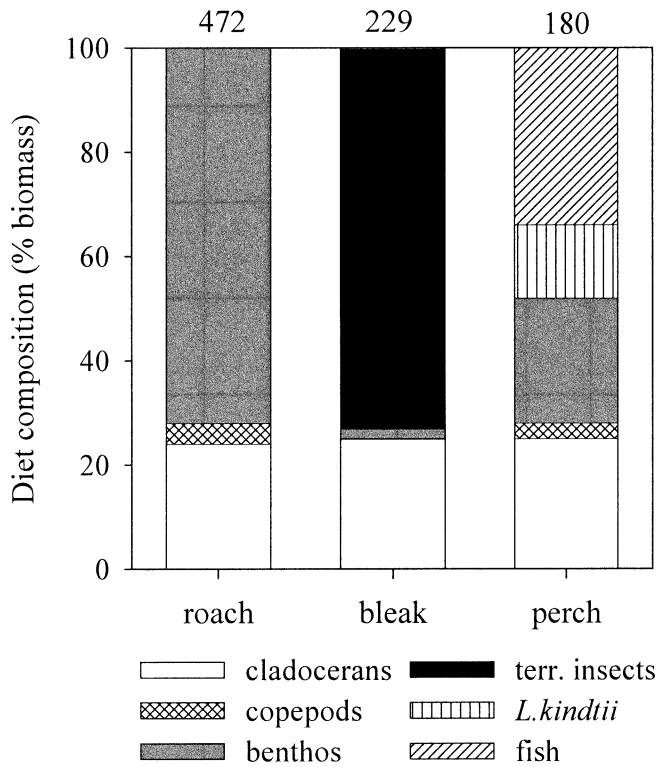


Fig. 3. Overall diet composition (% prey biomass) of the three dominant fish species roach, bleak, and perch from gill net catches in Lake Großer Vätersee in 2001 and 2002 (perch in 2002 only). The number of diet inspections is given above the bars.

806 and 1,392 mg d⁻¹ (Fig. 5) with a seasonal sum of 210.6 g or 0.335 μg L⁻¹. In comparison with the average SRP concentration in the lake of 3.06 μg L⁻¹, this amounted to 10.96% (Table 3).

The modeled total annual insect fall-down to a circle-shaped lake with a surface area of 0.01 km² and a half-diameter of 56.5 m resulted in 111.74 kg fwt that would support 716,600 bleak km⁻² if diet and age structure were similar to those of the Lake Großer Vätersee population (Fig. 6a). With increasing lake area, the supported population size declines sharply to 228,600 ind. km⁻² in a 0.1 km² lake, or 72,200 ind. km⁻² in a 1 km² lake (Fig. 6a). Applied to Lake Großer Vätersee (0.121 km²), the assumed insect fall-down would support 208,200 bleak km⁻², about three times the density that was determined from the catches. The sensitivity of the model to a variation in both the coefficient a and the exponent b was strongly expressed only for very small lakes with a surface area of less than ~0.03 km² (Fig. 6a). For lakes of ~1 km² size, the scenario with both a high a coefficient and a high b exponent resulted in supported bleak densities almost identical to the standard scenario. About three times more bleak were supported if the flux of terrestrial invertebrates was assumed to be at the maximum level according to published studies (high), whereas simultaneously the decay rate was assumed to be low. In contrast, the terrestrial subsidy would support 5.2–20 times less bleak in comparison to the standard scenario if both flux and decay rates were simultaneously low or if low insect fluxes and

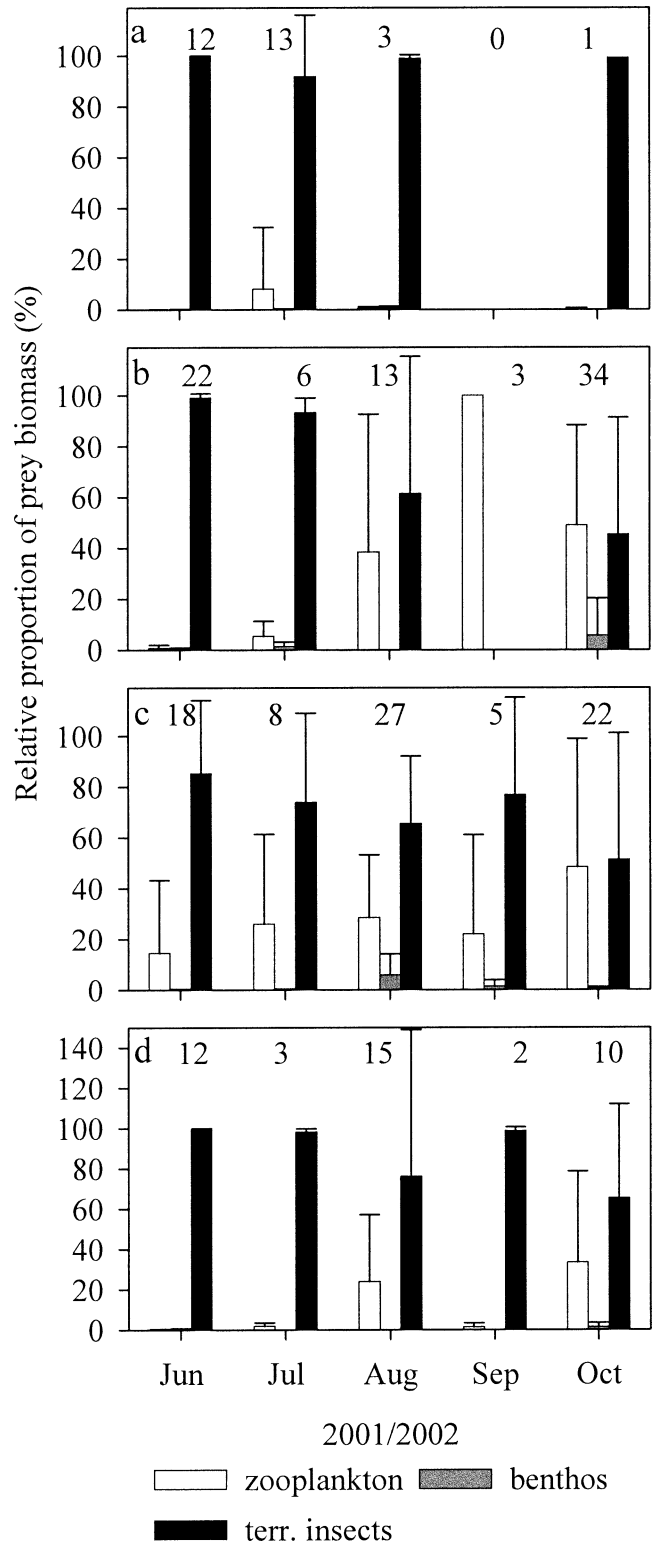


Fig. 4. Diet composition (% prey biomass) of four bleak age groups (a: 2+, b: 3+, c: 4+, d: 5+–7+) in Lake Großer Vätersee. The data represent average proportions from monthly samplings in both 2001 and 2002 (number of diet inspections above the bars).

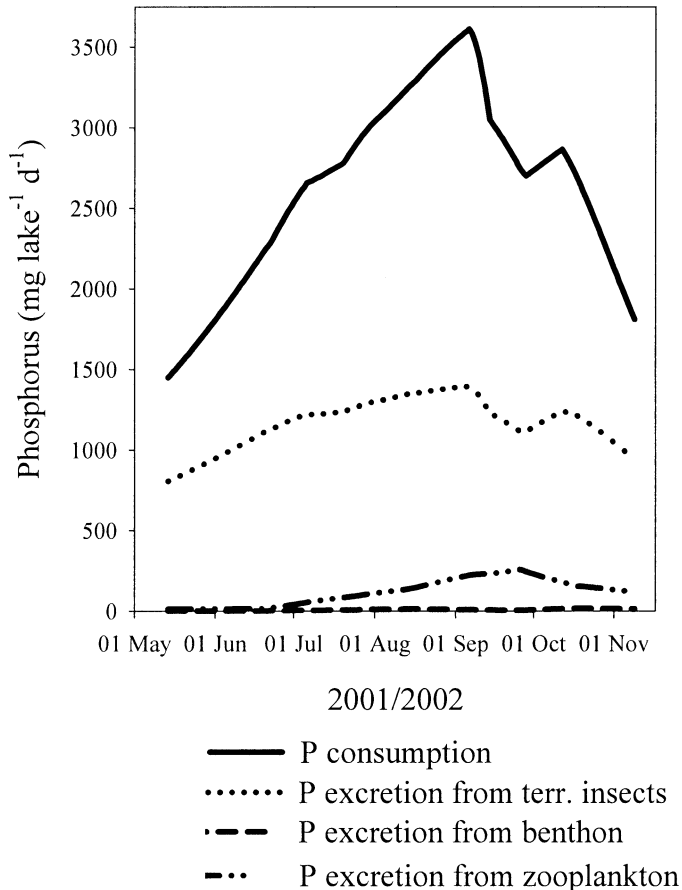


Fig. 5. Daily phosphorus consumption and excretion rates of bleak population ($\text{mg phosphorus in lake}^{-1} \text{d}^{-1}$) in Lake Großer Vätersee, calculated by a bioenergetics model as averages from 2001 and 2002.

high decay rates were combined (Fig. 6a). If the periphery length to lake area ratio was increased to either 1.5 or 2.0, the bleak density supplied by external insect biomass would increase accordingly (Fig. 6b). However, the impact of the decay rate on the maximum bleak density was still higher than the impact of the shoreline development factor, because overall highest values were found in both scenarios in which low decay rates b were applied (Fig. 6b).

Discussion

The data presented here show that uptake of lake-external phosphorus via terrestrial insects by the bleak population only moderately subsidized the internal phosphorus pools of the lake. Whereas the annual input of nutrients by feeding on external prey was almost two magnitudes lower than was the TP content of the lake, the excretion of highly reactive phosphorus by fish was about one magnitude lower than the average annual epilimnetic SRP concentration. These relatively low fractions were obtained even though biomass proportion of terrestrial insects on bleak's annual consumption was $\sim 84\%$. In contrast, the majority of nutrients taken up by bleak originated from terrestrial insects such that these fish obviously strongly relied on the lake-external food

sources. By assuming published rates of terrestrial insect flux to streams to occur also in Lake Großer Vätersee, our model scenarios show that a terrestrial prey subsidy to insectivorous fish may be of higher relevance only in small lakes.

Three sources of error in our calculations need to be mentioned. First, the calculated consumption of bleak was based on several assumptions, mainly according to insufficient accuracy in length measurements of prey items. We had to rely on the few occasions in which insect lengths could be determined in bleak guts after feeding. In all other situations, the pharyngeal bones of bleak destroyed the prey items considerably such that, in most cases, only parts of insect wings supported species determination. There are no comparative studies available in which average lengths of terrestrial insects in fish prey were determined in lakes. Therefore, we are aware of some uncertainty in the estimates of diet group proportions. However, with respect to our general hypotheses, even a proportion of terrestrial insects in the diet of bleak at the upper 95% CI (94% prey biomass), would increase the phosphorus consumption and phosphorus excretion by only $\sim 7\%$ or 8% , respectively, compared with the standard scenario (Table 3).

Second, the nutrient concentrations used in our balances were not directly obtained from animals in the lake or its terrestrial environment. Samples of terrestrial insects from the lake riparian habitats over the season, which may have been used to determine their phosphorus content, were not available. The situation was slightly better with the phosphorus concentration of bleak, in which the average was estimated from 310 samples out of four populations from the same geographical area with a relatively low variability ($0.68\% \text{ fwt} \pm 0.0044$, mean $\pm 95\% \text{ CI}$) (CI calculated from SD in Schreckenbach et al. 2001). Accordingly, by increasing the phosphorus content of bleak to the upper CI value, the total consumption of lake-external phosphorus and phosphorus excretion by bleak would have remained almost unchanged (Table 3).

In contrast, the published phosphorus concentrations of terrestrial insects were highly variable, ranging between 0.47 and 1.47% dry weight with both arithmetic mean and median at $\sim 0.85\% \text{ dry weight}$ that converts to $0.299 \pm 0.033\% \text{ fwt}$ (mean $\pm 95\% \text{ CI}$, calculated from supplementary material in Elser et al. 2000). Accordingly, the phosphorus consumption and phosphorus excretion were 11% and 16% higher, respectively, if the upper CI for the insect phosphorus content was applied (Table 3).

Third, the abundance estimates for bleak were based on a limited number of purse seine hauls. Purse seines were shown to catch small pelagic fish efficiently (Tischler et al. 2000), but individual catches may nevertheless strongly differ, in particular if shoaling fish have to be caught. Then, single hauls may encircle a shoal during one occasion but fail to catch any fish by the next haul. We have tried to minimize this sort of error by catching fish during the night only. Intensity of shoaling in response to potential encounter with visual predators normally declines during darkness (Pitcher and Parrish 1993) such that bleak were more evenly dispersed in the pelagic area during the night than during the day. Nevertheless, the variability in catch per haul remained high, with the abundance CI interval being almost

Table 3. Annual phosphorus (P) load from terrestrial insects by bleak feeding ($\text{g P lake}^{-1} \text{ season}^{-1}$) and proportion (%) on total lake TP, or annual P excretion by bleak from terrestrial insects ($\text{g P lake}^{-1} \text{ season}^{-1}$) and proportion on total lake SRP (%), compared between the scenario with average values and scenarios using the values of the upper 95% CIs for bleak density, proportion of terrestrial insects in bleak diet, P content of bleak, and P content of terrestrial insects.

Variable	Mean	Upper 95% CI	P load	% TP	P excretion	% SRP
Present			431.6	2.11	210.6	10.96
Bleak density (ind. km^{-2})	77,200	111,700	624.4	3.05	304.6	15.87
Insects in diet (% biomass)*	73.2	94.0	462.2	2.26	228.4	11.90
Bleak P content (% fwt)	0.68	0.684	431.6	2.11	209.9	10.94
Insect P content (% fwt)	0.30	0.333	479.0	2.34	244.2	12.72

* Weighted average of all age groups.

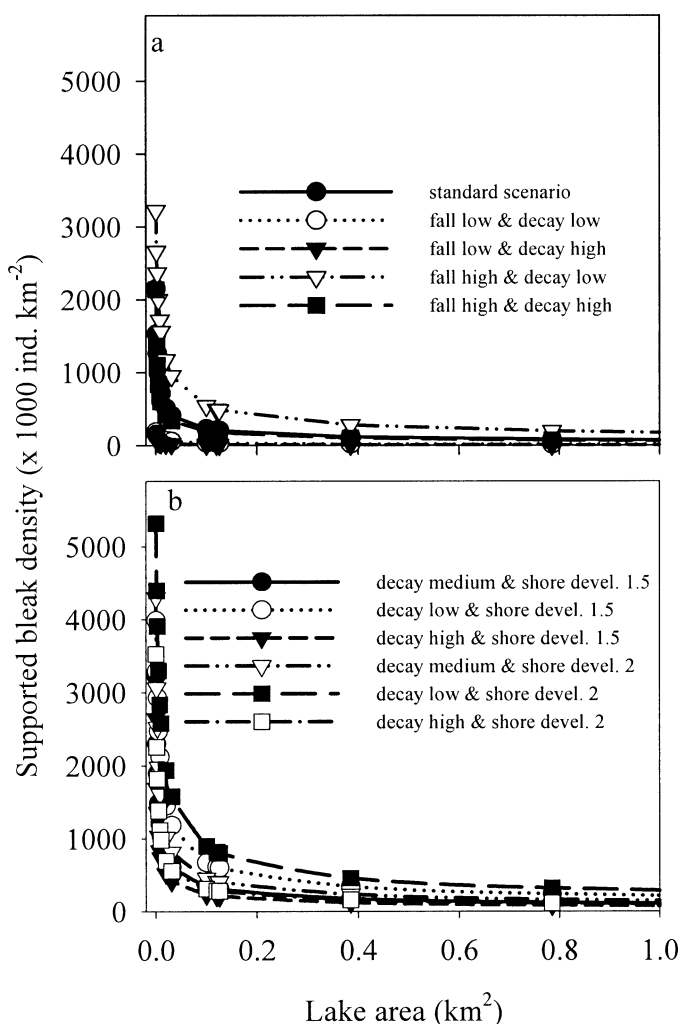


Fig. 6. Exponential decay model of the number of bleak (ind. km^{-2}) supported by terrestrial insects in dependence of the lake size (km^2). (a) The equation coefficient a (insect fall-down) was varied from the mean (standard scenario) to maximum (high) or minimum (low) literature data, whereas the decay rate b was varied to 150% (high) or 50% (low) of the standard scenario value. (b) The equation coefficient a (insect fall-down) was held at mean level, the decay rate b was varied to 150% (high) or 50% (low) of the mean value, and the periphery length to lake area ratio (shoreline development factor) was increased to either 1.5 or 2.0. For more details, see text.

as high as the arithmetic mean. Furthermore, the purse seine failed to catch juvenile bleak smaller than $\sim 4\text{--}5$ cm TL owing to the mesh size used. This weakness could be overcome only by assuming a constant annual mortality rate over all age groups and thus estimating the density of the juveniles from the abundances of the adults. As a consequence, however, the total population density estimate for bleak was very close to that derived from a combination of gill net catches and multiple mark-recapture estimates. Accordingly, we conclude that the population density of bleak in Lake Großer Vätersee was reliably estimated. Nevertheless, by applying the upper 95% CI of bleak abundance to the phosphorus estimates, both phosphorus consumption and phosphorus excretion by bleak would have been $\sim 45\%$ higher compared with the calculation with the mean bleak density (Table 3). This underlines that the calculations on the phosphorus budget were most sensitive to a reliable determination of fish densities.

Terrestrial subsidies to lake ecosystems have mainly been found for terrestrial carbon in form of DOM (Cole et al. 2000; Pace et al. 2004). These inputs may subsidize heterotrophic bacteria, zooplankton, and fish and may determine whether lakes function as sources or sinks of atmospheric carbon dioxide (Pace et al. 2004). Comparable balance estimates between autochthonous and allochthonous sources were not available for phosphorus or nitrogen except for general watershed budgets (Bennett et al. 1999). However, fish can serve as a link between watershed nutrients and food webs. The sediment-feeding gizzard shad (*Dorosoma cepedianum* Lesueur) in North American warmwater reservoirs is subsidized directly by allochthonous detritus and indirectly by phytodetritus from phytoplankton production stimulated by watershed subsidies (Vanni et al. 2005). Although fishes may act rather as a long-term nutrient sink, the excreted part of the phosphorus consumed is readily available to phytoplankton (Brabrand et al. 1990), and thus direct and indirect allochthonous sources of phosphorus for fish feeding may indirectly subsidize the primary production within a lake. In any case, we did not find strong evidence that the insectivorous bleak population subsidized the phosphorus pool in Lake Großer Vätersee, although their annual consumption rate consisted in major part of terrestrial insects. The relatively low proportions of phosphorus uptake and excretion in relation to in-lake phosphorus levels were attributable to both a low fish population density and a relatively large lake size. We cannot exclude, however, that there might

be some decisive subsidy of terrestrial-derived excreted SRP to lake phytoplankton during the late spring and summer months. In particular between May and July 2002, epilimnetic SRP concentrations were often $<2 \mu\text{g L}^{-1}$ (for seasonal data for previous years, see Kasprzak et al. 2000). The average lakewide daily excretion rates of bleak from terrestrial insects were $0.33 \mu\text{g phosphorus L}^{-1}$ but were highest during the summer (Fig. 5). Furthermore, excretion does not occur continuously but is pulsed on a diel scale and concentrated according to the spatial distribution of the bleak shoals in the lake. Therefore, it can be concluded that there might be a locally and temporally confined direct stimulation of phytoplankton growth by excreted phosphorus from riparian habitats that may even permeate through the food web. Accordingly, the relative contribution of external phosphorus to the lake budget depends on both the trophic state of the lake and the seasonality in phytoplankton production.

Allochthonous prey and nutrient subsidies have been thoroughly quantified in transversally coupled stream and riparian ecosystems or in longitudinally coupled stream and sea ecosystems (Wipfli 1997; Wipfli and Gregovich 2002). An even better understanding has been developed on the ecological role of the reciprocal subsidies of invertebrates between streams and their riparian zones (Nakano and Murakami 2001; Baxter et al. 2005). Beyond directly feeding the animals in the recipient habitat, allochthonous prey inputs also may have significant indirect effects that propagate throughout the recipient food webs (Baxter et al. 2005). Resources from donor habitats could support high densities of consumers, and these subsidized consumers could exert strong negative effects on their prey in the recipient habitats (Polis et al. 1997). A well-studied example is the increase of predatory spider density at a river shore that was subsidized by aquatic midges (Henschel et al. 2001; Sanzone et al. 2003). As a consequence, spiders depressed leafhopper densities, and this effect cascaded down to nettle plants, which were less damaged in areas on the river shore compared with more distant areals (Henschel et al. 2001). In contrast, other studies suggest that riverine insects subsidize riparian lizards but, in the short term, reduce the predation of lizards on terrestrial arthropod prey (Sabo and Power 2002). Similarly, Nakano et al. (1999) found that the terrestrial prey subsidy to Dolly Varden charr (*Salvelinus malma* Walbaum) buffered the effect of the fish predator on in-stream benthic prey. Such positive indirect interactions between prey that share predators may frequently occur when predators exhibit strong switching behavior (Baxter et al. 2005).

The results from the present study on bleak feeding on terrestrial insects in Lake Großer Vätersee supported the view that the external prey supports a moderate in-lake consumer density that would otherwise had to compete with zooplanktivorous fishes for the in-lake zooplankton prey resource. Consequently, although not experimentally tested, we assume that the terrestrial subsidy released the zooplankton from additional predation by bleak. Bleak is known to feed on aerial prey (Biro and Musko 1995), but fully zooplanktivorous populations were described as well (Chappaz et al. 1998). The dominant zooplanktivorous species in Lake Großer Vätersee were roach and perch, which have been

described as highly efficient zooplanktivorous feeders (Hjelm and Persson 2001). It can be assumed, therefore, that bleak is competitively inferior against both roach and perch while the fishes feed on scarce zooplankton resources. Indeed, zooplankton species and size structure in Lake Großer Vätersee reflect a strong top-down control by fishes, because *Eudiaptomus graciloides* was the numerically dominating crustacean species and the small *Daphnia hyalina* and *D. hyalina* \times *galeata* were the dominant cladocerans (Kasprzak et al. 2000). A limited zooplankton availability to the fish is further corroborated by the low annual growth rates of roach, indicated by an average length of 107 mm for 3+ fish (Haertel and Eckmann 2002). Consequently, competition for zooplankton among zooplanktivores may be intense, and bleak heavily relied on external nutrient sources to build up somatic biomass in this mesotrophic lake. Indeed, $\sim 6.6\%$ of phosphorus stored in the lakewide nonpiscivorous fish biomass of $27,200 \text{ kg km}^{-2}$ (H. Dörner unpubl. data) originated from terrestrial sources, but this percentage was exclusively attributable to bleak biomass. Generally, bleak abundances seem to increase with increasing trophic state of the lakes. A recent standardized fishing in north-German lowland lakes $>0.5\text{-km}^2$ surface area (for details, see Mehner et al. 2005) revealed that bleak catches in gill nets and chlorophyll-a concentration were positively correlated ($n = 54$, Spearman's $\sigma = 0.294$, $p = 0.031$) (T. Mehner unpubl. data). Accordingly, it can be assumed that only under the conditions of nutrient-limited primary production in the lake, are external nutrient sources required to support abundant bleak populations.

A second factor that strongly influenced the balance between terrestrial insect availability and in-lake fish density was the size of the lake. According to our model, terrestrial insects would subsidize bleak populations levels $>230,000 \text{ ind. km}^{-2}$ (i.e., comparable to the roach densities found in Lake Großer Vätersee) only in lakes with a surface area of $<0.1 \text{ km}^2$. This is attributable to the more favorable periphery length to surface ratio in the smallest lakes such that a longer shoreline as an insect source would need to supply a little water surface area only. Similarly, if the shape of lakes substantially deviates from an ideal circle with shoreline development factors being >1.0 , more fish per standard area were subsidized by external sources. A comparable effect of water size via the perimeter-to-area relationship has been found for the allochthonous subsidy of Virginia piedmont streams, in which streams of second order received much higher terrestrial invertebrate inputs per area compared with that of sixth-order streams (Cloe and Garman 1996). Furthermore, the high maximum proportions of external carbon sources within in-lake particulate organic matter (up to 55%) and zooplankton (50%) were experimentally confirmed in lakes of little size with $<0.03 \text{ km}^2$ surface area (Cole et al. 2000; Pace et al. 2004). Accordingly, there seems to be a general tendency that the relative importance of subsidy from donor to recipient systems declines with increasing system size (Polis et al. 1997).

The model scenarios show that the total insect flux to lakes is strongly influenced also by the rate by which the insect fall-down declines with increasing distance to the donor habitat. This process has rarely been quantified in any

system. Unfortunately, we also failed to quantify the insect fluxes to Lake Großer Vätersee. Direct measurement of insect subsidy to lakes would require an enormous spatial and temporal sampling effort to obtain reliable data for the entire lake surface over the seasonal course. The results of the present study indicate, however, that at least for small lakes surrounded by forests and containing insectivorous fish populations such as bleak in central Europe, a more detailed investigation may elucidate that forests also feed lakes.

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