Mass-balanced flow networks- Lake Constance data documentation

Updated 09/10/2019

Authors: Ursula Gaedke, Alice Boit

Lake name: Lake Constance

Contact person: Professor Dr. Ursula Gaedke (gaedke@uni-potsdam.de), Institute of Biochemistry and Biology, University of Potsdam, Maulbeerallee 2, 14469 Potsdam

If not available, try Dr. Dietmar Straile (Dietmar.straile@uni-konstanz.de), Limnological Institute, University of Constance (Konstanz)

Sampling site

Lake Constance (LC) is a temperate, large (476 km²), deep (mean depth = 101 m, max. depth 252 m), and warm-monomictic lake north of the European Alps of glacial origin. It has weak pelagic-benthic coupling, and little allochthonous input into the pelagic zone (Bäuerle and Gaedke 1998). The focal measuring site is in the north-western fjord-like arm of the lake (mean depth ca. 100 m, max. depth 146 m).

Lake Constance has a relatively deep and well-mixed epilimnion and a large pelagic zone. Since 1980, total P during winter mixing has declined from > 80 to < 15 μ g P/L. The trophic state has changed from meso-eutrophic to more oligotrophic conditions and phosphorus is the dominant limiting macronutrient in Lake Constance (Güde *et al.* 1998). Measured C:P ratios of phytoplankton and bacteria varied greatly throughout the growing season - their values indicated severe P limitation of algal production during summer and autumn (Hochstädter 2000). This restricts the maximum C gross growth efficiency for strictly algivorous consumers to between 20% and 25%, which is below their physiological maximum (Straile 1997), and suggests P limitation.

Datasets overview

We provide two datasets which provide the mass-balanced flows in units of carbon and phosphorus during 10 seasonal phases for the years 1987-1993 between 8 major compartments (highly aggregated functional groups) and the pool of detritus (see *Food web compartments* below).

As an illustration of these datasets, we show the carbon vs. phosphorus flows in characteristic seasonal phases averaged across the years 1987-1993 (Fig. 1). The datasets resolve this information by compartment, phase, and year.



Fig 1. Energy (carbon) and nutrient (phosphorus) flows in Lake Constance. (A–D) In-going flows of carbon between major compartments in winter (A), spring (B), Clear Water Phase (C), and summer to autumn (D). Data per phase is averaged across the years 1987-1993. Functional guilds aggregated into trophic compartments: Auto. = Autotrophs, Herb = Herbivores, Carn = Carnivores, Bac = Heterotrophic Bacteria, Bactv = Bacterivores. Excretion summarizes the release of dead particulate and dissolved organic matter (PDOM) by phytoplankton exudation, the consumers' feeding and metabolic activities (including sloppy feeding and non-grazing mortality). Arrows widths (compartment areas) are scaled relatively to the square root of the strength of the C-flows in μ gC m⁻² d⁻¹ (C-content of biomass in μ gC m⁻²). (E–H) Phosphorus (P) flows between major compartments in winter, late spring, Clear Water Phase, and late summer to autumn. Seasonal scaling for P is analogous to C.

Reproduced from Fig. 2 in Boit and Gaedke (2014), https://doi.org/10.1371/journal.pone.0090404.g002 .

Sampling methods

Sampling was carried out weekly during the growing season and approximately every two weeks in winter, at different depths at a central sampling site 147 m deep, in the northwestern part of the lake (Überlinger See) from 1987 to 1993. The abundance of all planktonic organisms was assessed by microscopy using advanced sampling and counting techniques. Individual body sizes were established by measuring either size frequency distributions (bacteria, APP, HNF), or average cell volumes of individual taxa (larger phytoplankton, ciliates, rotifers), or the individual length of the organisms (crustaceans). Original measurements of body size were converted to units of C using

measurements from Lake Constance or from the literature (for details see Gaedke (1992) and literature therein).

Production was measured *in situ* for bacteria (Simon and Tilzer 1987, Simon *et al.* 1998), APP (Gaedke and Weisse 1998), and phytoplankton (Häse 1998, Tilzer 1991). Production estimates for zooplankton were gained from a combination of *in situ* and laboratory techniques (Geller 1991, Müller 1989, Weisse 1998) and from mass-balanced flow matrices (see Mass-balanced carbon and phosphorus flows below).

The carbon and phosphorous flows were reconstructed using a mass-balanced model (Gaedke and Straile 1994a) which takes measurements of biomass and production as input data (see *Mass-balanced carbon and phosphorus flows* below).

Food web compartments

In the datasets, the food web in Lake Constance is represented by 8 living compartments and a detrital compartment labelled as follows:

1. Bacteria, 2. Phytoplankton (all eucaryotic phytoplankton) and Autotrophic Picoplankton (APP, i.e., cyanobacteria), 3. Heterotrophic Nanoflagellates (HNF), 4. Ciliates (protist zooplankton), 5. Rotifers (Multicellular zooplankton), 6. predominantly herbivorous crustaceans (mostly filter-feeding cladocerans commonly known as "water fleas" of the genera *Daphnia* and *Bosmina*, and calanoid copepods, e.g., the genera *Eudiaptomus*), 7. Carnivorous crustaceans (mostly raptorial feeders such as cyclopoid copepods and the cladoceran genera *Leptodora* and *Bythotrephes*), and 8. Planktivorous pelagic fish, and 9: detrital compartment (PDOM, consisting of particular and dissolved organic matter).

Mass-balanced carbon and phosphorus flows

The mass-balanced carbon and phosphorus flows are based on the long-term *in situ* measurements described above. The model builds upon earlier investigations of seasonally resolved, balanced C flow diagrams elucidating the flow of energy and the trophic structure of the pelagic food web of Lake Constance (Gaedke and Straile 1994a, Straile 1998). These studies revealed a very tight balance between primary production and the cumulative C demands of all consumers in summer and autumn, suggesting energy-limited growth of herbivores and carnivores, and high trophic-transfer efficiencies (Gaedke and Straile 1994b).

Based on the comprehensive measurements of plankton abundance and production (see Sampling methods above), the quantitative carbon flow networks were established for ten successive time intervals (see *Seasonal phases* below) throughout the years 1987-1993. For each phase and for all 9 individual compartments, the network fulfils the mass-balanced conditions. This means, that the inputs and outputs of both C and P are balanced around each compartment i.e., the sum of all inputs matched the sum of all loss terms in both units of C and P, and to the entire system, e.g., primary production balances the sum of respiration and sedimentation. The mass-flow networks further satisfy the assumption that the maximum gross growth efficiency (i.e., the ratio between production and ingestion) of consumer compartments is restricted to 33% in units of C (Gaedke and Straile 1994b, Straile 1997) and to 80% in units of P (Hessen and Andersen 1990). This upper limit was met by using realistic diet compositions (Gaedke *et al.* 2002) and parameters in the model. Bacterial respiration was calculated as the difference between consumption and production since excretion of organic compounds was regarded as negligible. To balance the flux charts, bacterial

consumption had to equal the total egestion of the other compartments minus sedimentation. Dark respiration of phytoplankton was taken as 20% of primary production. Allocation of prey production to omnivorous predators was derived from the relative share of each predator to total predator production, unless experimental evidence suggested a different diet composition (Gaedke and Straile 1994a, Straile 1998). The release of any particulate or dissolved C and P by heterotrophs was subsumed as egestion, i.e., as the difference between ingestion and the sum of production and respiration.

P fluxes were estimated by converting the respective mass-balanced C flux charts (Gaedke and Straile 1994a, Straile 1998) into units of P using the measured C:P ratios as described in Hochstädter (2000). The C:P ratio of each prey compartment were used to estimate P fluxes to consumer compartments, while the net P uptake by phytoplankton and bacteria was obtained from the algal and bacterial C:P ratio and their respective (measured) net C production. Egestion of P was calculated as the difference between nutrient input into a compartment and its nutrient outflow and was allocated to the nonliving compartment.

Seasonal phases

Each of the seven years of investigation was subdivided into 7–10 different time intervals (phases) to track seasonal changes in the mass-balanced flows (Geller 1991). The beginning and end of each time interval, lasting between 14 to 102 days and comprising 2–12 sampling dates, were not fixed to certain dates but determined according to changes in the numerous physical, chemical, and biological parameters during each year (for details see Straile [1998]).

Seven main seasonal phases are based on a definition according to Stüber (1998):

1: late winter, 2: early spring without stable stratification, 3: late spring without subsequent deep mixing; 4: cwp, 5: summer, 6: autumn, 7 early winter.

The conversion of the slightly older 10-phase system used in the datasets 1987 – 1993 to the 7 phase system (Stüber 1998) is as follows:

- Phase 1, 2, 3, and 4 are identical in both systems (late winter until CWP). Phase 2.5 is a transition phase which is unique to 1991 because it had characteristics of both phases 2 and 3 in the 10-phase systems. Note that phases 3 does not exist in all years 1987-1993, so that phase 4 follows directly on phase 2 (e.g., 1988).
- Phase 5 in the 10-phase system should be allocated to phase 5 in the 7-phase system (summer with still high daphnids after the CWP).
- Phase 6: exists only in 1987, can be converted to phase 5 in the 7-phase system.
- Phase 7 in the 10-phase system should be allocated to phase 5 in the 7-phase system ("proper" summer)
- Phase 8 in the 10-phase system should be allocated to phase 5 in the 7-phase system (late summer). In the 7-phase system phase 5 is defined to end on September 30 whereas phase 8 in the 10-phase system goes once beyond it and sometimes ends a bit earlier but the match is okay (plus/minus one sampling date)
- Phase 9 in the 10-phase system should be allocated to phase 6 in the 7-phase system. In the 7-phase system the period of phase 6 is defined as 1.10. to 15.11. which matches reasonably well with phase 9 in the 10-phase system.

• Phase 10: can be matched to phase 7 (=early winter) in the 7-phase system although the starting date is somewhat more flexible in the 10-phase system.

Depth-integration and unit conversion

Fluxes are given in units of carbon and phosphorus is given here in $[\mu gC/m^3/day]$ for each of the 10 seasonal phases. This implies the data is depth-averaged over the water column of the uppermost 0-20m (roughly the euphotic zone) and projected onto a volumetric unit of $1m^3 [\mu gC/m^3]$. Other authors prefer an areal unit per square meter. The conversion factor from the areal unit $\mu gC/m^2$ to $\mu gC/m^3$ is 1/20 because each cubic meter within the 20m-deep water column is thought to contain 1/20 of the depth-integrated biomass per square meter.

Datasets description

Dataset 1:

Filename: "Dataset1_LakeConstance_MassBalancedFlows_Carbon_DepthIntegrated"

This dataset (n = 1856) contains the mass balanced flows [μ gC/m³/day] in units of carbon of 8 major compartments and averaged across each of 10 seasonal phases from 1987-1993. Data is averaged over 0-20m depth. "Source" and "Sink" indicate the compartment number (see *Food web* above) and the direction of the flow (from source to sink).

Column headers

- A. Year
- B. Phase
- C. Source
- D. Sink
- E. C-Flux [μgC/m³/day]

Dataset 2:

Filename: "Dataset2_LakeConstance_MassBalancedFlows_Phosphorus_DepthIntegrated"

This dataset (n = XXX) contains the mass balanced flows $[\mu gP/m^3/day]$ in units of phosphorus of 8 major compartments and averaged across each of 7 seasonal phases from 1987-1993. Data is averaged over 8-20m depth. "Source" and "Sink" indicate the compartment number (see *Food web* above) and the direction of the flow (from source to sink).

Column headers

- A. Year
- B. Phase
- C. Source
- D. Sink
- E. P-Flux [μgP/m³/day]

References

General references on Lake Constance

- Bäuerle E, Gaedke U (1998) *Lake Constance: characterization of an ecosystem in transition*. Stuttgart, Germany: Schweizerbartsche Verlagsbuchhandlung.
- Boit, A. & U. Gaedke (2014) Benchmarking Successional Progress in a Quantitative Food Web. *PLoS* One 9(2): e90404

Specific references for this dataset

- Gaedke U, Straile D (1994a) Seasonal changes of the quantitative importance of protozoans in a large lake An ecosystem approach using mass-balanced carbon flow diagrams. *Mar Microbial Food Webs* 8: 163–188.
- Gaedke U, Straile D (1994b) Seasonal changes of trophic transfer efficiencies in a plankton food web derived from biomass size distributions and network analysis. *Ecological Modelling* 75/76:435–445.
- Gaedke U, Hochstädter S, Straile D (2002) Interplay between energy limitation and nutritional deficiency: Empirical data and food web models. *Ecological Monographs* 72: 251–270.
- Gaedke U, Weisse T (1998) Seasonal and interannual variability of picocyanobacteria in Lake Constance (1987–1996). Arch Hydrobiol Spec Issues: Advances in Limnology 53: 143–158.
- Geller W, Berberovic R, Gaedke U, Müller H, Pauli HR, *et al.* (1991) Relations among the components of autotrophic and heterotrophic plankton during the seasonal cycle 1987 in Lake Constance. *Verh Int Verein Limnol* 24: 831–836.
- Güde H, Rossknecht H, Wagner G (1998) Anthropogenic impact on the trophic state of Lake Constance during the 20th century. *Archiv für Hydrobiologie, Special issues: Advances in Limnology* 53:585–108.
- Häse C, Gaedke U, Beese B, Seifried A, Tilzer M (1998) Phytoplankton response to reoligotrophication in large and deep Lake Constance: Photosynthetic activity and chlorophyll concentration. Arch Hydrobiol Spec Issues: Advances in Limnology 53: 143–158.
- Hessen, D. O., and T. Andersen. 1990. Bacteria as a source of phosphorus for zooplankton. *Hydrobiologia* 206:217–223.
- Hochstädter S (2000) Seasonal changes of C:P-ratios of seston, bacteria, phytoplankton and zooplankton in a deep, mesotrophic lake. *Freshwater Biology* 44:453–464.
- Müller H (1989) The Relative Importance of Different Ciliate Taxa in the Pelagic Food Web of Lake Constance. *Microbial Ecology* 18: 261–273.
- Simon and Tilzer (1987) Bacterial response to seasonal changes in primary production and phytoplankton biomass in Lake Constance. J. Plankton Res. 9: 535-552.
- Simon M, Bunte C, Schulz M, Weiss M, Wünsch C (1998) Bacterioplankton dynamics in lake Constance (Bodensee): Substrate utilization, growth control, and long-term trends. Arch. Hydrobiol. Spec. Issues Advanc. Limnol. 53:195-221.
- Straile D (1997) Gross growth efficiencies of protozoan and metazoan zooplankton and their dependence on food concentration, predator–prey weight ratio, and taxonomic group. *Limnology and Oceanography* 42:1375–1385.

- Straile, D (1998) Biomass allocation and carbon flow in the pelagic food web of Lake Constance. Archiv für Hydrobiologie, Special issues: Advances in Limnology 53:545–563.
- Stüber K (1998) Der Einfluss unterschiedlicher Nährstoff- und Wetterbedingungen auf die saisonale Planktonentwicklung im Bodensee. Diploma thesis, University of Constance, 186 p., available on request from gaedke@uni-potsdam.de
- Tilzer MM, Gaedke U, Schweizer A, Beese B, Wieser T (1991) Interannual variability of phytoplankton productivity and related parameters in Lake Constance: No response to decreased phosphorus loading? J. Plankton Res. 13: 755-777.
- Weisse T, Müller H (1998) Planktonic protozoa and the microbial food web in Lake Constance. Arch Hydrobiol Spec Issues: Advances in Limnology 53: 223–254.