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Carbon steady-state model of the planktonic food web of Lake Biwa, Japan

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SUMMARY

1. A steady-state model of carbon flows was developed to describe the summer planktonic food web in the surface mixed-layer of the North Basin in Lake Biwa, Japan. This model synthesised results from numerous studies on the plankton of Lake Biwa.
2. An inverse analysis procedure was used to estimate missing flow values in a manner consistent with known information. Network analysis was applied to characterise emergent properties of the resulting food web.
3. The system strongly relied on flows related to detrital particles. Whereas primary production was mainly by phytoplankton >20 µm, microzooplankton were active and mainly ingested detritus and bacteria.
4. The main emergent property of the system was strong recycling, through either direct ingestion of non-living material by zooplankton, or ingestion of bacteria after degradation of detritus to release dissolved organic carbon.

Keywords: detritus, food web, lake, plankton, static model

Introduction

In spite of the wealth of biological information on the pelagic communities in lake ecosystems, the available data in single lakes have rarely been assembled into food webs. Even if trophic interactions, nutrient recycling and material budget have been described roughly, details on material flows among community components are unknown. In order to understand the processes that sustain ecosystems and to assess the role of each process, it is necessary to synthesise biological data in trophic webs, illustrating quantitatively the material flows that connect community components. However, it is almost impossible to

obtain all of these flows from field observations because of methodological problems in measuring everything. A modelling approach can overcome this difficulty. The last decade has seen the rapid development of modelling methods aimed at describing and analysing the flows of matter and energy in aquatic ecosystems. Among these approaches, Vézina & Platt (1988) developed an inverse analysis technique to describe marine planktonic food webs in a model that coupled the flows of carbon and nitrogen. The method makes it possible to estimate the flows of material between trophic components that are difficult to determine directly and thus to estimate quantitatively a complete set of flows within the food web. Because of the power of inverse analysis, a number of studies have applied this approach to analyse flows among trophic components in various aquatic ecosystems, which include lakes (Vézina & Pace, 1994), marine sediments (Eldridge & Jackson,

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1993) and atoll lagoons (Niquil *et al.*, 1998, 1999, 2001). These studies show that inverse analysis is useful for determining the relative importance of trophic channels that have not been quantitatively detected by *conventional* field observations. It must be noted, however, that substantial knowledge on the biological processes among trophic components of an ecosystem is necessary to apply inverse analysis successfully.

Lake Biwa is the largest lake in Japan and one of the ancient lakes of the world. It supplies water to 14 million people living in Kinki regions, which contain 0.25% of the global human population. As a result, Lake Biwa is a very important ecosystem, both ecologically and economically. A number of studies have described the seasonal succession and population dynamics of phytoplankton, bacteria and micro- (mostly protozoans) and mesozooplankton (mostly crustaceans) (Nagata, 1984, 1986; Kawabata, 1987; Nakano, 1992; Kawabata & Urabe, 1996; Gurung *et al.*, 2001; Yoshida *et al.*, 2001a). Trophic interactions between these components have been intensively studied during the past 20 years (Nagata *et al.*, 1996; Urabe *et al.*, 1996; Gurung, Nakanishi & Urabe, 2000; Yoshida *et al.*, 2001b; Kagami *et al.*, 2002). Several studies have examined the relative importance of factors regulating the production, growth and abundance of phytoplankton (Frenette, Vincent & Legendre, 1996; Robarts *et al.*, 1998; Urabe *et al.*, 1999a; Kagami & Urabe, 2001) and bacteria (Nagata, 1988; Nakano, 1992; Gurung & Urabe, 1999; Gurung *et al.*, 2001), and the roles of micro- (mostly protozoans: Nakano, 1994; Takahashi *et al.*, 1995a) and mesozooplankton (mostly metazoans: Urabe, Nakanishi & Kawabata, 1995) in nutrient regeneration. In addition, allochthonous inputs (Yoshimizu *et al.*, 2002) and sinking fluxes of organic matters (Nakanishi *et al.*, 1992; Takahashi *et al.*, 1995b; Yoshimizu *et al.*, 2001) were measured in conjunction with primary production and grazing experiments.

The extensive observations made in Lake Biwa make inverse analysis possible. In the present study, we applied this method to the pelagic community in order to describe quantitatively the full set of carbon flows between trophic components. We consider only carbon flows because ecological (trophic interactions) and physiological (metabolism) processes can be easily described in terms of carbon. We focus on the layer above the thermocline during summer in the

North Basin of the lake because most field data correspond to this spatio-temporal window.

Methods

Study site

Lake Biwa is located on Honshu Island, Japan at (35°11.5'N, 135°58.8'E). This mid-latitude temperate zone lake is divided in two basins (Fig. 1), the mesotrophic North Basin (616 km², average depth of 45.5 m) and the eutrophic South Basin (58 km²; average depth of 3.5 m). It has a maximum depth of 104 m. Water enters the lake through 34 rivers, with more than 99% of this water arriving in the North Basin. Epilimnetic water from the North Basin flows into the South Basin, from which it flows into the Seta River.

Inverse analysis and application

Methods. The inverse approach of Vézina & Platt (1988) describes each trophic component (compartment) in terms of all the possible flows in to or out of it. While non-steady-state conditions can be described by including flows that accumulate mass, we have

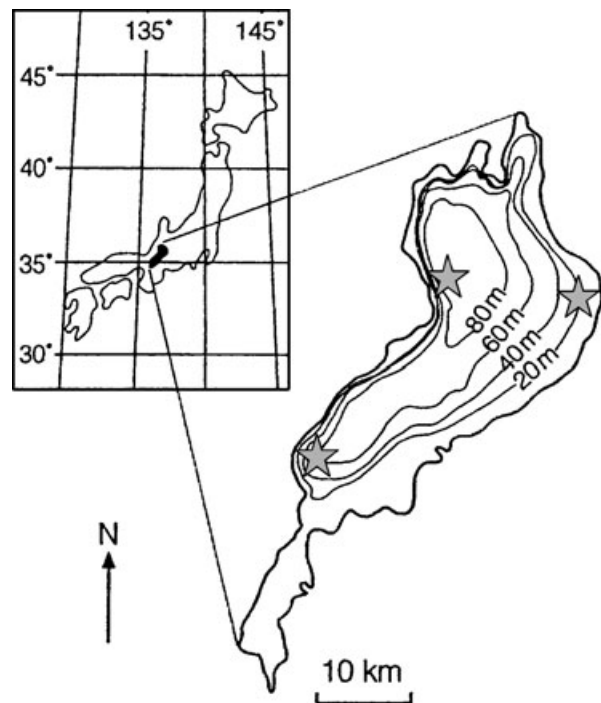


Fig. 1 Map of Lake Biwa showing the sampling sites (stars) used in the present study (from Frenette *et al.*, 1996).

made a steady-state assumption that does not account for growth. The total flows in and out of each compartment must be equal for the system to be in balance, which leads to a mass-balanced equation describing each compartment. Field determinations of rates of planktonic processes, such as photosynthetic and grazing rates, allow us to incorporate data into the model by formulating additional linear equations that express the observations in terms of flows. The equations describing the system and the data can be written:

$$A \times r = b \quad (1)$$

where A is a matrix of coefficients, r is the vector of flows (unknowns) and b contains the solution vector of the equalities.

Because the number of flows (unknowns, here 38) exceeds the number of equations (mass balance + data estimates, here 8 + 18), the system is mathematically underdetermined and has an infinity of solutions. Vézina & Platt (1988) applied two additional criteria to obtain a single solution. The first was a set of constraints limiting the rates and efficiencies of biological processes. These were expressed as inequalities for linear combinations of flows. The system of inequalities can be written:

$$G \times r \geq h \quad (2)$$

where G is a matrix of coefficients and h is the boundaries vector of inequalities.

Applying such constraints reduced the domain of solutions, but it still allowed an infinite number of possible solutions. The second criterion was based on a parsimony principle which assumes that the 'best' values for the flows are those which form the smallest Euclidean norm (Vézina, 1989). These two additional criteria led to a single solution vector describing the flows between pairs of compartments of the system or between components that are in and out of the system. The algorithmic technique was described in Vézina & Platt (1988).

Compartments. We separated organic matter in the surface mixed layer into eight compartments (Table 1). The six living compartments were: three size classes of phytoplankton, two size classes of zooplankton and one class of heterotrophic bacteria; the two non-living compartments were particulate and dissolved organic matter. Mixotrophic organisms

Table 1 Descriptions and abbreviations of the eight food web compartments used in the model

Description	Abbreviation
Phytoplankton <2 µm	ph1
Phytoplankton 2–20 µm	ph2
Phytoplankton >20 µm	ph3
Heterotrophic bacteria	bac
Microzooplankton (Zooplankton <100 µm)	mic
Mesozooplankton (Zooplankton >100 µm)	mes
Detritus (non-living material >0.7 µm)	poc
Dissolved organic carbon (non-living material <0.7 µm)	doc

present in the lake (e.g. *Uroglena americana*, Urabe, Gurung & Yoshida, 1999b) were not collected into a specific compartment but the flows associated with them were allocated to phytoplankton or zooplankton according to metabolic characteristics: primary production was allocated to phytoplankton and phagotrophic intake to zooplankton. Mixotrophs were neglected when calculating biomass in compartments.

Possible flows. The group of allowed flows, all positive, makes up what is called the *a priori* model (listed in Table 2). Although bacteria cannot consume detritus directly, they can consume it indirectly by consuming dissolved organic carbon (DOC) solubilised from detritus. Bacteria can be consumed by both microzooplankton and mesozooplankton (e.g. non-pigmented nano-flagellates and *Daphnia galatea*, Nagata, 1988). Mesozooplankton can also consume all sized of phytoplankton but microzooplankton can consume only the two smaller groups (ph1, ph2). The smallest cells (ph1 and bac) are not lost by sinking. Carbon from bacteria that die, such as from viral lysis, flows directly to DOC. Exchange of detritus and DOC outside the system is allowed, with information about the net exchange included as data. Such exchanges are primarily by river flows, but do include exchanges between inshore and offshore areas and between the surface mixed layer and deep water and sediments.

Available data and their incorporation into model equations. The three sampling sites selected (stars in Fig. 1) were located in the North Basin and had bottom depths of 20–70 m. We used data collected between June and September. The thermocline depth varied between approximately 10 and 20 m (Nagata, 1988) and approximately 15 to 20 m (Mitamura,

Table 2 Flows of the steady-state model, with abbreviations used in Fig. 2. For each flow, the value given is obtained by the inverse analysis

Description	Flow number	Flow name	Inferred value (mg C m ⁻² day ⁻¹)	Sensitivity Index
Gross phytoplankton production for ph1	1	gpp-ph1	155	0.61
Gross phytoplankton production for ph2	2	gpp-ph2	323	0.21
Gross phytoplankton production for ph3	3	gpp-ph3	1100	0.07
Respiration by ph1	4	ph1-res	50	0.77
Grazing of ph1 by microzooplankton	5	ph1-mic	24	2.93
Grazing of ph1 by mesozooplankton	6	ph1-mes	69	0.07
ph1 detrital POC production	7	ph1-poc	10	0.71
DOC excretion by ph1	8	ph1-doc	2	0.71
Respiration by ph2	9	ph2-res	91	0.66
Grazing of ph2 by microzooplankton	10	ph2-mic	0	–
Grazing of ph2 by mesozooplankton	11	ph2-mes	204	0.04
ph2 detrital POC production	12	ph2-poc	23	0.06
DOC excretion by ph2	13	ph2-doc	5	0.06
ph2 sinking	14	ph2-out	0	–
Respiration by ph3	15	ph3-res	352	0.12
Grazing of ph3 by mesozooplankton	16	ph3-mes	209	0.07
ph3 detrital POC production	17	ph3-poc	429	0.54
DOC excretion by ph3	18	ph3-doc	65	2.83
ph3 sinking	19	ph3-out	45	0.07
Microzooplankton respiration	20	mic-res	185	0.11
Grazing of microzooplankton by mesozooplankton	21	mic-mes	81	0.14
Microzooplankton egestion	22	mic-poc	417	0.11
DOC excretion by microzooplankton	23	mic-doc	124	0.58
Mesozooplankton respiration	24	mes-res	205	0.10
Mesozooplankton egestion	25	mes-poc	437	0.11
DOC excretion by mesozooplankton	26	mes-doc	145	0.46
Grazing of mesozooplankton by larger organisms	27	mes-out	149	0.11
DOC consumption by bacteria	28	doc-bac	920	0.10
Respiration by bacteria	29	bac-res	460	0.06
Grazing of bacteria by microzooplankton	30	bac-mic	422	0.05
Grazing of bacteria by mesozooplankton	31	bac-mes	25	0.27
Bacteria mortality	32	bac-doc	13	6.16
Non-living POC dissolution to DOC	33	poc-doc	494	0.24
Grazing of non-living POC by microzooplankton	34	poc-mic	360	0.25
Grazing of non-living POC by mesozooplankton	35	poc-mes	349	0.22
Sinking of non-living POC	36	poc-out	137	0.12
Net import of POC (import-export)	37	out-poc	23	0.25
Net import of DOC (import-export)	38	out-doc	73	0.20

Bold values are directly determined by field observations (Table 3). res, respiration; gpp, gross primary production; out, outside the system considered. The Sensitivity Index gives the average value for all the simulations of the sensitivity analysis.

Kawashima & Maeda, 2000), deeper than the euphotic zone (8–11 m; Mitamura *et al.*, 2000). In order to describe all flows on an areal basis (mg C m⁻² day⁻¹), we integrated volumetric data from the surface to 20 m. Data that we used were in published studies (Table 3). Their translation into linear combinations of flows is given in Table 4.

In order to balance the flows in and out of the total system, we had to modify the primary production estimates. Yoshimizu *et al.* (2001) estimated primary

production rates of 990 mg C m⁻² day⁻¹ for micro-phytoplankton (ph3) and 430 mg C m⁻² day⁻¹ for smaller phytoplankton (ph1 + ph2). Note that as they estimated the primary production rates using ¹³C by incubating lake water for 4 h, the measured rate is between net and gross production rates. Recent estimates for a pelagic site indicated that the annual import of allochthonous organic matter averaged 46 g C m⁻² year⁻¹, while lateral export was 11 g C m⁻² year⁻¹ (Urabe & Yoshioka, 2006). The difference

Table 3 Values used for the inverse analysis, calculated from published field observations. Vertical water-column integration was over the mean depth of the layer above the thermocline, i.e. 20 m. Abbreviations are from Table 1

Process	Value (mg C m ⁻² day ⁻¹)	Reference
Gross primary production of ph1 and ph2	496	Yoshimizu <i>et al.</i> (2001)
Gross primary production of ph3	1143	Yoshimizu <i>et al.</i> (2001)
Total sinking	182	Yoshimizu <i>et al.</i> (2001)
Sinking of phytoplanktonic cells (ph2 and ph3)	45	Nakanishi <i>et al.</i> (1992)
Respiration of phytoplankton	493	Nakanishi <i>et al.</i> (1992)
Respiration of bacteria	460	Nakanishi <i>et al.</i> (1992)
Respiration of zooplankton	390	Nakanishi <i>et al.</i> (1992)
Exudation of DOC by the phytoplankton	6.6% of net primary production	Nakanishi <i>et al.</i> (1992)
POC egestion by zooplankton	854	Urabe <i>et al.</i> (1995)
Grazing of ph1 by mesozooplankton	69	Urabe <i>et al.</i> (1996), Kawabata & Urabe (1996)
Grazing of ph2 by mesozooplankton	204	Urabe <i>et al.</i> (1996), Kawabata & Urabe (1996)
Grazing of ph3 by mesozooplankton	209	Urabe <i>et al.</i> (1996), Kawabata & Urabe (1996)
Bacterial production	447	Gurung <i>et al.</i> (2002)
Mesozooplankton production	149	Gurung <i>et al.</i> (2002)
Carbon import as POC and DOC	96	Urabe & Yoshioka (2006)
Carbon import as POC	0.24 × 96	Yoshimizu <i>et al.</i> (2002), Urabe & Yoshioka (2006)
DOC consumption by bacteria	2 × bacterial respiration	Gurung <i>et al.</i> (2002)
Bacteria grazing efficiency by mesozooplankton as a percentage of nanoalgae grazing efficiency	30%	Nagata & Okamoto (1988), Urabe & Watanabe (1990), Yoshida <i>et al.</i> (2001a)

Table 4 Linear equations used as complements for the mass balance equations, to take into account field estimates. Abbreviations are from Tables 1 & 2

Equation number	Equation
1	$gpp-ph1 + gpp-ph2 = 496$
2	$gpp-ph3 = 1143$
3	$ph2-out + ph3-out + poc-out = 182$
4	$ph2-out + ph3-out = 45$
5	$ph1-res + ph2-res + ph3-res = 493$
6	$bac-res = 460$
7	$mic-res + mes-res = 390$
8	$ph1-doc + ph2-doc + ph3-doc - 0.066 gpp-ph1 - 0.066 gpp-ph2 - 0.066 gpp-ph3 + 0.066 ph1-res + 0.066 ph2-res + 0.066 ph3-res = 0$
9	$mic-poc + mes-poc = 854$
10	$ph1-mes = 69$
11	$ph2-mes = 204$
12	$ph3-mes = 209$
13	$bac-mic + bac-mes = 447$
14	$mes-out = 149$
15	$out-poc + out-doc = 35$
16	$out-poc = 8.4$
17	$doc-bac - 2 bac-res = 0$
18	$bac-mes - 0.118 ph3-mes = 0$

between the inflow and outflow of organic carbon ($35 \text{ g C m}^{-2} \text{ year}^{-1} = 96 \text{ mg C m}^{-2} \text{ day}^{-1}$) represents the net annual import rate of allochthonous organic

matter. Hence, the total organic carbon entering the system was $990 + 430 + 96 = 1516 \text{ mg C m}^{-2} \text{ day}^{-1}$. Total respiration rate of whole organisms (autotrophic and heterotrophic planktonic organisms) in the water column above the 20 m depth was $1343 \text{ mg C m}^{-2} \text{ day}^{-1}$ (Nakanishi *et al.*, 1992) and sinking rate of POC to deeper layers was $182 \text{ mg C m}^{-2} \text{ day}^{-1}$ (Yoshimizu *et al.*, 2001). According to Urabe *et al.* (1996), net production of mesozooplankton from June to September corresponded to 10.5% of the primary production rate ($149 \text{ mg C m}^{-2} \text{ day}^{-1}$). Assuming that all the net production of mesozooplankton was consumed by fish that left from the system, the sum of flows leaving the system was $1343 + 182 + 149 = 1674 \text{ mg C m}^{-2} \text{ day}^{-1}$, a value larger than the total organic carbon entering the system. The two sets of measurements can be reconciled if the estimates of primary production rate mentioned above are increased by 11%, thus being closer to gross production than net production. We increased, therefore, the gross primary production estimates of ph3 to 1100 and ph1 + ph2 to $478 \text{ mg C m}^{-2} \text{ day}^{-1}$, respectively, (total gross production: $1578 \text{ mg C m}^{-2} \text{ day}^{-1}$) in order to balance the inputs and outputs. No quantitative information was available on the microzooplankton grazing, except that its grazing on bacteria was close to

bacterial production (Gurung *et al.*, 2000). The rates of grazing by mesozooplankton on the three size classes of phytoplankton in the water column were calculated using the weight-specific grazing rate estimated by Urabe *et al.* (1996) and the average mesozooplankton biomass during summer at the same pelagic site (Kawabata & Urabe, 1996).

From June to September, *Eodiaptomus japonicus*, *Daphnia galeata* and *Diaphanosoma brachyurum* were the dominant mesozooplankton species, comprising 66%, 20% and 8% of the mesozooplankton carbon biomass, respectively (Kawabata & Urabe, 1996; Yoshida *et al.*, 2001a). Although the latter two species can graze bacteria as efficiently as they can phytoplankton >20 µm, the first one does not graze bacteria at all (Nagata & Okamoto, 1988; Urabe & Watanabe, 1990). Thus, roughly 70% (66 of 94) of mesozooplankton, in term of biomass, could not graze bacteria. Therefore, bacterial grazing by mesozooplankton was estimated assuming that their grazing efficiency on bacteria was 30% of that on phytoplankton >20 µm.

Sinking of total organic matter and phytoplankton cells, respiration of living compartments, phytoplankton exudation of DOC and bacterial production rates for the summer were estimated from published data. The egestion rate of particulate organic carbon (POC)

by zooplankton was calculated by multiplying the weight-specific particle elimination rate averaged from June to September [$0.33 \text{ mg (mg DW)}^{-1} \text{ day}^{-1}$, Urabe *et al.*, 1995] by the average dry-weight at the surface (255 µg DW L^{-1} , Urabe *et al.*, 1996). Using this rate and the biomass distribution in the water column (Kawabata & Urabe, 1996), the flow from zooplankton to POC was calculated.

Inequalities. Thresholds for biological and physical processes were applied to constrain the calculated values to ranges that resulted in realistic values. Vézina & Platt (1988) and Vézina & Pace (1994) gathered published information on different planktonic processes in order to estimate these realistic limits. We used their values (listed in Table 5) with one exception, i.e. the upper limit for phytoplankton respiration was modified from 30 to 32% of gross primary production to be consistent with values estimated by Nakanishi *et al.* (1992) in Lake Biwa.

Network analysis

The Network 4.2 Program (Ulanowicz, 1999) was used to calculate network indices for the carbon flows derived from our inverse analysis. The sum of all

Table 5 List of minimum and maximum values used as biological constraints for the inverse analysis. Abbreviations are from Tables 1 & 2

Constraint	Lower bound	Upper bound	Reference
Respiration of ph1, ph2 and ph3	5% of gpp	32% of gpp	Vézina & Platt (1988), Nakanishi <i>et al.</i> (1992)
Respiration of mic and mes	3% of their ingestion		Vézina & Pace (1994)
Ingestion of microzooplankton		$5.46 \times B_{mic} \times \exp(0.0693T)$	Vézina & Platt (1988)
Ingestion of mesozooplankton		$0.73 \times B_{mes} \times \exp(0.0693T)$	Vézina & Platt (1988)
Degradation of dead phytoplankton to DOC (ph1, ph2 and ph3)	10% of (gpp - res - poc)		Vézina & Pace (1994)
Exudation of DOC by ph1, ph2 and ph3	2% of (gpp - res)	55% of (gpp - res)	Vézina & Pace (1994)
Excretion of DOC by mic and mes	10% of their ingestion		Vézina & Pace (1994)
Assimilation efficiency of mic and mes [(ing - poc)/ing]		90%	Vézina & Platt (1988)
Net production efficiency of bac [(ing - poc - res)/ing]	10%	40%	Vézina & Platt (1988)
Gross production efficiency of mic [(ing - poc - doc - res)/ing]	10%	60%	Vézina & Platt (1988)
Gross production efficiency of mes [(ing - poc - doc - res)/ing]		40%	Vézina & Platt (1988)
All flows are non-negative	0		

B_{mic} = biomass of microzooplankton [147 mg C m^{-2} , derived from the percentage of total zooplankton biomass in Haga, Nagata & Sakamoto (1995)]. B_{mes} = biomass of mesozooplankton [491 mg C m^{-2} , Urabe *et al.* (1995)]. T = average temperature [17.4 °C , Haga *et al.* (1995)].

fluxes passing through a compartment is called its *throughput*. It is equal to the sum of entering as well as exiting fluxes for a system at equilibrium. *Recycling* is carbon involved in cyclic pathways, i.e. carbon coming back to the compartment it left (Ulanowicz, 1986). The cycling activity of each compartment was estimated as the fraction of its throughput involved in recycling (Fasham, 1985). We also estimated the Finn Cycling Index (FCI; Finn, 1976), which is the ratio of the sum of carbon flows in cyclic pathways to the sum of all carbon flows in the system. The ratio detritivory/herbivory is calculated as the sum of flows of consumption of non-living material divided by the sum of flows of ingestion of autotrophic organisms.

Sensitivity analysis

A sensitivity analysis was performed to assess the dependence of the calculated fluxes on variations in the values of the field values (right hand value in the equations of Table 4). The 18 data values were varied by $\pm 20\%$ one at a time and a new set of flows calculated for this perturbed situation. Results for each flow were expressed as a sensitivity index SI (e.g. Richardson *et al.*, 2004):

$$\text{SI for } i\text{th flow} = (|f_{i,p} - f_{i,o}|/f_{i,o})/0.2 \quad (3)$$

where $f_{i,p}$ and $f_{i,o}$ are the values for the i th flow in the perturbed and original situations. A value of 1 indicates that the 20% variation of the field value leads to a 20% variation in the considered flow value.

The sum of input flows (primary production and imports) was always kept equal to $1674 \text{ mg C m}^{-2} \text{ day}^{-1}$. The same was true for the sum of output flows (respiration flows, sinking and exports). When the +20% variation increased an input flow, the other input flows were reduced by amounts proportional to their initial values such that the total input was constant. A similar readjustment was made for the -20% variation, and for the output flows.

The SI values are averaged per flow, for all the simulations realised and per simulation, for all the obtained flows.

Results

Input and output flows

The resulting estimates for integrated flows are given in Table 2 and illustrated in Fig. 2. Of the total input

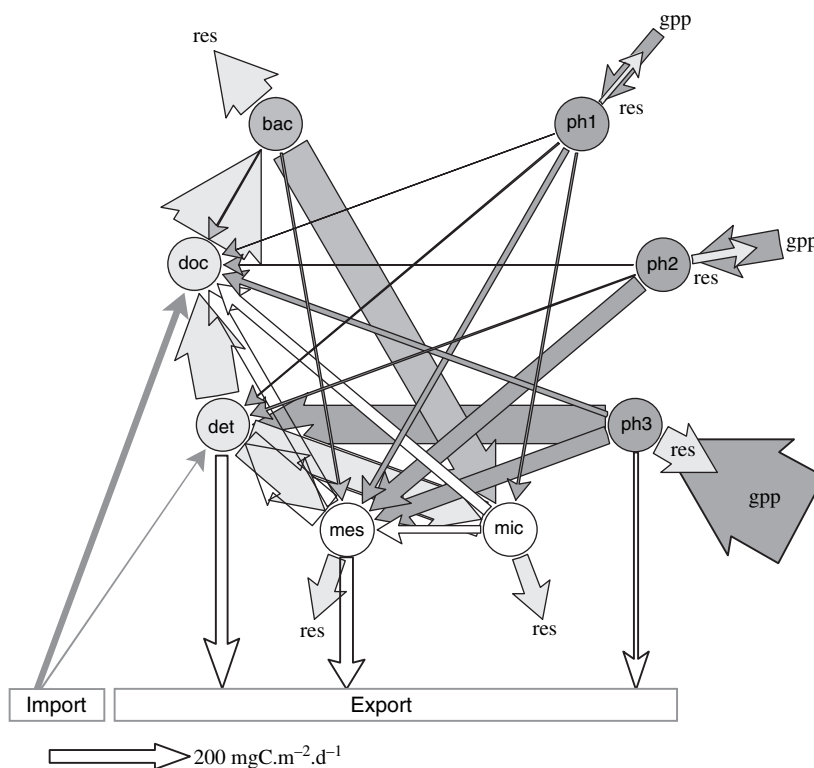


Fig. 2 Inverse solution for the planktonic food web flows in the North Basin of Lake Biwa (20-m layer above the thermocline, during an average summer season). res, respiration flows; gpp, gross primary production flows. Abbreviations for the compartments are given in Table 1. Each carbon flow is represented by an arrow, and the width of each arrow is proportional to the calculated value.

of 1674 mg C m⁻² day⁻¹ to the pelagic community, 66%, 19% and 9% are from the photosynthetic activities of phytoplankton >20 µm, nanophytoplankton (2–20 µm) and picophytoplankton (<2 µm), respectively. The net allochthonous input of 73 mg C m⁻² day⁻¹ for DOC and 23 mg C m⁻² day⁻¹ for POC (Yoshimizu *et al.*, 2002; Urabe & Yoshioka, 2006) is very low compared with primary production.

Respiration flows account for 80% (1343 mg C m⁻² day⁻¹) of the carbon output from the system. Among the living compartments, bacteria have the highest respiration (460 mg C m⁻² day⁻¹), followed by phytoplankton >20 µm (352 mg C m⁻² day⁻¹), mesozooplankton (205 mg C m⁻² day⁻¹) and microzooplankton (185 mg C m⁻² day⁻¹). The remaining 20% of the output goes to consumption of mes (149 mg C m⁻² day⁻¹, i.e. 9%) and sedimentation by detritus (137 mg C m⁻² day⁻¹) and phy3 (45 mg C m⁻² day⁻¹).

Null flow

Some allowed flows are zero. This tends to results when there are no data or constraints requiring them. In the present study, there are only two such flows, the sedimentation of phy2 and ph2 consumption by microzooplankton. The mesozooplankton requirement being high, this group consumed all the available ph2 production, leaving none for microzooplankton. We imposed a combined phy2 and phy3 sedimentation flux using the results of Nakanishi *et al.* (1992); the analysis assigned it all to the larger phytoplankton, the ph3. This is reasonable if the nanophytoplankton are efficiently grazed by zooplankton and removed before sinking out.

Throughputs and turnovers

Six of eight compartments have high throughput values, ranging from 1339 to 805 mg C m⁻² day⁻¹ (Table 6). The two highest values (1339 and 1100 mg C m⁻² day⁻¹) correspond to detrital POC and phytoplankton >20 µm. The next, slightly lower values (937–920 mg C m⁻² day⁻¹) are for mesozooplankton, DOC and bacteria, followed by microzooplankton (805 mg C m⁻² day⁻¹). The lowest values are 323 and 155 mg C m⁻² day⁻¹, for nanophytoplankton and picophytoplankton, respectively.

There are large differences among the compartments in the turnover rate (throughput divided by

Table 6 Throughputs (sum of entering flows) and turnover rates (biomass/throughput) for each living compartment

	Throughput (mg C m ⁻² day ⁻¹)	Biomass (mg C m ⁻²)	Turnover rate (day ⁻¹)
ph1	155	943*	0.16
ph2	323	616*	0.52
ph3	1100	1851*	0.59
bac	920	642 [†]	1.43
mic	805	147	5.48
mes	937	491	1.91

*Urabe *et al.* (2002); [†]Urabe *et al.* (2005).

biomass; Table 6). The picophytoplankton have a very low turnover rate (0.16 day⁻¹) compared with the intermediate values of the other phytoplankton groups. Heterotrophic compartments are high, particularly the microzooplankton who consume 5.48 times their biomass per day. This rate is, however, less than the upper limit of 18 day⁻¹ included as a constraint (Table 5).

Internal flows

Six of the 24 internal flows are >400 mg C m⁻² day⁻¹: DOC consumption by bacteria (920 mg C m⁻² day⁻¹), detritus degradation to dissolved material (494 mg C m⁻² day⁻¹), loss to detritus by mesozooplankton (437 mg C m⁻² day⁻¹), by phytoplankton >20 µm (429 mg C m⁻² day⁻¹) and by mesozooplankton (427 mg C m⁻² day⁻¹), and consumption of bacteria by mesozooplankton (417 mg C m⁻² day⁻¹). All flows affecting detritus are high. The formation of detritus (including organism mortality) makes up 52% and 47% of the microzooplankton and mesozooplankton throughputs, respectively. Zooplankton excretion of DOC is also large, 15% of their totals. As a consequence, the production rates of these two zooplankton compartments are low (10% and 16% for mic and mes).

Most carbon photosynthesised by picophytoplankton (ph1) goes to mesozooplankton (44%) or is respired (32%). The carbon photosynthesised by nanophytoplankton (ph2) goes mostly to mesozooplankton (63%). The gross primary production of microphytoplankton (ph3) goes to detritus (39%), is respired (32%), or is consumed by mesozooplankton (19%).

The diet of microzooplankton is composed of bacteria (52%), followed by detritus (45%) and picophytoplankton (3%). Mesozooplankton ate detri-

tus (37%), microphytoplankton (22%), nanophytoplankton (22%), microzooplankton (9%) picophytoplankton (7%) and bacteria (3%).

For total consumption in the system, the detritivory/herbivory ratio is 3.22, indicating that most heterotrophic production relies on non-living material.

Recycling

The FCI is 33%, indicating that 33% of the carbon flows are part of cyclic pathways. The cycling activity of each compartment is 0% for autotrophs, 41% and 26% for POC and DOC, 26% for bac and 37% and 23% for mic and mes.

Sensitivity analysis

The sensitivity analysis (Table 7) shows that the field input with the greatest impact is the efficiency with which bacteria take up DOC (SI = 2.21) followed by bacterial respiration (SI = 1.66), primary production by phytoplankton >20 µm (SI = 1.45), total phytoplankton respiration (SI = 1.41) and bacterial production (SI = 1.33). Numerous perturbations of a field result have a very small effect on the calculated flow values, with SI values between 0.2 and 0.35. The lowest SI is for the sinking of phytoplankton (0.04).

The flow most affected by changing the input data in the sensitivity analysis is the bac-DOC flow, corresponding to bacterial mortality (mean SI = 6.16), mainly as a result of changing the uptake efficiency of DOC by bacteria. The grazing of picophytoplankton by microzooplankton is the second most affected flow (SI = 2.93), mainly because of its sensitivity to changes in rates of primary production and phytoplankton respiration. The third more sensitive flow is the DOC excretion by microphytoplankton (SI = 2.83).

The detritivory to herbivory ratio varies between 2.55 and 3.52. The smallest value results from decreasing gross primary production by phytoplankton >20 µm. The largest value results from increasing DOC uptake efficiency of bacteria.

Discussion

Several choices were made when developing the *a priori* model. Our level of aggregation used only three phytoplankton and two zooplankton compartments.

These relatively few groupings cannot fully describe the complex planktonic food web. However, a more detailed food web would require a greater level of experimental data than exists. We did not include the uptake of DOC by protozoa (Sherr & Sherr, 1988; Marchant & Scott, 1993) because the process is known to exist in the ocean but we had no information on its extent in lakes. Without any results about its size over even enough information to constrain the flow, we could not represent it adequately. As noted earlier, we did not include the flow of material directly from detritus because it was represented by flow through detritus to DOC.

We did not include fish feeding directly because it was represented as an outflow of carbon. This description of the role of fish implies that they do not graze on the other planktonic organisms nor do they provide an additional carbon source as a result of migrations to either the benthos of the littoral zone and subsequent egestion. Any additional inputs of detrital material would only reinforce the main characteristic of a system highly relying on the consumption of non-living material.

Comparative data are needed to discuss the emergent properties. In order to do so, we built a comparative Table 8 using two different approaches, both for mass balances models. The first one consisted in taking directly indices published in the literature about lake planktonic food webs at different periods for Lakes Paul (WI, U.S.A.) and Konstanz (Germany and Switzerland). Vézina & Pace (1994) estimated flows during three consecutive years for Lake Paul using an inverse analysis. The results presented here represent the ranges of values for those 3 years. Gaedke & Straile (1994) made their own estimates of monthly flows for Lake Konstanz from measurements and literature data. The results in Table 8 are for their summer period.

The second approach for accumulating values of emergent properties was to calculate indices using network analysis when the published flow values had sufficient detail. The only lake where such data are available is Lake Kinneret (Israel; Stone *et al.*, 1993), for which a method of linear programming similar to our inverse analysis was used to describe an average year. The results in Table 8 concern the Lake Kinneret model for August to September. The results for three other, non-lacustrine; planktonic food webs were added to the comparison, all concerning whole-year

Table 7 Result of the sensitivity analysis. Each field estimate (right hand value in Table 4) is modified by minus (-) or plus (+) 20%

	SI	D/H
Gross primary production of ph1 and ph2		
-	0.62	3.04
+	0.84	2.80
Gross primary production of ph3		
-	1.45	2.55
+	NS	NS
Total sinking		
-	NS	NS
+	0.35	3.06
Sinking of phytoplanktonic cells (ph2 and ph3)		
-	0.04	3.22
+	0.04	3.22
Respiration of phytoplankton		
-	1.41	2.85
+	NS	NS
Respiration of bacteria		
-	NS	NS
+	1.66	3.34
Respiration of zooplankton		
-	NS	NS
+	NS	NS
Exudation of DOC by the phytoplankton		
-	0.13	3.18
+	0.31	3.13
POC egestion by zooplankton		
-	0.33	2.90
+	0.35	3.41
Grazing of ph1 by mesozooplankton		
-	0.33	3.15
+	0.33	3.15
Grazing of ph2 by mesozooplankton		
-	0.84	3.15
+	NS	NS
Grazing of ph3 by mesozooplankton		
-	0.27	3.50
+	0.31	2.85
Bacterial production		
-	1.33	3.20
+	NS	NS
Mesozooplankton production		
-	0.29	3.30
+	0.29	3.14
Carbon import as POC and DOC		
-	0.20	3.16
+	0.20	3.28
Carbon import as POC		
-	0.26	3.15
+	0.25	3.16
DOC consumption by bacteria		
-	NS	NS
+	2.21	3.52
Bacteria grazing efficiency by mesozooplankton		
-	0.26	3.15
+	0.25	3.15

SI = Sensitivity Index, averaged for all the flows of the simulated model. NS means that there was no solution to the system of equations with the constraints. D/H = ratio detritivory/herbivory.

Table 8 Comparison of the present model for Lake Biwa with several models from the literature

Reference	Lake Biwa	Lake Paul	Lake Konstanz	Lake Kinneret	Takapoto Atoll	English Channel	Celtic Sea
Present paper							
Main contributor to primary production (% of PP)	Phyto. >20 µm (70)	Vézina & Pace (1994) ND	Gaedke & Straille (1994) ND	Stone <i>et al.</i> (1993) non-pyrrophytes (95)	Niquil <i>et al.</i> (2001) Phyto. <3 µm (74)	Vézina & Platt (1988) ND	Vézina & Platt (1988) ND
Phytoplankton grazing by microzooplankton as a percentage of all zooplankton grazing on phytoplankton	4.8	72–98	30–70		82	23	18
phy-mic/(phy-mic + phy-mes) (%)							
mic-mes/mic throughput	10	ND	26–28 (7–13% in flood time)	26	38	37	46
Microbial food web efficiency (microzooplankton efficiency) (%)							
(mic-mes + bac-mes)/mes throughput	11	2–5	ND	16	29	23	20
link as a % of mesozooplankton demand (%)							
Bacteria production efficiency	46	15–18	ND	60	3	60	58
bac-mic/doc-bac (%)							
Respiration phytoplankton/total outputs (%)	29	ND	ND	40	8	23	10
Resp bacteria/total outputs (%)	27	ND	ND	10	17	6	8
Resp zooplankton/total outputs (%)	23	ND	ND	22	39	37	48
Export/total outputs (%)	20	ND	ND	26	36	34	35
FCI (%)	33	ND	ND	11	21	12	16
Detritivory/herbivory	3.22	ND	ND	0.88	1.4	0.43	0.38
Diet of mic in % of:							
phytoplankton	3			2	27	92	62
bacteria	52			91	2	8	38
non-living material	45			0	64	0	0
zooplankton	0			7	7	0	0
Diet of mes in % of:							
phytoplankton	51			70	4	53	65
bacteria	3			7	0	16	9
non-living material	37			0	19	0	0
zooplankton	9			23	31	31	26
Diet of zooplankton in % of:							
phytoplankton	29			53	14	59	65

Table 8 (Continued)

	Lake Biwa	Lake Paul	Lake Konstanz	Lake Kinneret	Takapoto Atoll	English Channel	Celtic Sea
bacteria	26			29	1	15	14
non-living material	41			0	40	0	0
zooplankton	5			18	21	26	21

ND not documented. For a better homogeneity, we allocated the protozoa to 'microzooplankton' and the metazoan plankton to 'mesozooplankton'. FCI, Finn Cycling Index [percentage of carbon flows in cyclic pathways; Finn (1976)].

*In the model of Takapoto Atoll, the mesozooplankton also grazed on benthic material.

food webs obtained by inverse analysis, i.e. the lagoon of Takapoto Atoll (French Polynesia; Niquil *et al.*, 2001) and models of euphotic zones in the English Channel and the Celtic Sea (Vézina & Platt, 1988).

The main source of carbon in Lake Biwa is photosynthesis by microphytoplankton (>20 µm). Phytoplankton were not separated into size fractions in the published lake models. Stone *et al.* (1993) did separate pyrophyte and non-pyrophyte nanoplanktonic algae in their models of Lake Kinneret for March to April and August to September. The relative contributions of these two groups were very different in the two periods, with non-pyrophyte nanoalgae representing 27% of photosynthesis in March to April and 95% in August to September. Photosynthesis during the summer is dominated by larger algae in Lake Biwa, unlike Lake Kinneret, but its variability is larger at Lake Kinneret.

Two of these studies included non-photosynthetic inputs. In Takapoto, grazing of mesozooplankton on the benthos was an important input. In Lake Biwa, non-photosynthetic inputs represent only 6% of the total input. The dominance of the >20 µm phytoplankton results large consumption of autotrophic organisms by mesozooplankton (51% of their diet, Table 8). This dominance was even stronger in Lake Kinneret, but the consumption of detritus by zooplankton was not considered as a possible flow in that study (Stone *et al.*, 1993).

Carbon from the planktonic system of Lake Biwa leaves evenly distributed among phytoplankton, bacteria, zooplankton respiration and export (sinking, and consumption of mesozooplankton production by non-planktonic animals). The main differences between it and Lake Kinneret are the higher phytoplankton respiration and lower bacterial respiration at Lake Kinneret, whereas zooplankton respiration is similar fraction of carbon outputs in both. In the studies of marine environments, phytoplankton and bacterial respiration were less important in carbon output than in Lake Biwa and zooplankton were mostly responsible for the removal of carbon.

In Lake Biwa, the direct link from phytoplankton to zooplankton is less important than the indirect link through non-living compartments, comprising two pathways: direct consumption of particulate detritus by meso- and microzooplankton and their consumption of bacteria. Bacterial production depends on the DOC excreted by the various living and dead com-

partments. The bacterial path is important in Lake Biwa, with major pathways going from living compartments to particulate detritus to DOC to bacteria, which are in turn consumed by microzooplankton. Thus, detritivory in one form or another plays a major role in secondary production. However, micro- and mesozooplankton differ in their use of newly photosynthesised versus recycled matter in their diets. Autotrophic matter is available mainly as phytoplankton >20 µm, which is grazed mostly by mesozooplankton. As a result, phytoplankton represent 3% and 51% of micro- and mesozooplankton diet. Because of the production rates for phytoplankton <20 µm, microzooplankton must rely on detritus and bacteria.

Given the species composition of mesozooplankton, the conclusion that the microbial assemblage contributes little to the diet of mesozooplankton is reasonable. From June to September, a calanoid copepod, *E. japonicus*, is the dominant mesozooplankton (Yoshida *et al.*, 2001a). This species grazes minimally on bacteria (Nagata & Okamoto, 1988). In addition, Nagata *et al.* (1996) showed experimentally that small flagellates accounted for <5% of the total carbon consumption by mesozooplankton when *E. japonicus* was dominant. *Eodiaptomus japonicus* can stimulate the growth rate of bacteria, probably through nutrient regeneration and substrate supply (Yoshida *et al.*, 2001b). Our results, together with those of previous studies, imply that the microbial assemblage predominantly respire carbon and regenerate nutrients, with only a relatively small flow to higher trophic levels, especially when calanoid copepods are dominant. There are several indices in the literature for estimating the importance of the microbial food web in the functioning of the plankton community. Gaedke & Straile (1994) used microbial food web efficiency, the ratio is the consumption of microzooplankton by mesozooplankton divided by the ingestion by microzooplankton (or its throughput). They describe this ratio as the quantification of how much microzooplankton makes the organic carbon available to macro-consumer. According to this ratio, Lake Biwa is the least efficient of systems in Table 7 at transferring carbon from microzooplankton to mesozooplankton. Although the throughput of microzooplankton is very high, the carbon goes mainly to detritus, DOC, and respiration. Only 10% of the microzooplankton throughput is transferred directly to mesozooplank-

ton. The one system with similar values for this index (7–13%) is the period following a summer flood in Lake Konstanz.

Vézina & Pace (1994) used a different index for estimating the microbial link. They calculate the consumption of heterotrophic microorganisms (bacteria and microzooplankton) by mesozooplankton as a percentage of mesozooplankton ingestion. This index is similar for Lake Biwa and marine systems. The difference between Lake Biwa and Lake Kinneret in August to September is not as strong as for the microbial food web efficiency previously discussed, but points in the same direction, i.e. a lowest efficiency of transfer from heterotrophic microorganisms to the macro-consumer in Lake Biwa. The index indicates that Lake Paul (Vézina & Pace, 1994) had an even lower efficiency than Lake Biwa.

Despite a high activity of bacteria and microzooplankton (dominated by protozoa), the dominant link to macro-consumers is not through the consumption of bacteria or microzooplankton, but through direct consumption of detritus by mesozooplankton. This may reflect the inability of mesozooplankton to graze efficiently on large algae. Also, the present results explain why the sinking flow was as low as 11% of primary production in spite of predominance of large less efficiently grazed algae: carbon in these algae was grazed after entering the detrital pool. Predominance of such large algae is a characteristic of the Lake Biwa plankton community (Kawabata & Nakanishi, 1994).

This interpretation about the dominance of recycling in the functioning of the Lake Biwa planktonic system is reinforced by the comparison of two network analysis indices, i.e. the FCI, which calculates the percentage of carbon flows involved in cyclic pathways and the ratio of detritivory to herbivory. These two indices are very high for Lake Biwa relative to both Lake Kinneret and marine systems (Table 8). The very high FCI in Lake Biwa stresses the importance of recycling compared with direct consumption of autotrophic compartments. The ratio detritivory/herbivory is even higher than the value observed in the lagoon of Takapoto Atoll, whereas this coral reef system highly depends on the consumption of detrital material for sustaining its high activity. This pattern is consistent with the above description of the planktonic system in Lake Biwa, which is based on high recycling of organic matter; the latter relies on direct consumption of detrital carbon by the heterotrophic

compartments. This conclusion is robust, as the detritivory to herbivory ratio is very high for all the simulations of the sensitivity analysis.

The use of the inverse analysis for estimating missing flow value was essential in this case, even if many of the flows were already well documented. The flows involving detritus were deduced from the calculation (i.e. from field data and physiological constraints), despite our inability to experimentally discriminate of living from non-living fine particles.

Detritus has a prominent role in this system with relatively low allochthonous carbon inputs. However, it could be more general observation as non-living particulate matter usually makes up a majority of the carbon content in lakes and most mesozooplankton cannot discriminate between living and non-living particles within their edible size ranges. This role for detritus in lakes is consistent with recent results showing the potential important place of detritus in mesozooplankton diet (Jeppesen *et al.*, 1999; Pilati, Wurtsbaugh & Brindza, 2004). It may be even stronger than observed in marine ecosystems (Lampitt, Noji & von Bodungen, 1990; Maar *et al.*, 2004). However, experimental confirmation of this detritivory for mesozooplankton and, especially, microzooplankton in Lake Biwa would be of great interest.

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