Chapter 25
The Fate of Organic Carbon

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Abstract In Lake Kinneret, the majority of photosyntetically produced organic carbon (OC) is cycled through the microbial loop. Taken together, bacterial production (BP) and bacterial respiration (BR), i.e., bacterial carbon demand (BCD), accounted for about 65 % of gross primary production (GPP), measured biweekly and averaging 2.3 g C m^{-2} day^{-1} during the last decade (2001–2011). Community respiration (CR) was 2.1 g C m^{-2} day^{-1}. The major contributors to total CR were bacterial and phytoplankton respiration (~80%) while zooplankton respiration accounted for the reminder. Most (~ 83 %) of the OC input were eventually respired, ~3 % lost to outflows, while ~15 % of the total OC input were transferred annually to the sediments. Here oxic mineralization is gradually replaced by anoxic processes as a function of the availability of suitable electron acceptors. After the depletion of oxygen in the hypolimnion, sulfate (500 μM) becomes the dominant oxidant. Depending on the settling flux of OC sedimentary sulfate reduction (SR) rates were measured from 0.01 to 1.67 μmol cm^{-3} day^{-1} in December and July, respectively. SR is the dominant anaerobic terminal decomposition process in Lake Kinneret and is responsible for the accumulation of sulfide in the hypolimnion to concentrations up to 400 μM. Methanogenesis is restricted to those sediment layers that are depleted of sulfate (below 3–5 cm). Seasonal profiles and 13C signatures of dissolved methane in the

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sediment pore water of Lake Kinneret have indicated anaerobic methane oxidation in the deeper sediments (below 20 cm), with Fe(III) as electron acceptor. Lake Kinneret resembles the first aquatic ecosystem where the existence of this process could be verified. Changes in the watershed and lake environment are suggested as possible causes for the apparently significant declines in bacterial numbers, BP, and BCD that have taken place over the last decade in Lake Kinneret.

Keywords Heterotrophic bacteria · Respiration · Bacterial production · Growth efficiency · Sulfate reduction · Sediments · Methanogenesis · Methanotrophy · Benthic boundary layer · Net heterotrophic · Net autotrophic

25.1 Heterotrophic Bacterial Production, Respiration, and Growth Efficiency

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25.1.1 Heterotrophic Bacteria in Organic Carbon Processing

As in most lakes, so too in Lake Kinneret, the metabolic activities of aerobic heterotrophic bacteria are major drivers of organic carbon (OC) cycling (Cole et al. 1988; del Giorgio and Williams 2005a). In Sect. 15.1, the patterns of bacterial abundance (BA) based on 4′,6-diamidino-2-phenylindole (DAPI) counts and some phylogenic and morphological data relating to Lake Kinneret bacteria are presented. Here, we shall show data concerning various aspects of bacterial metabolic activity and their far-reaching impacts on OC cycling of the lake.

25.1.2 Bacterial Production

The first set of monthly bacterial production (BP) measurements were made using the ^{3}H-thymidine method (Riemann et al. 1982) from June 1988 through May 1993 at five depths at Station A (location in Fig. 1.1 of Chap. 1). Routine measurements, using ^{14}C-leucine (Kirchman et al. 1985) were resumed only in 2001 on samples collected at Sta. A from 1, 5, 10, 20, 30, and 40 m and mid-thermocline depth. (For the ^{3}H-thymidine method, empirical conversion factors were used; literature values were used for the ^{14}C-leucine method.) The annual means for the two data sets (1988–1993 and 2001–2011) are shown in Fig. 25.1. Although the mean annual BP values for both periods appear to be very similar, it should be noted that during the first period sampling was much less frequent or complete than in 2001–2011. The former data set was used for the first models of carbon cycling in Lake Kinneret that emphasized and quantified the central role of the bacteria in carbon flux in this ecosystem (Stone et al. 1993; Berman and Stone 1994; Hart et al. 2000).

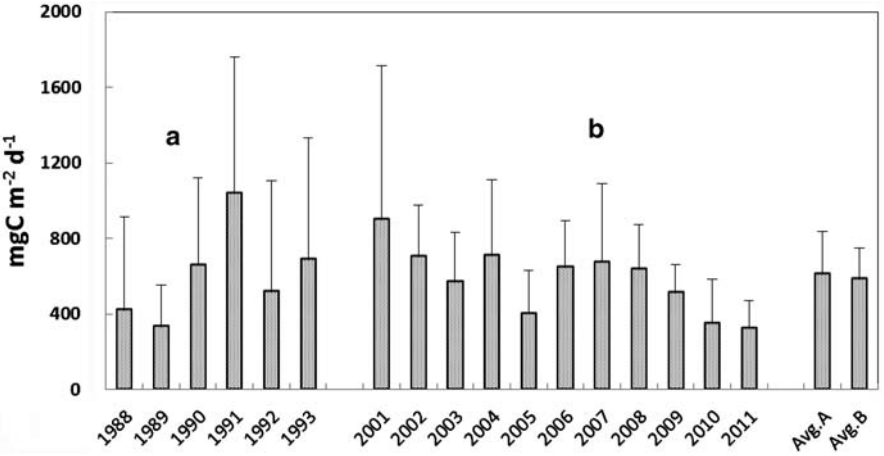

Fig. 25.1 Annual means (mg C m^{-2} d^{-1}) and standard deviations of bacterial production (*BP*) in the euphotic zone, 0–15 m at Sta. A. **a** From 1988 to 1993, measured with ^{3}H-thymidine. **b** From 2001 to 2011 measured with ^{14}C-leucine

From 2001 to 2011, the mean annual BP in the lake epilimnion was 558 ± 179 mg C m^{-2} day^{-1} with annual values ranging from 902 to 1,320 mg C m^{-2} day^{-1} in 2011 and 2001, respectively. Semiannual means of BP are given in Table 25.1. On a semiannual basis, BP ranged from 12 to 38 % (mean 25 %) and from 18 to 57 % (mean 38 %) of gross primary production (GPP) and net primary production (NPP), respectively. Until 2008, mean semiannual BP was always greater in January–June as compared to July–December, a pattern that also corresponded with PP levels. However, from 2009 through 2011, this pattern reversed, as has also been reported for primary production (see Chap. 24). Furthermore, as noted in Chap. 15, in the years from 2001 to 2011, there was a significant trend ($r^2 = 0.93$, $p < 0.0001$, $n = 11$) to lower annual average BA that coincided with a significant decrease ($r^2 = 0.57$, $p = 0.004$, $n = 11$) in BP; the annual means of BA and BP were also significantly correlated ($r^2 = 0.43$, $p = 0.028$, $n = 11$). The marked drop in BP has had a significant impact on OC flows within the lake system (see below).

The declines in the annual averages of both BA and BP in the epilimnic water do not appear to be correlated to any change in annual averages of phytoplankton biomass, primary production, or chlorophyll. Nevertheless, the apparently real and significant declining trend in BP and the changes in semiannual patterns of primary production and BP (Table 25.1; Fig. 25.1) appear to reflect a definite slowing down in the rate of OC cycling in the lake over the last decade. This trend may be a further indication of the profound ecosystem shift that has occurred (and is probably still ongoing) since the mid-1990s (Zohary and Ostrovsky 2011).

As previously reported for the period 2001–2007 (Berman et al. 2010), strong correlations were obtained from 2001 to 2010 between semiannual BP and total community respiration (CR; $r^2 = 0.67$, $p = < 0.0001$, $n = 22$). A rather weaker, but still significant correlation was observed between semiannual BP and GPP ($r^2 = 0.22$, $p = 0.03$, $n = 22$) from 2001 to 2011.

Table 25.1 Semiannual means of gross primary productivity (GPP, calculated as 1.5 *14C-measured primary productivity (see Chap. 24)), phytoplankton respiration (*PR*), community respiration (*CR*), bacterial productivity (*BP*), bacterial respiration (*BR*), and zooplankton respiration (*ZR*) from 2001 to 2011

	January–June						July–December					
	GPP	PR	CR	BP	BR	ZR	GPP	PR	CR	BP	BR	ZR
2001	2,610	780	2,460	990	1,120	560	2,350	710	2,150	810	970	480
2002	2,350	700	2,310	740	1,070	530	2,150	640	1,710	660	710	360
2003	3,050	910	3,190	720	1,520	760	1,850	550	1,560	420	670	340
2004	2,870	910	3,370	870	1,640	820	2,210	680	1,660	550	650	330
2005	1,770	530	1,940	400	940	470	1,990	600	1,450	400	570	280
2006	2,470	740	2,080	660	890	450	2,030	610	1,700	630	730	360
2007	2,520	760	2,920	840	1,440	720	1,960	590	2,090	510	1,000	500
2008	2,450	650	1,500	700	570	290	2,360	680	1,550	560	580	290
2009	2,130	670	1,420	510	500	250	2,220	630	1,720	510	730	360
2010	2,390	730	1,970	310	820	410	2,340	710	1,840	390	750	380
2011	1,980	590	1,410	300	540	270	2,850	860	nd	350	nd	nd
Average	2,420	725	2,234	640	1,005	503	2,210	660	1,743	526	736	368
SD	350	112	660	221	380	189	260	80	215	131	137	68

All values are in mg C m^{-2} day^{-1}
SD standard deviation, *nd* not defined

25.1.3 Bacterial Growth Rates and Turnover Times

The estimation of cell-specific C incorporation rates (expressed as fg C $cell^{-1}$ day^{-1} and calculated as BP/BA from samples taken monthly at five depths in Sta. A) from 2001 through 2011 falls within the expected ranges. Overall mean cell-specific carbon uptake for epilimnic depths (0–15 m) was 18.0 ± 1.2 fg C $cell^{-1}$ day^{-1}. Assuming a mean bacterial cell content of 30 fg C bacterial $cell^{-1}$ (Stone et al. 1993; Hart et al. 2000), this would give a mean carbon turnover (doubling) time of 3.1 ± 0.4 days. Note that despite the large decreasing trends observed in both the annual mean BA and BP, the ratio BP:BA (i.e., cell-specific carbon uptake) showed no significant trend and remained more or less constant throughout the period 2001–2011.

For hypolimnic depths (samples taken close to 40 m), mean cell-specific carbon uptake was distinctly slower with much higher variability (13.4 ± 5.8 fg C $cell^{-1}$ day^{-1}), and with longer turnover times (7.3 ± 10.9 days). These values for samples from the anaerobic hypolimnion should be viewed with caution since the actual BP measurements were not made under strictly anaerobic conditions. Nevertheless, because metabolic efficiency would be expected to be lower in anaerobic than aerobic environments (Fenchel and Finlay 1995), it is reasonable that bacteria in the hypolimnion would have considerably slower C uptake rates and turnover times than epilimnic bacteria.

The above values for cell-specific carbon uptake and turnover times were based on the assumption that all DAPI-counted bacterial cells (Chap. 15) were metabolically active. Berman et al. (2001) used three different staining techniques,

each of which detected different aspects of cellular state or metabolic activity to assess the proportion of active bacteria within the total counted population. Their data indicated that in Lake Kinneret, usually only a small fraction (probably < 20 %) of the entire bacterial assemblage was metabolically active at any given time. In this case, the active bacterial population would have cell-specific carbon uptake rates of ~ 90 fg C $cell^{-1}$ day^{-1} and turnover times of about 14–15 h. Unfortunately, no studies have been made in Lake Kinneret of the impact on bacterial cell turnover of lysis by bacteriophage (Suttle 2007).

Berman et al. (2001) also observed that even apparently inactive bacteria could become highly active under appropriate conditions (Choi et al. 1999). This "switching on" might occur as a result of nutrient inputs caused by upwelling events, or on a more localized scale, because of inputs from protistan or zooplankton excretion or sloppy feeding (Jumars et al. 1989) or from algal cell lysis (Berman and Wynne 2005). Thus, the bacterial populations in the lake should be regarded as a dynamic mixture with various components functioning at different degrees of activity at any given moment, constantly modulating their physiological activities to changes in their localized environment.

25.1.4 Bacterial Respiration, a Major Fraction of Total Community Respiration

Bacterial respiration (BR) was estimated using the method suggested by Berman et al. (2004, 2010) as follows:

$$BR = CR - PR - ZR \quad (1)$$

where CR is community respiration, PR is phytoplankton respiration, and ZR is zooplankton respiration. CR was directly measured by the ΔO_2 method (Sect. 25.2). PR was calculated as 0.3* GPP derived as 1.5* primary production (PP) determined by routine ^{14}C measurements of PP (Sect. 24.1). Based on previous studies (Berman and Pollingher 1974; Berman et al. 1995), these PP values were assumed to be close to NPP.

Some explanation of the ZR term is required. Historically, crustaceans (cladocera and copepods) together with the rotifers were included in the category of "zooplankton" (Gophen 1978). Hambright et al. (2007) used the term "microzooplankton" to describe the assemblage of rotifers, numerous ciliated and flagellated protists, and nupliar stages of copepods. In their previous work, Berman et al. (2010) used ZR values based on routine monitoring measurements of the crustacean and rotifer biomasses multiplied by experimentally determined group-specific respiration rates (Gophen 1981) to obtain BR (Eq. 1 above); however, similar ZR values were calculated by assuming that ZR ranged from 0.33 to 0.5 BR (for details, see Berman et al. 2010). There are no data available on ciliate or flagellate respiration in the lake and no explicit mention of protist respiration has been made in previous studies. In

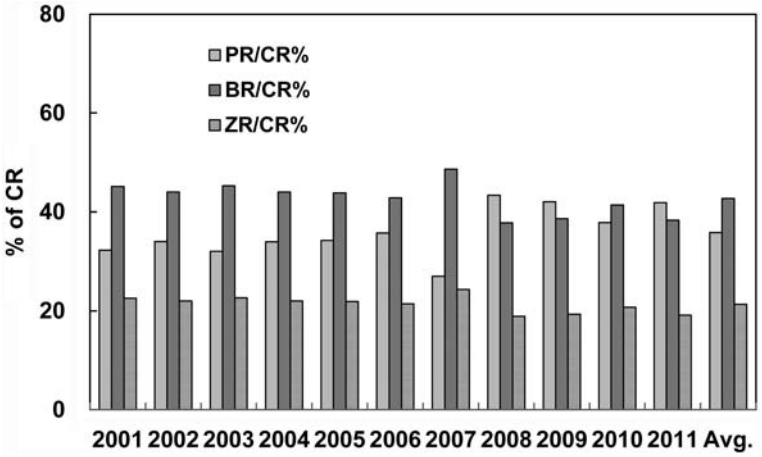

Fig. 25.2 Relative contribution to total community respiration (*CR*) by phytoplankton (*PR*), bacteria (*BR*), and zooplankton (*ZR*), based on annual means from 2001 to 2011 (Table 25.2), Sta. A. (Note: 2011 values are based on January–June data only)

the present study, ZR was taken to include both crustacean and microzooplankton respiration and assigned a value of 0.5 BR; therefore

$$\mathrm{BR} = (\mathrm{CR\text{-}PR})/1.5 \tag{2}$$

This implies that the directly measured values for crustacean ZR in Berman et al. (2010) were overestimated and that the ZR values used in their study included respiration of the protists as well as crustaceans and rotifers. (Note: Fish respiration, based on biomass, has been estimated at between 3 and 5% of CR (Stone et al. 1993), which is below the sensitivity of this method; therefore, this source of respiration has been omitted.)

The semiannual means of BR (Eq. 2) from 2001 to 2011 are given in Table 25.1. There was a strong, positive correlation between BR and BP ($r^2=0.41$, $p=0.0018$, $n=21$), although the decrease in BR during this period was only weakly significant ($r^2=0.20$, $p=0.0412$, $n=21$). Generally, with the exception of 2009 and 2010, BP levels were higher in January–June than in July–December as might be expected because of the higher levels of phytoplankton biomass and GPP at this season (see Sect. 24.1).

The relative proportions contributed annually by PR, BR, and ZR to total CR are shown in Fig. 25.2. The 10-year averages of PR, BR, and ZR as percentages of CR were 36, 43, and 21%, respectively. With the exception of 2008 and 2009, BR was always the major component of CR. As previously observed (Hart et al. 2000; Berman et al. 2004, 2010), ZR was consistently the smallest contributor to CR ranging from 14 to 24% on an annual basis and showing no clear trend during these years.

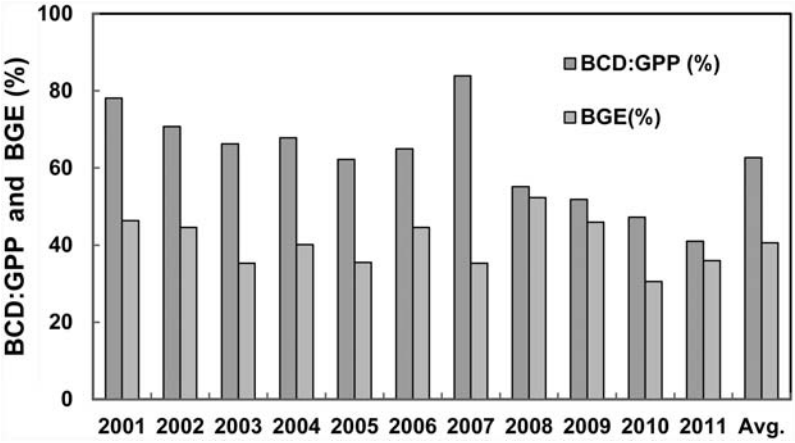

Fig. 25.3 Annual means of bacterial carbon demand: gross primary production (*BCD:GPP*) and bacterial growth efficiency (*BGE*) from 2001 to 2011, Sta. A. (Note: 2011 values are based on January–June data only)

25.1.5 Bacterial Carbon Demand and Bacterial Growth Efficiencies

Previous studies (Berman et al. 2004, 2010) had shown high levels of bacterial carbon demand (BCD; defined as BP+BR) in Lake Kinneret, consistent with the generally high levels of BP and BR. As shown in Table 25.1 and Fig. 25.3, a large proportion of GPP was cycled through the epilimnic bacterial community. These are high, but by no means impossible levels for BCD:GPP (Table 25.2). Even in the absence of external inputs, the total bacterial carbon uptake by heterotrophic bacteria and by secondary and tertiary consumers can sometimes exceed GPP because of recycling within the system (Strayer 1988), as was shown to be the case for Lake Michigan (Scavia 1988). For the years 2001–2007, Berman et al. (2010) reported annual mean BCD:GPP% of 75 ± 17% for the entire period 2001–2010; however, BCD:GPP% decreased to 65 ± 13% as a result of the sharp drop in BCD since 2007. There was an overall slight but significant decrease ($r^2 = 0.46$, $p = 0.029$, $n = 10$) in BCD from 2001 to 2010.

BCD levels tended to be somewhat higher during the first half of the year (average 66 ± 14%) than in the second half (60 ± 10%) with the notable exception of 2009 and 2010. In these years, BCD fluxes were only about half of those measured in peak years, although GPP levels did not show a similar drop. BCD reached a maximum of 84% during the *P. gatunense* bloom of 2007 (Table 25.2). It is reasonable to assume that this seasonal pattern reflects the increased cycling by heterotrophic bacteria of dissolved organic carbon (DOC) derived directly or indirectly from the larger biomasses of phytoplankton usually present in winter–spring than in summer–fall. Sherr et al. (1982) demonstrated that bacterivorous

Table 25.2 Semiannual means of bacterial carbon demand (*BCD*), bacterial growth efficiency (*BGE*), bacterial production: gross primary production (*BP:GPP*) and *BCD:GPP*, 2001–2011 at Sta. A

	January–June				July–December			
	BCD mg C m^{-2} day^{-1}	BP:GPP (%)	BCD:GPP (%)	BGE (%)	BCD mg C m^{-2} day^{-1}	BP:GPP (%)	BCD:GPP (%)	BGE (%)
2001	2,110	38	81	47	1,780	34	76	46
2002	1,810	32	77	41	1,380	31	64	48
2003	2,240	24	73	32	1,090	23	59	38
2004	2,510	30	87	35	1,200	25	54	46
2005	1,340	23	76	30	970	20	49	41
2006	1,560	27	63	43	1,360	31	67	47
2007	2,290	34	91	37	1,510	26	77	34
2008	1,290	29	53	56	1,140	24	48	49
2009	1,010	24	47	51	1,240	23	56	41
2010	1,130	13	47	27	1,140	16	49	34
2011	810	15	41	36	nd	12	nd	nd
Average	1,645	26	67	39	1,281	24	60	42
SD	552	7	17	8	223	6	10	5

SD standard deviation, *nd* not defined

flagellates increased the decomposition rate of the dinoflagellate carbohydrate thecae by increasing the rate of recycling of nutrients, which stimulated bacterial activity. Thus, the heterotrophic flagellates could be a driver for the increased bacterial (i.e., microbial loop) carbon demand during dinoflagellate blooms in the lake.

Over the period 2001–2010, there was a significant trend of decreasing BCD:GPP measured in winter–spring but not in summer–fall. The drop in both the absolute amounts of BCD and the ratio of BCD:GPP in the winter–spring season may have resulted from the trend to fewer *Peridinium* years. In any event, the decrease in the flux of OC via the microbial loop may be connected with lower levels of BP and BA (see above and Chap. 15).

In contrast to BCD, annual mean bacterial growth efficiencies (BGE; defined as BP/(BP+BR)) showed no consistent, significant change over the period 2001–2011 (Fig. 25.3). The overall, average annual BGE (41 ± 6 %) was very similar to that reported for the years 2001–2007 (Berman et al. 2010). In general, estimates for BGE levels in this lake tend to be higher than in most reported freshwater systems. However, it is presently unclear whether these high BGE estimates are accurate or reflect some inherent difference between various methods used for estimating BGE. In the present study, we have assumed that the respiration of protists is included in the ZR term; thus, BR refers to bacterial respiration only. The indirect method of calculating BR (and hence BGE) used here has not been widely used. Most BR measurements reported in the literature to date have utilized experimental data from 1-μm filtered water to directly estimate BR; this approach also has some limitations (see Berman et al. 2010). Future research should compare results obtained with both the above approaches to estimate BR and BGE.

25.1.6 What Caused the Significant Drop in BP, BA, and BCD From 2001 Through 2010?

As documented elsewhere (Chaps. 10 and 11), the most visible evidence of ecosystem change in Lake Kinneret has been the disruption of the regular seasonal pattern of phytoplankton development (as typified by late winter–early spring blooms of *P. gatunense* with dominance of small chlorophytes in summer–fall) to highly erratic dinoflagellate blooms and the increasing dominance of N_2-fixing cyanobacteria especially in summer–fall. Here, we have shown that dramatic changes have also occurred both in the abundance (Chap. 15) and in the metabolic activity of the bacterial populations from 2001 to 2011.

Not much is known about limiting factors for the bacterial populations in this lake. Zohary et al. (2000) found that P addition enhanced bacterial degradation of dinoflagellate thecae in Lake Kinneret water. Pinhassi and Berman (2003), working with samples taken from near-surface lake waters, found that P appeared to be limiting BP and growth at most times. Additionally, similarly to previous research (Berman et al. 1993), they found that the availability of Fe or chelators could play an important role in regulating bacterial metabolism and growth even in Lake Kinneret where ambient concentrations of total Fe are relatively high. These observations might suggest two possible causes for the significant continuous decreases in BP, BA, and BCD levels from 2001 to 2011 documented here: (1) From the mid-1990s, major hydrological changes in the catchment area have altered the amounts and characteristics of organic chelators and/or Fe and other trace metal ions flowing into the lake. (2) Prolonged periods of low lake levels and low volume winter inflows may have been responsible for the increasing abundance of N_2-fixing cyanobacteria (Chap. 12). These cyanobacteria would be expected to compete more effectively with the heterotrophic bacteria for relatively scarce available nutrients, especially P and Fe, than the previously dominant chlorophytes and dinoflagellates. In any event, there appears to be little doubt that a profound shift in carbon cycling has taken place over the last decade in Lake Kinneret.

25.2 Community Respiration

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25.2.1 Background

Dark pelagic respiration (hereafter, CR) is a major flux in biogeochemical cycles, being the largest sink for organic matter and oxygen in freshwater lakes (del Giorgio and Williams 2005b; Pace and Prairie 2005). Traditionally, CR has been measured as oxygen depletion (ΔO_2) in dark bottles ("dark respiration"). A basic assumption

Table 25.3 Community respiration (*CR*) in Lake Kinneret measured at different periods

Period	Method	CR		Reference
		g O_2 m^{-2} day^{-1}	g C m^{-2} day^{-1}	
1964–1965	ΔO_2	7.6	2.28	Hepher and Langer 1969
1972	Carbon budget	6.27	1.88	Serruya et al. 1980
1970–1990	Oxygen budget	3.18	0.95	Nishri et al. 1998
1996–1998	$^{18}[O_2]$	19.4	5.82	Luz et al. 2002
2001–2010	ΔO_2	6.86	2.06	This study

of the oxygen method is that CR rates in the light and dark are similar. Although this assumption has been controversial (Pringault et al. 2007, 2009), in most ecological situations, differences between light and dark CR appear to be insignificant (Winberg 1960; Aristegui et al. 1996; Gazeau et al. 2007).

The first systematic determinations of CR in Lake Kinneret were made by Hepher and Langer (1969), who used the ΔO_2 method. Subsequently, lake CR has been estimated from the budget of OC (Serruya et al. 1980), from daily changes in the pool of dissolved oxygen (Nishri et al. 1998) and using $^{18}O_2$ (Luz et al. 2002). From 2001, CR was monitored biweekly at the central pelagic Sta. A (see location in Chap. 1, Fig. 1.1), using the ΔO_2 method. This involved in situ incubations of water from five depths (0, 1, 5, 10, and 15 m) in dark bottles over 24 h. A factor of 0.3 was used to convert mg O_2 L^{-1} to mg C L^{-1} (i.e., Respiration Quotient, RQ = 0.8). In natural aquatic environments, an RQ of 0.8 may be more accurate than the often used RQ = 1 for CR because the respiration of organic matter includes proteins and lipids in addition to carbohydrates (Winberg 1960; Geider 1997; Robinson 2008).

25.2.1.1 Community Respiration in Lake Kinneret (1964–2010)

Estimates of CR in the lake, based on measurements made by a variety of methods, are shown in Table 25.3. The annual average value of CR for the period from 2001 to 2010, when the most detailed monitoring of this parameter was carried out, is surprisingly close to early estimates obtained in 1964–1965 (Hepher and Langer 1969) and in 1972 (Serruya et al. 1980). Although it is tempting to suggest that this similarity of CRs attests to a relative stability in the rates of aerobic decomposition of organic matter over the decades, we note that the early data are based on relatively few actual measurements. Much lower CR values (3.18 g O_2 m^{-2} day^{-1} or 0.95 g C m^{-2} day^{-1}) were calculated by Nishri et al. (1998) for the period 1970–1990, based on oxygen mass balance calculations. It seems probable that these CR values were considerably underestimated because they are much lower than values for average daily primary production (1.54 g C m^{-2} day^{-1}) measured by the ^{14}C method for the same period (Berman et al. 1995; Yacobi 2006). Furthermore, it seems unlikely that lower CR would occur during a period of overall higher standing stock algal biomass. In contrast, extremely high CR values were reported by Luz et al. (2002) for the years 1996–1998 using the $^{18}O_2$ method (Table 25.3).

25.2.1.2 Community Respiration from 2001 to 2010

Berman et al. (2010) reported that from 2001 to 2007, annual CR averaged 7.28 g O_2 m^{-2} day^{-1}. Community respiration was consistently higher in winter–spring than in summer–fall by an average factor of 1.48 (±0.37). It was also correlated closely with BP as well as with parameters of phytoplankton biomass (Chl) and photosynthetic activity.

The average annual values for CR for the period 2001 to 2010 (Fig. 25.4a) averaged 6.86±1.91 g O_2 m^{-2} day^{-1} and ranged from 4.93±2.53 g O_2 m^{-2} day^{-1} in 2009 to 9.91±6.18 g O_2 m^{-2} day^{-1} in 2007. Daily levels of CR varied very widely from 0.61 to 31.7 g O_2 m^{-2} day^{-1}. The highest CR values (>15 g O_2 m^{-2} day^{-1}) were recorded in spring during intense dinoflagellate blooms ("*Peridinium* years," when maximum phytoplankton biomass exceeded 100 g m^{-2}; Zohary et al. 2012) that occurred in 2003, 2004, and 2007; in years without such blooms ("non-*Peridinium* years"), the spring maxima of CR were smaller or even absent. The discrepancy between these two annual patterns of CR is most clearly shown by comparing the monthly CR recorded in 2004 and 2009 (Fig. 25.4b). Community respiration was much higher during the first half of 2004 than in 2009; subsequent monthly differences between these years were minimal. It seems reasonable to assume that the greater input of OC that occurred as a result of the *Peridinium* blooms provided the substrate for enhanced respiration rates recorded during these years. During dense dinoflagellate blooms, high CR values were measured even when the upper water layer (0–15 m) was supersaturated (up to 130%) with oxygen. On these occasions, GPP should be higher than the corresponding measured CR values which ranged from 4.50 to 31.7 g O_2 m^{-2} day^{-1} (1.35–9.51 g C m^{-2} day^{-1}) assuming no significant allochthonous inputs of OC. Such high values for GPP greatly exceed primary production rates measured with the ^{14}C method during *Peridinium* blooms. In general, the ^{14}C method as used in the long-term studies in Lake Kinneret gives values close to NPP (Berman and Pollingher 1974); during dense *Peridinium* blooms, the ratio of GPP:NPP was close to 2 (see Chap. 24.1).

The mean monthly CR (averaged for the period 2001–2010) is shown in Fig. 25.4c. Despite the large variability shown in these measurements, there was nevertheless a clear trend of higher CR in the late winter–spring months (April, May). Overall, CR was consistently higher in winter–spring than in summer–fall by a factor of 1.44, consistent with the generally higher levels of phytoplankton biomass measured during the former season.

25.2.2 Contributions of Major Biological Groups to CR

Phytoplankton, heterotrophic bacteria, and zooplankton (including protista) all contribute to the total measured CR in the epilimnic waters of Lake Kinneret. Some attempts have been made to measure directly respiration rates for heterotrophic bacteria (Berman et al. 1979), phytoplankton (Berman and Gerber 1980; Berman and Kaplan 1984a, 1984b), and zooplankton (Gophen 1981). The first estimates

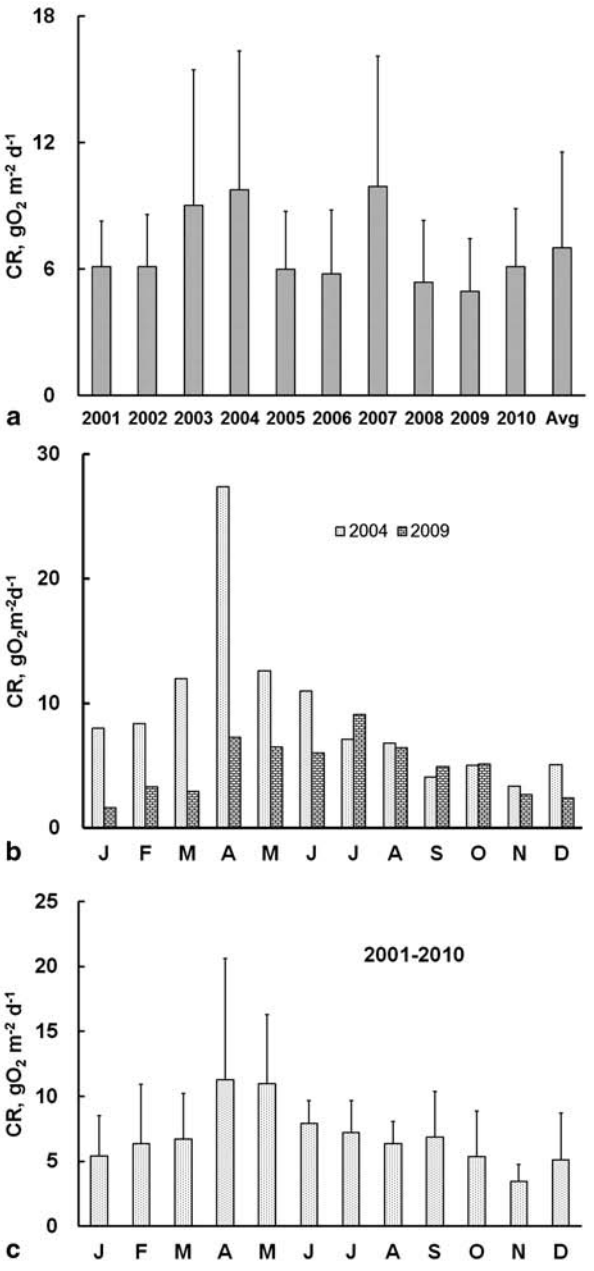

Fig. 25.4 Lake Kinneret community respiration (*CR,* g O_2 m^{-2} d^{-1}) recorded at Sta. A, 2001–2010. **a** Annual averages and overall average (*Avg*). **b** Monthly *CR* for a "*Peridinium* year" (2004) and "non-*Peridinium* year" (2009). The annual mean contributions of dinoflagellates to total phytoplankton biomass were 65.5% in 2004 and 38.4% in 2009. **c** Multi-annually averaged monthly *CR* for the period 2001–2010. Whiskers in **a** and **c** indicate standard deviation (*SD*)

for the specific contribution of the major planktonic biological groups to overall lake CR were derived from carbon mass balances measured from 1989 to 1992 (Hart et al. 2000). These indicated (Fig. 25.5) that heterotrophic bacterial and PF

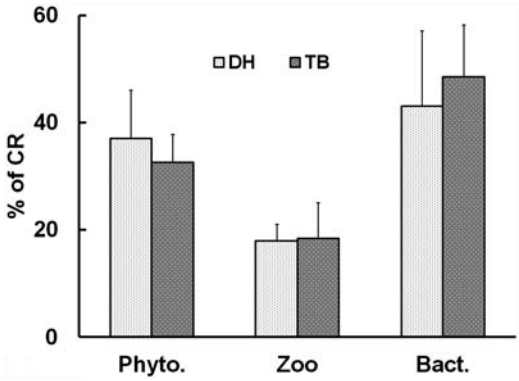

Fig. 25.5 The relative contributions of three groups of planktonic organisms to total community respiration (*CR*). DH (D. Hart): estimates based on Hart et al. (2000) for the years 1989–1992; TB (T. Berman): estimates based on Berman et al. (2010) for the years 2001–2010. Whiskers indicate standard deviation (*SD*)

contributed about equally (~40 % each) to total CR, with only ~20 % contributed by zooplankton (cladocera, copepoda, rotifers) and protozoa (ciliates and flagellates). The contribution of fish respiration was at most only a few percent of total CR.

The data on dry weight-specific respiration (mg O_2 $mgTSS^{-1}$ day^{-1}) associated with seston dominated by different algal groups are presented in Table 26.3 of Chap. 26.

Berman et al. (2004, 2010) introduced a method of estimating the relative amounts of respiration contributed annually by PR, BR, and ZR to total CR. Using this approach, the calculated, overall, 10-year (2001–2011) averages of PR, BR, and ZR of CR were 36, 43, and 21 % of CR, respectively (details in Fig. 25.2, Sect. 25.1). With the exception of 2008 and 2009, BR was always the major component of CR, slightly higher than PR. As previously estimated (Hart et al. 2000; Berman et al. 2004, 2010), ZR was consistently the smallest contributor to CR, ranging from 14 to 24 % on an annual basis and showing no clear trend during these years. Note, the contribution of fish respiration to total CR was excluded here because it was assumed to be too low to be within the resolution of this method.

25.3 Sulfate Reduction

Ora Hadas and Riki Pinkas

25.3.1 Introduction

Anaerobic mineralization of organic matter is mediated by a series of bacterial metabolic pathways such as nitrate reduction and manganese and iron reduction with sulfate reduction and methanogenesis being the terminal processes in the anaero-

bic decomposition of organic matter (Oremland and Polcin 1982; Ingvorsen and Jorgensen 1984; Capone and Kiene 1988). Sulfate-reducing bacteria (SRB) play a key role in the mineralization processes in marine sediments, but significant sulfate reduction rates have also been reported for freshwater sediments, despite low sulfate concentrations in the pore water (King and Klug 1982; Landers and Mitchell 1988). This finding suggests that SRB in freshwater have acquired high-affinity sulfate uptake systems to cope with the low sulfate concentrations (Smith and Klug 1981; Ingvorsen and Jorgensen 1984). High substrate affinities of SRBs for acetate, H_2, and other electron donors can account for the inhibition of methanogenesis in sulfate-rich environments (Lovley and Klug 1986; Skyring 1988), although syntrophism in methanogenic environments is not excluded (Plugge et al. 2011). Although until recently sulfate reduction was considered a strict anaerobic process (Postgate 1984), we know today that SRBs may thrive under oxidizing conditions in which they respire with nitrate or even oxygen (Canfield and Des Marais 1991; Frund and Cohen 1992; Cypionka 2000).

Sulfate reduction is one of the major driving forces in the maintenance of deep water anoxia in Lake Kinneret. As in other sites, sulfate reduction forms the basis of the biological sulfur cycle in this lake. The factors controlling the rate of sulfate reduction are: (1) availability of organic matter from decomposing material, mostly planktonic carbon in the water column; (2) ambient SO_4^{2-} concentration; (3) redox potential; (4) temperature; and (5) pH (Westrich and Brenner 1988).

The conditions in Lake Kinneret hypolimnion and sediments regarding those controlling factors were followed closely at Sta. A (station location map in Fig. 1.1 of Chap. 1) during 1988–1989. Two other stations Sta. G and the shallow Sta. S were studied during different seasons in 1991 and 1992. The findings are summarized below.

25.3.2 Sources of Organic Matter

The annual average of total phytoplankton biomass was similar in 1988 and 1989 (73 g wet wt m^{-2} in 1988 and 74 g wet wt m^{-2} in 1989). In 1988, the highest biomass (225 g wet wt m^{-2}) was observed in February due to a bloom of the filamentous diatom *Aulacoseira granulata* (182 g wet wt m^{-2}) whereas the *Peridinium* peak appeared in May (124.7 g wet wt m^{-2}). In 1989, the *Peridinium* peak was in March–April (166, 184 g wet wt m^{-2}), contributing more than 90 % of the total phytoplankton biomass; no significant biomass of *Aulacoseira* was observed in 1989 (Table 25.4).

The heavy filaments of *A. granulata* appear in the water column in times of high turbulence, and at the end of the turbulent period, they sink toward the sediments (mixed water column), supplying fresh organic material to the sediments. These blooms supplied the organic matter for sulfate reduction by SRBs in the hypolimnion and sediments, where anoxia existed, sulfate was available, and temperature and pH were also suitable, as discussed below.

Table 25.4 Monthly mean total, *Peridinium gatunense* and *Aulacoseira granulata* biomass (g w.w. m^{-2}) at the trophogenic layer at Sta. A, and sulfate reduction rates (mmol m^{-2} $month^{-1}$)

Month	Total biomass		*Peridinium*		*Aulacoseira*		SO_4^{-2} reduced	
	1988	1989	1988	1989	1988	1989	1988	1989
January	91.7	97.2	11.2	21.3	58.5	NS	152	100
February	225	99	24.8	43.2	182	NS	260	115
March	126.7	166.4	61	157.2	54.8	NS	–	137
April	91.5	183.9	83.4	177.7	NS	NS	229	148
May	134.2	108	124.7	97.9	NS	NS	216	–
June	58.2	35.4	40.7	14.6	NS	NS	527	193
July	35.4	44.7	23.6	24	NS	NS	880	580
August	18.3	31.2	1.7	11.5	NS	NS	421	305
September	25	28.5	2.6	5.6	NS	NS	416	169
October	36.7	24.2	3.8	7.3	NS	NS	207	224
November	23.6	28.6	3.4	15	NS	NS	146	239
December	27.7	28.5	6.8	16.6	NS	NS	119	46

NS not significant

25.3.3 Sulfate and Sulfide Concentrations

Hypolimnion: Strong seasonal variations in sulfate and sulfide concentrations in the hypolimnion of Lake Kinneret were found. Levels of sulfate ranged from 531 to 547 μM during holomixis and dropped to minima of 198–219 μM in December, at the end of the stratification period. An inverse pattern was observed for sulfide concentrations, 0 during the mixing period and reaching maxima of 309 and 366 in 1988 and 1989, respectively, just before overturn (Fig. 25.6). The decrease in sulfate concentrations corresponded stoichiometrically to the increase in that of sulfide, suggesting that intensive sulfate reduction was occurring in the hypolimnion of the lake, with sulfide accumulating as a result of sulfate reduction. The higher sulfide concentrations in 1989 compared with 1988 were probably due to a smaller hypolimnion volume, due to lower water levels (1,555 and 1,296 million m^3 in 1988 and 1989, respectively).

Sediments: The highest sediment pore water sulfate concentrations were found during the mixing period in February, 438 μM at 0.3 cm depth in 1988 and 781 μM at 0.6 cm depth in 1989 due to turbulence, oxygen diffusion into the first few millimeters and bioturbation by transitory dwellers (e.g., *Leydigia* sp., Cladocera), and some copepods and chironomids. Minimum values were detected toward the end of the stratification period, 8–20 μM, of sulfate in November–December 1988 (Fig. 25.7). In some years, no sulfate is detected in December below 1.5 cm.

25.3.4 Arylsulfatase

When sulfate concentrations are low, the enzymatic activity of arylsulfatases may supply part of the sulfate demands of SRB in the sediments. In Lake Kinneret, the activity of arylsulfatase varied with depth and season (Hadas and Pinkas 1992,

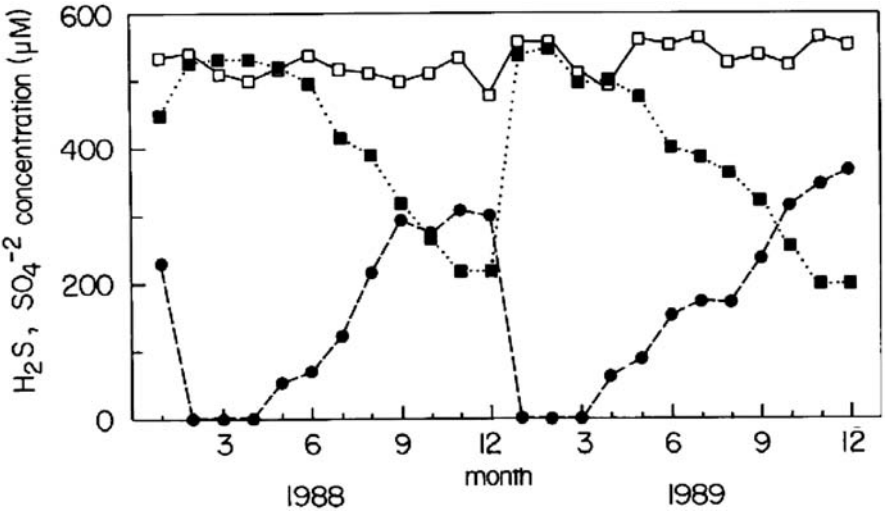

Fig. 25.6 Monthly average concentrations (µM) of sulfate at 10-m depth (*empty squares*) and sulfate (*full squares*) and sulfide (*circles*) at 40-m depth at Sta. A in Lake Kinneret, 1988–1989. (Reproduced from Hadas and Pinkas 1995a with permission from Wiley)

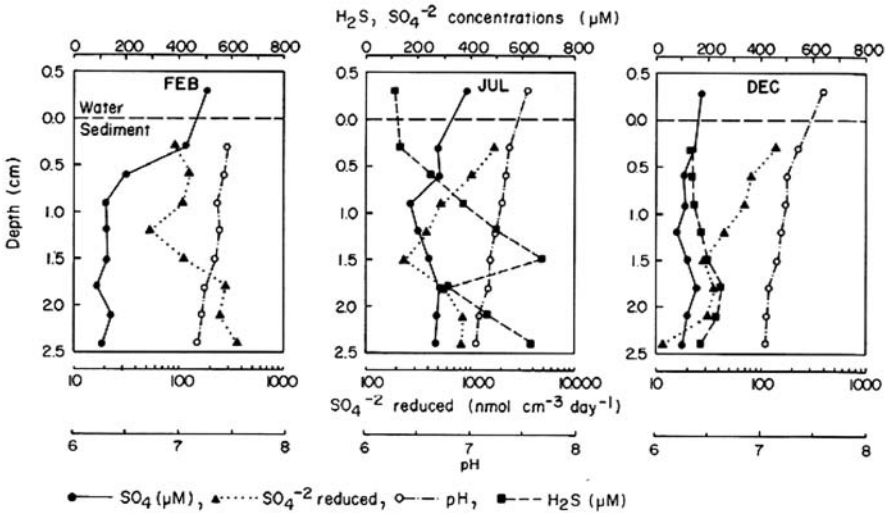

Fig. 25.7 Depth profiles of H_2S and SO_4 concentrations and pH and sulfate reduction rates in different seasons in Lake Kinneret sediments and overlying water. (Reproduced from Hadas and Pinkas 1995a with permission from Wiley)

1997). Maximum activity was found in the sediments in July (670 nmol *p*-nitrophenol, PNP, g w.w.$^{-1}$ h^{-1}) and December, and minimum in February. The lower activity in February was correlated with high SO_4^{-2} available. During the stratified period,

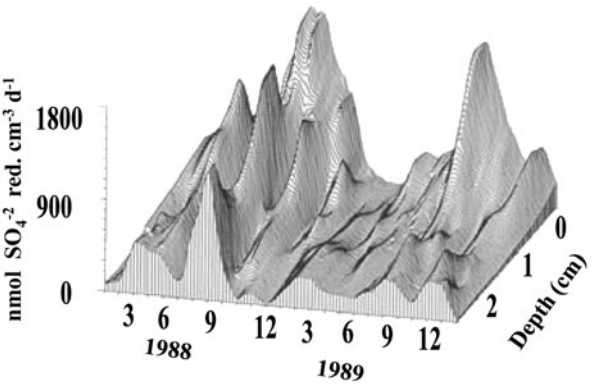

Fig. 25.8 Time–depth distribution of rates of sulfate reduction in Lake Kinneret sediments in 1988–1989. (Reproduced from Hadas and Pinkas 1995a with permission from Wiley)

intensive sulfate reduction resulted in decrease in SO_4^{-2} concentrations and increase in arylsulfatase activity. At the decline of the *Peridinium* bloom, supplying organic matter and sulfate esters, high arylsulfatase activity was induced (Hadas and Pinkas 1992, 1997).

25.3.5 Redox, Temperature, and pH

The pH in the sediment cores decreased with depth and ranged between 7.45 and 7.05 with no seasonal variation (Fig. 25.7). The temperature of the hypolimnion at Sta. A is in the range of 14–16 °C and does not vary during the year, with interannual variations averaging 2 °C. There is a drop in redox potential in the sediment due to availability of organic matter, high microbial activity, and depletion of oxygen at the beginning of summer. These conditions enabled intense sulfate reduction activity (Figs. 25.7 and 25.8).

25.3.6 Sulfate Reduction Rates

Sediment cores were taken with a Tessenow gravity sampler (Tessenow et al. 1977) at Sta. A (Central, 42 m depth) during 1988–1989 and at Sta. G (Northern, 22 m) influenced by the Jordan River, and Sta. S (shallow, 10 m) representing sediments covered with oxic water the whole year. Sampling was carried out at different seasons of the year, corresponding to the thermal stratification and *Peridinium* bloom: (1) in February during full mixing at the beginning of the *Peridinium* bloom, (2) in July after the crash of the bloom, and (3) in December during stable stratification. Sulfate reduction rates were measured by the method of Jorgensen (1978) using $Na_2{}^{35}SO_4$ as described previously (Hadas and Pinkas 1992, 1995a, 1995b).

25.3.6.1 Hypolimnion

According to the stoichiometric equation:

$$2(CH_2O)_n + SO_4^{-2} \rightarrow 2HCO_3^- + H_2S \quad (3)$$

2 mol of OC are oxidized per mole of sulfate reduced. The accumulation of H_2S in the hypolimnion was accompanied by a decrease in SO_4^{-2} concentrations of 0.31 and 0.35 mM in 1988 and 1989, respectively (Fig. 25.6). The average hypolimnion volume of the lake was 1,555 and 1,296 million m^3 in 1988 and 1989, respectively. Accordingly, 964×10^6 and 907×10^6 mol C could have been oxidized in 1988 and 1989 via sulfate reduction. The total accumulated yearly phytoplankton biomass was about 150,000 t wet weight. Since most of it was *Peridinium* with 20% C content, about 36 and 39% of the phytoplankton biomass could have been oxidized via sulfate reduction in the hypolimnion in 1989 and 1988, respectively. This is in agreement with the reports that 50% of the primary production may be decomposed by SRB in the hypolimnion (Smith and Oremland 1987; Canfield 1989).

25.3.6.2 Sediments

The rate of sulfate reduction in Lake Kinneret sediments varied seasonally (Figs. 25.7, 25.3) and was dependent on both the availability of sulfate in the pore water and organic matter supplied from the epilimnion and reaching the sediments. The relative fraction of organic matter reaching the sediments depends on the timing of the algal bloom and the shape of the isotherms. An early bloom of *Peridinium* (or other species) and a long mixing period would usually increase the amount of organic matter reaching the sediments (Serruya et al. 1974). At the beginning of summer, the crash of the *Peridinium* bloom resulted in an increased input of fresh organic matter.

During thermal stratification, the phytoplankton is mostly decomposed in the epilimnion and the supply of organic matter reaching the sediments is low resulting in lower sulfate reduction rates in autumn (Fig. 25.3). During the mixing period, although sulfate concentrations are high, the limited supply of organic matter resulted in low sulfate reduction rates. An exception was February 1988, in which a second peak of sulfate reduction occurred due to the *A. granulata* bloom sinking toward the sediments (no thermal barrier) and providing fresh organic matter (Fig. 25.3).

High sulfate reduction rates were observed in July 1988 throughout the whole 2.4-cm depth sediment core, reaching a maximum of 1,699 nmol SO_4^{-2} reduced cm^{-3} day^{-1} at 0.3-cm depth (Figs. 25.7 and 25.8). These high rates were also observed in June and August at the upper layers of the sediments. In November and December, due to the strong thermal stratification, depletion of organic matter, and of sulfate, lower rates were measured (14 and 80 nmol SO_4^{-2} reduced cm^{-3} day^{-1}). In 1989, the sulfate reduction peak occurred in July at 0.3-cm depth and, at least at this depth, was as high as in 1988 (Figs. 25.7 and 25.8). Lower rates were observed

Table 25.5 Semiannual and annual monthly average carbon oxidized through sulfate reduction (mmol C m^{-2} $month^{-1}$) and carbon supplied by primary production (mmol C m^{-2} $month^{-1}$) in the sediments at Sta. A

Month	Carbon oxidized through sulfate reduction (mmol C m^{-2} $month^{-1}$)[a]		Carbon supplied by primary production (mmol C m^{-2} $month^{-1}$)	
	1988	1989	1988	1989
January–July	754±557	424±366	575±150	496±53
August–December	524±293	393±194	370±170	361±152
January–December	650±451	410±287	493±183	440±122

[a] Based on the assumption that 2 mol of carbon are oxidized per mol of sulfate reduced

in December, just before the overturn (12 nmol SO_4^{-2} reduced cm^{-3} day^{-1} at 2.4-cm depth; Hadas and Pinkas 1995a).

The integrated values of sulfate reduction in the sediments in 1989 were only 63% of those in 1988. The difference in the phytoplankton composition and the higher productivity during the first half of the year (January–June), 2,300 and 2,000 mg C m^{-2} day^{-1} in 1988 and 1989, respectively, could probably account for part of the difference in sulfate reduction rates between those years (Table 25.5). Furthermore, the mixing period of the lake was a month longer in 1988 than in 1989, resulting in higher amounts of organic matter reaching the sediments. Only 10% of the carbon fixed by photosynthesis reaches the sediments (Serruya 1978). Based on this value, the phytoplankton primary production reaching the bottom could account for most or all the potential sulfate reduction in the sediments at Sta. A (Table 25.5). $\delta^{13}C$ of the organic matter in the sediments have shown values lower by 4‰ as compared to the organic matter sinking from lake water indicating diagenetic processes in the sediments (Stiller and Magaritz 1974).

25.3.7 Sulfate Reduction Rates at Stations G and S as Compared to Station A (Based on the Years 1990–1992)

Station G, located in the northern part of the lake, is mostly influenced by the inflow of the Jordan River. The Jordan and its tributaries bring relatively high amounts of particulate organic matter. The sediments at station G are rich in detrital elements (Fe, P, Mn) as the result of deposition of suspended matter associated with the early floods. High sulfate reduction rates were observed immediately after the first heavy rainfalls in December 1991. Another peak (1,350 nmol SO_4^{-2} reduced cm^{-3} day^{-1}) was recorded in July at the crash of the *Peridinium* bloom when organic matter and sulfate were available. During drought years when the contribution of the Jordan River was small, low sulfate reduction rates were recorded (Hadas and Pinkas 1995b).

Station S (10 m depth, in the littoral at the western side of the lake) is exposed to an oxygenated water column during the whole year; however, the sediments at Station S are anoxic and oxygen penetrates to less than 0.6 mm. At low lake levels, if less organic matter was available, low sulfate reduction rates were recorded

(6–48 nmol SO_4^{-2} reduced cm^{-3} day^{-1} in February, 1991). During periods of low water levels (e.g., 1990–1991) shoreline vegetation (*Tamarix jordanis* and *Phragmites australis*) developed on the exposed shores. This vegetation decomposed after being covered by the rising water (like in 1992), supplying fresh organic material that resulted in high sulfate reduction rates.

25.3.8 Prospective

The main trigger for the sulfate reduction process in Lake Kinneret was the decline and decomposition of the *Peridinium* bloom. In years of low water levels, the bloom started early (February), peaked in April, and declined in May–June supplying fresh organic material to the hypolimnion and sediments. At high water levels (usually correlated with cold and rainy winters), the bloom of *A. granulata* added to the organic fraction supplied to the sediments. During the past 2 decades, the characteristic annual bloom of *Peridinium* does not appear every year, and in some years other species (e.g., *Mougeotia*) are the main phytoplankton contributing to the primary production. Sulfate reduction rates calculated from sulfate concentration profiles using a numerical model and based on profiles in 2008 ("non-*Peridinium* year," Adler et al. 2011) showed values in the range of the rates measured by Hadas and Pinkas (1995a) without the peaks measured in July after the degradation of the *Peridinium* bloom. The changes in the phytoplankton composition pattern of the lake and invasion of new species with different seasonal distribution patterns and bloom timing may have an impact on sulfate reduction in the hypolimnion and sediments and on the mineralization processes of organic matter in the lake.

25.4 Methanogenesis

Werner Eckert and Orit Sivan

Methanogenesis is a key terminal process in the anaerobic decomposition of organic matter that dominates in the absence of other electron acceptors such as nitrate, ferric iron, and sulfate. It is meditated by methanogenic bacteria (MB), a diverse group of microorganisms, all belonging to the Archaea. They are responsible for ~70% of the globally produced methane estimated at 500–600 Tg CH_4 per year (Conrad 2009). This biologically produced methane derives mainly from the reduction of CO_2 with hydrogen (hydrogenetic methanogenesis), or from the fermentation of acetate (acetoclastic methanogenesis), which is split into CH_4 and CO_2 and, to a lesser extent, from other C −1 compounds (Whitman et al. 1991). In aquatic environments, methanogenesis is primarily a sedimentary process controlled by the prevailing sulfate concentrations due to the competition between MB and SRB for

common substrates. Even in freshwater sediments that are relatively poor in sulfate, SRB can outcompete MB (Lovley and Klug 1983) restricting the process of methanogenesis to the deeper sediment layers that are depleted of SO_4^{2-}. Nevertheless, methanogenesis was repeatedly confirmed as the dominant process in the final mineralization of organic matter (Kuivila et al. 1989; Sinke et al. 1992). On a global scale, the contribution of aquatic ecosystems to the atmospheric methane budget is relatively small (3 %)—a fact that seems to disagree with the well-established importance of methanogenesis in carbon cycling (e.g., Rudd and Taylor 1980). This apparent contradiction is the result of the activity of methane-oxidizing prokaryotes, or methanothrophs, that in aquatic environments effectively attenuate the sedimentary CH_4 flux by oxidizing upward diffusing methane in the presence of suitable electron acceptors (Conrad 2009). For a long time, methanotrophy was regarded as a strictly aerobic process performed by gamma- or alpha-proteobacteria (e.g., Trotsenko and Murrell 2008). However, increasing evidence suggests the existence of a group of Archaea capable of anaerobic oxidation of methane (AOM). AOM was estimated to consume the methane equivalent to 20 ± 5 % of the present atmospheric methane flux (Valentine and Reeburgh 2000).

In Lake Kinneret, both methanogenesis and methanotrophy were unexplored processes until 1998. At that time, a scientific program was launched aimed at learning about methane evolution in the water column, its role in the lake's carbon cycle, and physiological aspects of methanogenesis. The study of hypolimnetic methane accumulation together with that of sulfide during several annual lake cycles showed that the biogeochemical processes in the lake are tightly linked to the physical forcing of the water column (Eckert et al. 2002). During the stratified period, strong daily westerly winds lead to the formation of a benthic boundary layer (BBL) that is characterized by enhanced microbial activity. As such, oxygen and nitrate are depleted first in this ~ 10 m thick BBL delineated by a sharp drop of the oxygen-reduction potential, as exemplified by the April profile in Fig. 25.9. Only when the upper hypolimnion, with its significantly lower microbial activity (e.g., rate of oxygen consumption was shown to be ca. four times lower in this layer; Eckert et al. 2002), has turned anoxic as well, does the chemocline rise to the depth of the thermocline (August profile in Fig. 25.9). In the absence of suitable electron acceptors, sedimentary release causes the continuous increase of CH_4 into the hypolimnion with near-bottom concentrations reaching up to 400 µmol L^{-1} (Eckert and Conrad 2007). The peaks of both solutes in the upper hypolimnion are likely the result of BBL mixing due to internal wave braking followed by advection across the laminar hypolimnion (Eckert et al. 2002; Chap. 9, physics). Compared to other freshwater systems, this concentration is relatively high. Similar quantities measured in the hypolimnion of some temperate lakes in the northern USA (L. Paul: 250 µmol L^{-1}; L. Peter: 600 µmol L^{-1}, and L. Hummingbird: 300 µmol L^{-1}, Bastviken et al. 2008) could be attributed to low sulfate (< 60 µmol L^{-1}) and high DOC concentrations (> 500 µmol L^{-1}; Houser et al. 2003). But Lake Kinneret generates such concentrations at a tenfold higher sulfate and five times lower DOC. Conditions are similar for Lakes Konstanz and Lugano where CH_4 concentrations in the anaerobic zone remain significantly lower at 120 µmol L^{-1} (Schmidt and Conrad 1993) and 80 µmol L^{-1} (Liu et al. 1996),

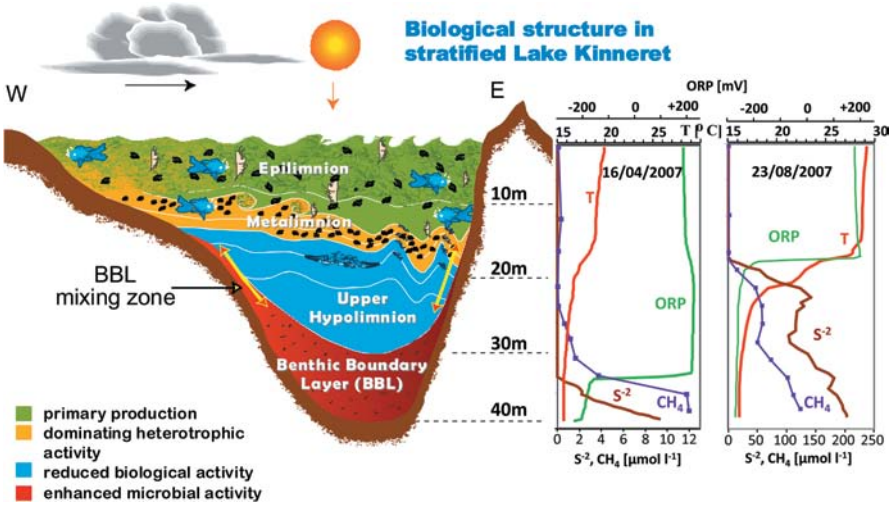

Fig. 25.9 Biological stratification in Lake Kinneret during summer in response to physical forcing. Microbial activity is highest in the benthic boundary layer and the metalimnion, and lowest in the laminar "upper hypolimnion." The effect of the stratification on the evolution of biochemical processes in the water column is indicated in the right panel by the sulfide (S^{2-}), CH_4, oxidation reduction potential (*ORP*), and temperature (*T*) profiles from April and August. (Reproduced from Eckert et al. 2002 with permission from Springer)

respectively. The only environmental parameter that may explain the relative high methane concentrations in Lake Kinneret is the elevated temperature in comparison to temperate lakes (Thebrath et al. 1993).

During the stratified period, the accumulation pattern of methane in the hypolimnion of Lake Kinneret follows closely that of sulfide (Fig. 25.10), with annual average concentrations around 3 and 6 mol m^{-2}, respectively. The relative impact of both processes on the mineralization of OC was elaborated further by Eckert and Conrad (2007), who established a carbon budget for Lake Kinneret. Sulfate reduction was identified as the dominant process in the decomposition of organic matter that seasonally settles into the hypolimnion (~20 mol C m^{-2} $year^{-1}$), accounting for 60 % of the C input. Methane release represented 30–40 % including that of methane gas ebullition. The latter constituted approximately 25 % of the sedimentary methane flux (Eckert and Conrad 2007), a figure that was confirmed by echosounder measurements (Ostrovsky 2003; Ostrovsky et al. 2008; Ostrovsky and Tegowski 2010).

Physiological studies targeting methanogenesis in the sediment of Lake Kinneret have indicated extreme substrate limitation, with methane production from acetate being partly due to syntrophic oxidation coupled with hydrogenotrophic methanogenesis rather than direct acetoclastic cleavage (Nüsslein et al. 2001, 2003; Schwarz et al. 2008). Molecular analysis of the microbial community structure in the upper 10 cm of profundal sediments revealed that the numbers of archaea and bacteria,

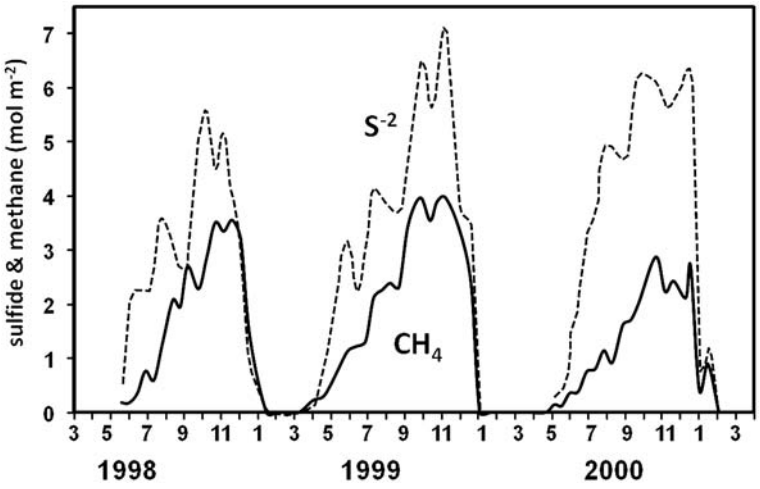

Fig. 25.10 Seasonal patterns of near-bottom dissolved methane and total sulfide concentrations in the hypolimnion of Lake Kinneret during the years 1998–2000. (Reproduced from Eckert and Conrad 2007 with permission from Springer)

quantified by real-time polymerase chain reaction (PCR), amounted to about 10^8 and 10^{10} 16S rRNA gene copies cm^{-3} sediment, respectively, suggesting that Archaea account for only a minor fraction (approximately 1 %) of the total prokaryotic community (Schwarz et al. 2007a, 2007b). Since methanogenesis is carried out by Archaea only, this observation supports the overall assumption that methanogenesis plays only a minor role in the carbon cycle of the Lake Kinneret.

Seasonal profiles of dissolved methane in the pore water of intact sediment cores from the centrally located Sta. A (see location in Fig. 1.1a, Chap. 1) typically show a prominent increase in sediment depth with a maximum around 10 cm (Fig. 25.11a, redrawn from Adler et al. 2011). Below the peak zone, dissolved methane decreases again to concentrations similar to those measured in the upper sediment layers. Model results (Adler et al. 2011) as well as incubation experiments suggest that this decline is the result of a methane sink in the deeper lake sediments. Apparently, methanogenesis is not substrate limited in this zone, based on the DOC profile that is characterized by increasing concentrations with depth (Fig. 25.11a). Thus, the hypothesis evolved that methane production may be balanced by methane consumption.

The assumption of AOM could be further manifested by means of the $\delta^{13}C$ signatures measured within the zone of deep methane decrease (Fig. 25.11b, modified from Sivan et al. 2011). The $\delta^{13}C$-CH_4 profile shows a decrease from −60 ‰ at 1-cm depth to about −65 ‰ at 7-cm depth and then an increase to a maximum of −53.5 ‰ at 24 cm, an increase that can only be explained by methanotrophy, in which the residual methane becomes isotopically heavier. Besides this geochemical evidence for AOM in deep Kinneret sediments, Sivan et al. (2011) suggested

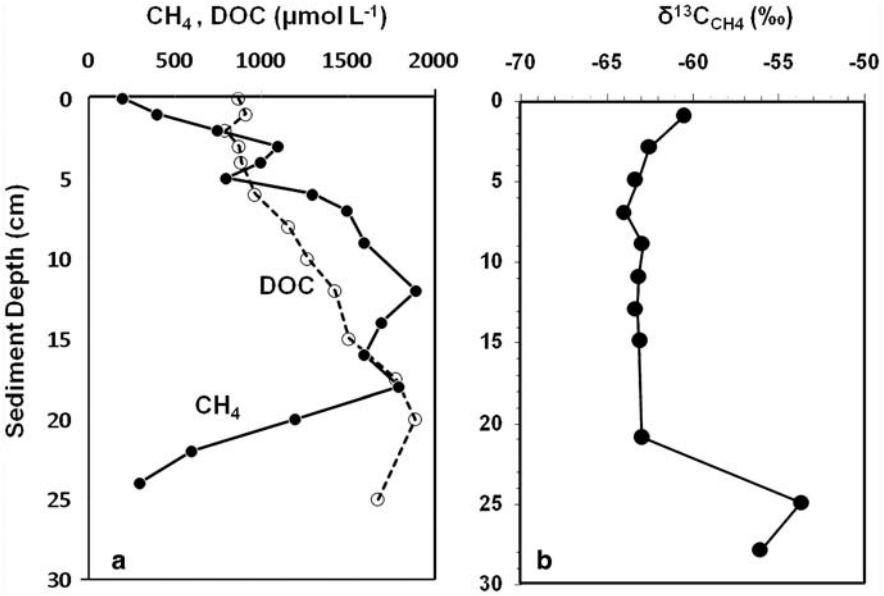

Fig. 25.11 Sediment pore water depth profiles of **a** dissolved methane and dissolved organic C (*DOC*) and **b** $\delta^{13}C$–CH_4 signature measured in intact sediment cores sampled in August 2009 at Sta. A at the center of Lake Kinneret (location in Fig. 1.1 of Chap. 1). (The *DOC* profile represents unpublished data of Bar Or and Eckert; CH_4 and $\delta^{13}C$ profiles are redrawn from Sivan et al. 2011—Copyright 2014 by the Association for the Sciences of Limnology and Oceanography, Inc.)

that AOM is likely driven by iron (Fe) reduction, a hypothesis that was verified by dissolved iron concentration and isotopic profiles measured in the pore water of intact sediment cores and by Fe(III)-amended mesocosm studies.

Analysis of seasonal sediment cores from Sta. A revealed that below the sediment water interface sulfate reduction is the dominant process throughout the year with rates peaking at around 1.5×10^{-12} mol cm^{-3} s^{-1} and declining exponentially with depth (Fig. 25.12). Methanogenesis starts at ~3 cm depth with maximum rates of 4×10^{-13} mol cm^{-3} s^{-1} at 5–12 cm depth, followed by decreasing methane concentrations below the maximum methane production zone. Apparently, this decline is caused by AOM taking place at a rate of about 5×10^{-14} mol cm^{-3} s^{-1} (Adler et al. 2011). To explain the average annual hypolimnetic CH_4 accumulation of 3 mol m^{-2} (Fig. 25.10) with the reported rates of methanogenesis requires a 20–25 cm-thick sedimentary zone of methane production—a presumption that matches well our measured profiles (Fig. 25.12).

In summary, the study of methane cycling in Lake Kinneret revealed some unique features in comparison to other freshwater lakes. Besides the relatively high concentrations of dissolved CH_4 in spite of high sulfate and low DOC concentrations, there is the important discovery of sedimentary AOM with ferrous iron, shown for the first time ever in a natural aquatic system.

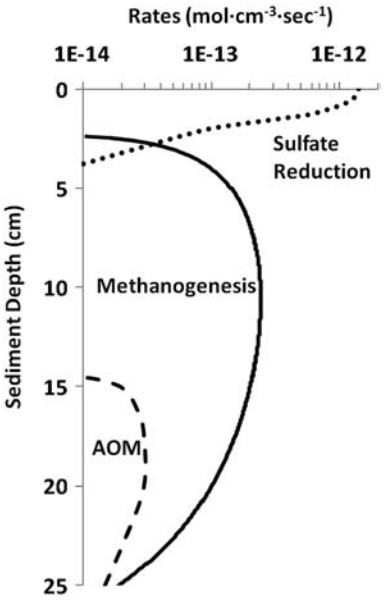

Fig. 25.12 Geochemical model output of the changes with sediment depth of rates of sulfate reduction (*dotted line*), methanogenesis (*full line*), and anaerobic methane oxidation (*AOM, dashed line*) in Lake Kinneret. (Drawn from data published by Adler et al. 2011 and Sivan et al. 2011)

25.5 Fluxes of Organic Carbon in the Epilimnion

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25.5.1 Organic Carbon Sources and Sinks in Lake Kinneret

The first delineation of carbon flows in the Lake Kinneret system was by Serruya et al. (1980) who emphasized the different patterns observed during the "*Peridinium* season" and during the summer–fall. In winter–spring, the major OC input was from primary production during the regular annual dinoflagellate bloom by large *Peridinium* cells that were mostly not grazed by zooplankton but broken down in the water column by heterotrophic bacteria. By contrast, in summer–fall, primary production was carried out by smaller phytoplankton, mostly chlorophyta, that were readily grazed by the resident cladocerans, which in turn provided sustenance for copepods and fish. Later studies provided more detailed quantitative descriptions of carbon fluxes in the lake ecosystem, based on more extensive data including bacterial and protozoan (ciliates and flagellates) participation in OC cycling (Stone et al. 1993; Hart et al. 2000). Here, we present an overview of OC fluxes in the lake, based on data from 2001 to 2010.

Table 25.6 Lake Kinneret: Annual, averaged, daily organic carbon fluxes in the epilimnion (0–15 m) for the years 2001 through 2010

Year	Input	Sink		Ratio	Balance
	GPP	CR	SED	SED/GPP (%)	GPP-CR-SED
2001	2,480	2,310	540	22	−370
2002	2,240	2,010	*nd*	*nd*	*nd*
2003	2,450	2,370	*nd*	*nd*	*nd*
2004	2,540	2,520	360	14	−340
2005	1,880	1,700	300	16	−120
2006	2,250	1,890	300	13	60
2007	2,240	2,500	400	18	−660
2008	2,400	1,530	380	16	490
2009	2,170	1,570	340	16	260
2010	2,360	1,900	280	12	180
Average	2,301	2,030	360	16	−63
SD	200	350	80	3	

GPP calculated as $1.5 \times {}^{14}$C-measured primary production, except for years when *Peridinium* bloomed (shown in bold) when the GPP for January–June was calculated as $2 \times {}^{14}$C-measured primary production; CR measured by ΔO_2 method; and SED measured in sediment traps positioned 11 m above the bottom to avoid the impact of resuspension (Ostrovsky and Yacobi 2010). Allochthonous organic C inputs are generally ~1 % of GPP. Ratios of SED:GPP are given as percentages, *nd* not defined

GPP Gross primary production, *CR* community respiration, *SED* sedimentation are given in mg C m^{-2} day^{-1}

In Table 25.6, we show the major, annual, averaged daily OC fluxes for the years 2001–2010; during this period, *Peridinium* blooms occurred only in 2003, 2004, and 2007. Table 25.6 shows only the major autochthonous OC input, GPP (calculated from routine measurements of ^{14}C primary production, see Sect. 24.1), and sinks (CR, measured with ΔO_2, see Sect. 25.2 and sedimentation, SED, determined from direct measurements with sediment traps). These fluxes are also shown separately for the winter–spring and summer–fall seasons in Table 25.7.

By far, the major input of OC into Lake Kinneret was from GPP by phytoplankton (Sect. 24.1), with GPP estimated as $1.5 \times {}^{14}$C-measured primary production, except for January–June 2003, 2004, and 2007, when, during *Peridinium* blooms, GPP was calculated as $2.0 \times {}^{14}$C-measured primary production. Minor additional inputs were from chemoautotrophic bacteria (Sect. 24.2), watershed inflows, direct rainfall, benthos, littoral vegetation, and dust. The major loss of OC derived from community respiration (Sect. 25.2), followed by losses from sedimentation (Fig. 25.13). Other losses through outflows via the National Water Carrier, local water consumption (including water to the Kingdom of Jordan), and to the southern Jordan River were very small.

Note that the data (given as mg C m^{-2} day^{-1}) in Tables 25.6 and 25.7 were derived from measurements made in the epilimnion (here, taken as the water layer from 0 to 15 m) and show only the major OC fluxes in this system. Neither OC production nor OC losses have been quantified in the deeper waters of the lake (average lake depth ~24 m). In addition, we have not included in these tables autochthonous

Table 25.7 Lake Kinneret: Semiannual, averaged, daily organic carbon fluxes (January–June and July–December) in the epilimnion (0–15 m) for the years 2001 through 2010

Year	January–June						July–December					
	Input	Sink		Ratio	Sink	Ratio	Input	Sink		Ratio	Sink	Ratio
	GPP	CR	SED	SED:GPP (%)	BCD	BCD:GPP (%)	GPP	CR	SED	SED:GPP (%)	BCD	BCD:GPP (%)
2001	2,610	2,460	850	33	2,110	81	2,350	2,150	220	9	1,770	75
2002	2,350	2,310	*nd*	*nd*	1,810	77	2,140	1,710	*nd*	*nd*	1,380	64
2003	3,050	3,190	*nd*	*nd*	2,240	73	1,840	1,560	*nd*	*nd*	1,090	59
2004	2,870	3,370	470	16	2,510	87	2,210	1,660	250	11	1,200	54
2005	1,770	1,940	400	23	1,340	76	1,990	1,450	190	10	970	49
2006	2,470	2,080	390	16	1,560	63	2,030	1,700	200	10	1,360	67
2007	2,520	2,920	500	20	2,280	90	1,960	2,090	300	15	1,510	77
2008	2,450	1,500	440	18	1,280	52	2,360	1,550	330	14	1,140	48
2009	2,130	1,420	450	21	1,010	47	2,220	1,720	240	11	1,240	56
2010	2,390	1,960	310	13	1,130	47	2,340	1,840	240	10	1,140	49
Average	2,460	2,320	480	20	1,730	70	2,140	1,740	250	11	1,280	60
SD	340	640	150	6	510	15	170	220	40	2	220	10

GPP, CR, SED (defined in legend for Table 25.6), and BCD (bacterial C demand = bacterial production + bacterial respiration) are given in mg C m^{-2} day^{-1}. GPP was calculated as explained in the legend of Fig. 25.1; CR measured by ΔO_2 method; and SED measured in sediment traps positioned 11 m above the bottom to avoid the impact of resuspension (Ostrovsky and Yacobi 2010). Ratios of SED:GPP and BCD:GPP are given as percentages. Years when *Peridinium* bloomed are shown in bold

SD standard deviation, *nd* not defined

inputs of OC resulting from chemoautotrophic activity. Chemoautotrophic inputs may add somewhere between ~5 and 10% OC on an annual basis, but these have not been consistently monitored and occur only in aerobic/anaerobic interfaces such as in the metalimnion and sediment–water interface (Sect. 24.2). Additional inputs of allochtonous OC into Lake Kinneret brought by river inflows from the watershed (Chap. 18), direct rainfall, benthos, littoral vegetation, and dust constitute a very small percentage (~1–2%) of the GPP and have not been included in Tables 25.6 and 25.7. Other losses that occur but are not shown in these tables include OC removed in fish biomass by commercial fishing and birds, and in the water outflows to the National Water Carrier, to the southern Jordan River, to local water consumers, and to the Kingdom of Jordan (Chap. 31). In total, these OC losses are estimated to be not greater than ~1–5% of GPP.

The major sink for OC was always CR; annual losses by SED averaged 16% varying from 12 to 22% of GPP (Table 25.6). Note that CR data in Table 25.6 were based on measurements that did not include respiration by fish, estimated to be <3% of CR (Hart et al. 2000). Overall, the 10-year record of the difference "Inputs-Sinks" indicated that some further inputs and sinks not shown in Table 25.6 could be required to better balance the OC budget; however, these "missing" components were quantitatively minor. Also, inherent problems in the measurements of GPP, CR and SED add a measure of uncertainty to the data.

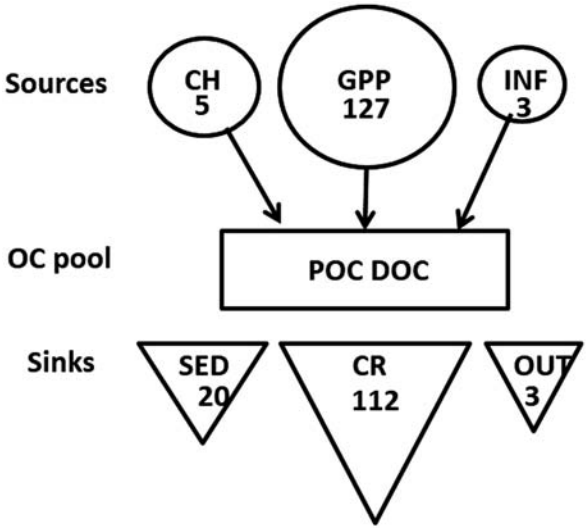

Fig. 25.13 Organic carbon (*OC*) fluxes for the epilimnic waters of Lake Kinneret based on averaged annual rates from 2001 to 2010. Sources of *OC* are gross primary production (*GPP*), chemosynthesis (*CH*), and inputs (*INF*) from watershed inflows and dust. Sinks of *OC* are community respiration (*CR*), sedimentation (*SED*), and outflows (*OUT*) via the National Water Carrier, southern Jordan River, and pumping for local water consumption and to the Kingdom of Jordan. The *OC* pool in the lake is comprised of particulate and dissolved *OC* (*POC* and *DOC*). The numbers represent annual *OC* fluxes as tons C lake$^{-1} \times 1{,}000$, based on lake surface area = 151 km^2 measured for an average lake depth of 24 m

Clear differences in OC semiannual flux patterns over the period 2001–2010 were observed (Table 25.7). With few exceptions, the relative amounts of GPP, CR, and SED were usually greater in the first half of the year in comparison with the second half of the year, resulting from the higher levels of primary production and nutrient inputs in winter–spring (Table 25.8). This was particularly evident with respect to GPP and CR in 2003, 2004, and 2007 when dense blooms of *Peridinium* occurred. In winter–spring season of these years, measured rates of CR exceeded those of GPP, presumably due to the high intrinsic respiration of the dinoflagellate bloom and subsequently to elevated rates of bacterial respiration linked to the breakdown of the phytoplankton biomass.

The ratio between GPP (winter–spring) and GPP (summer–fall) in any given year ranged from 0.9 to 1.7 (average 1.2 ± 0.2) whereas the ratio between SED (winter–spring) and SED (summer–fall) was always higher, ranging from 1.3 to 3.9 (average 2.0 ± 0.8). This suggests that the main reason for the lower average percentage of summer–fall SED:GPP (11 ± 2 %) compared to winter–spring SED:GPP (20 ± 6 %) was because more of the autochthonous particulate organic carbon (POC) generated by GPP was lost by respiration or transformation to DOC in the second half of the year. This observation implies that the POC formed in the latter half of

Table 25.8 Ratios of winter–spring to summer–fall averages of gross primary production (*GPP*), community respiration (*CR*), sedimentation (*SED*), and bacterial C demand (*BCD*) measured in Lake Kinneret, 2001–2010, and the multiannual average and standard deviation (*SD*), (*nd*: not defined)

	GPP	CR	SED	BCD
2001	1.1	1.1	3.9	1.2
2002	1.1	1.4	nd	1.3
2003	1.7	2.1	nd	2.0
2004	1.3	2.1	1.9	2.1
2005	0.9	1.3	2.1	1.4
2006	1.2	1.2	2.0	1.1
2007	1.3	1.4	1.7	1.5
2008	1.0	1.0	1.3	1.1
2009	1.1	0.8	1.9	0.8
2010	1.0	1.1	1.3	1.0
Average	1.2	1.3	2.0	1.4
SD	0.2	0.4	0.8	0.4

the year was relatively more labile (i.e., less POC reached the lake bottom) than the POC formed in winter–spring. Another possible reason for the observed difference in SED: GPP is a more efficient recycling of POC within the epilimnion in summer and fall (see Chap. 27).

The annual averages of CR (Table 25.6) were weakly correlated to GPP ($r^2 = 0.47$; $p = 0.028$; $n = 10$); a much stronger correlation ($r^2 = 0.67$; $p = 0.004$; $n = 10$) was found between CR and GPP measured for the January–June season only (Table 25.7). No significant relationship was observed for CR and GPP in the latter half of the year. Curiously, no correlations were found between GPP and SED or, less surprisingly, between CR and SED.

25.5.2 Net Autotrophic and Heterotrophic States of the Lake

In view of the unexpectedly high potential of lakes to act as sources or sinks of greenhouse gasses and to function as significant regulators of climate change on a global scale (Williamson et al. 2009), considerable interest has focused on their overall net autotrophic or heterotrophic status. Given the low OC external inputs, it is not surprising that the euphotic zone of Lake Kinneret is generally net autotrophic. However, when examined on a semiannual basis, measured CR was higher than GPP in the winter–spring (January to June in 2003, 2004, 2005, and 2007), indicative of net heterotrophic conditions. As noted, 2003, 2004, and 2007 were years with large *Peridinium* blooms with intrinsically high levels of respiration. Additionally, after the rapid die-off of the bloom, the dense phytoplankton biomass would be expected to undergo extensive degradation by heterotrophic bacteria, giving rise to heightened CR. In spring 2005, there was an unusual bloom of the filamentous green alga *Mougeotia* sp. (Zohary et al. 2012) which may have resulted in a net heterotrophic situation where CR > GPP (Table 25.7). Overall, however, despite relatively short, occasional periods of net heterotrophy, Lake Kinneret is clearly net autotrophic (see below).

25.5.3 Organic Carbon Flux Through the Microbial Loop

In early studies of OC cycling in Lake Kinneret (Serruya et al. 1980), the role of microorganisms was scarcely considered. However, later modeling studies of carbon fluxes in the lake indicated the central function of bacteria and protista in cycling of OC (Stone et al. 1993; Hart et al. 2000); this was subsequently confirmed by experimental measurements (Berman et al. 2004, 2010). As can be seen in Table 25.7, BCD (calculated as the sum of BP plus BR), a measure of the OC flux through the heterotrophic bacteria, was always a relatively high proportion of the total autochthonous OC inputs, ranging from 45 to 91 % of GPP in winter–spring and 48 to 77 % of GPP in summer–fall (for more details on BCD, see Sect. 25.1).

25.5.4 Generalized Organic C Budget for Epilimnic Waters of Lake Kinneret

We show a generalized diagram quantifying annual OC fluxes for the epilimnic waters of Lake Kinneret based on averaged annual rates from 2001 to 2010 in Fig. 25.13. Here, we have included estimates for minor inputs such as chemosynthetic primary production, OC in river inflows from the watershed, direct rainfall on the lake, benthos, littoral vegetation and dust, as well as minor OC sinks such as OC in outflows to the National Water Carrier, local water consumers, southern Jordan River outflow, and water supply to the Kingdom of Jordan.

The decade-long summary shown in Fig. 25.13 would imply that over this period, ~94 % of OC input derived from autochthonous, photosynthetic carbon fixation by lake phytoplankton. Possibly, this underestimates the contribution of chemosynthetically fixed OC (Sect. 24.2), albeit most chemosynthetic activity would not occur within the epilimnic waters of the lake. Most (~83 %) of the OC input was eventually respired. A considerable portion of the OC pool was taken up, recycled, and respired through the microbial communities; BCD accounted for ~65 % of GPP annually (Table 25.7). Reflecting the net autotrophic status of Lake Kinneret, about ~20,000 t C (~15 % of the total OC input) was transferred to the sediments annually.

References

Adler M, Eckert W, Sivan O (2011) Quantifying rates of methanogenesis and methanotrophy in Lake Kinneret sediments (Israel) using pore-water profiles. Limnol Oceanogr 56:1525–1535

Aristegui J, Montero MF, Ballesteros S, Basterretxea G, van Lenning K (1996) Planktonic primary production and microbial respiration measured by ^{14}C assimilation and dissolved oxygen changes in coastal waters of the Antarctic Peninsula during austral summer: implications for carbon flux studies. Mar Ecol Prog Ser 132:191–201

Bastviken D, Cole JJ, Pace ML, Van de Bogert MC (2008) Fates of methane from different lake habitats: connecting whole-lake budgets and CH4 emissions. J Geophys Res 113:G02024

Berman T, Gerber C (1980) Differential filtration studies of carbon flux from living algae to microheterotrophs, microplankton size distribution and respiration in Lake Kinneret. Microb Ecol 6:189–198
Berman T, Kaplan B (1984a) Diffusion chamber studies of carbon flux from living algae to heterotrophic bacteria. Hydrobiologia 108:127–135
Berman T, Kaplan B (1984b) Respiration of Lake Kinneret microplankton measured by carbon loss in the dark. Arch Hydrobiol Beih Ergeb Limnol 19:157–162
Berman T, Pollingher U (1974) Annual and seasonal variations of phytoplankton, chlorophyll and photosynthesis in Lake Kinneret. Limnol Oceanogr 19:31–54
Berman T, Stone L (1994) Musings on the microbial loop: twenty years after. Microbial Ecol 28:251–253
Berman T, Wynne D (2005) Assessing phytoplankton lysis in Lake Kinneret. Limnol Oceanogr 50:526–537
Berman T, Hadas O, Marchaim U (1979) Heterotrophic glucose uptake and respiration in Lake Kinneret. Hydrobiologia 62:275–282
Berman T, Kaplan B, Chava S, Parparova R, Nishri A (1993) Effects of iron and chelation on Lake Kinneret bacteria. Microb Ecol 26:1–8
Berman T, Stone L, Yacobi YZ, Kaplan B, Schlichter M, Nishri A, Pollingher U (1995) Primary production and phytoplankton in Lake Kinneret: a long-term record (1972–1993). Limnol Oceanogr 40:1064–1076
Berman T, Kaplan B, Chava S, Viner Y, Sherr BF, Sherr E (2001) Metabolically active bacteria in Lake Kinneret. Aquatic Microb Ecol 23:213–224
Berman T, Parparov A, Yacobi YZ (2004) Planktonic community production and respiration and the impact of bacteria on carbon cycling in the photic zone of Lake Kinneret. Aquat Microb Ecol 34:43–55
Berman T, Yacobi YZ, Parparov A, Gal G (2010) Estimation of long-term bacterial respiration and growth efficiency in Lake Kinneret. FEMS Microbiol Ecol 71:351–363
Canfield DE (1989) Sulfate reduction and oxic respiration in marine sediments: implications for organic carbon preservation in euxenic environments. Deep Sea Sci 36:121–138
Canfield DE, Des Marais DJ (1991) Aerobic sulfate reduction in microbial mats. Science 251:1471–1473
Capone DG, Kiene RP (1988) Comparison of microbial dynamics in marine and freshwater sediments: contrasts in anaerobic carbon catabolism. Limnol Oceanogr 33:725–749
Choi JW, Sherr EB, Sherr BS (1999) Dead or alive? A large fraction of ETS-inactive marine bacterioplankton cells, as assessed by reduction of CTC, can become ETS-active with incubation and substrate addition. Aquat Microb Ecol 18:105–115
Cole JJ, Findlay SEG, Pace ML (1988) Bacterial production in fresh and saltwater ecosystems: a cross-system overview. Mar Ecol Prog Ser 43:1–10
Conrad R (2009) The global methane cycle: recent advances in understanding the microbial processes involved. Environ Microbiol Rep 1(5):285–292
Cypionka H (2000) Oxygen respiration in *Desulfovibrio* species. Ann Rev Microbiol 54:827–848
del Giorgio P, Williams P (2005a) Respiration in aquatic ecosystems. Oxford University Press, Oxford, 324 pp
del Giorgio P, Williams P (2005b) The global significance of respiration in aquatic ecosystems: from single cells to the biosphere. In: del Giorgio P, Williams P (eds) Respiration in aquatic ecosystems. Oxford University Press, Oxford, pp. 267–303
Eckert W, Conrad R (2007) Sulfide and methane evolution in the hypolimnion of a subtropical lake: a three-year study. Biogeochemistry 82:67–76
Eckert W, Imberger J, Saggio A (2002) Biogeochemical evolution in response to physical forcing in the water column of a warm monomictic lake. Biogeochemistry 61:291–307
Fenchel T, Finlay BJ (1995) Ecology and evolution in anoxic worlds. Oxford University Press, Oxford
Frund C, Cohen Y (1992) Diurnal cycles of sulfate reduction under oxic conditions in cyanobacterial mats. Appl Environ Ecol 58:70–77

Gazeau FJ, Middelburg JM, Loijens JP et al (2007) Planktonic primary production in estuaries: a comparison of the ^{14}C, O_2 and ^{18}O methods. Aquat Microb Ecol 46:95–106
Geider RJ (1997) Photosynthesis or planktonic respiration? Nature 388:132
Gophen M (1978) Zooplankton. In: Serruya C (ed) Lake Kinneret. W Junk, The Hague
Gophen M (1981) Metabolic activity of herbivorous zooplankton in Lake Kinneret (Israel) during 1972–1977. J Plankton Res 3(1):15–24
Hadas O, Pinkas R (1992) Sulfate reduction process in sediments of Lake Kinneret, Israel. Hydrobiologia 235:295–301
Hadas O, Pinkas R (1995a) Sulfate reduction in the hypolimnion and sediments of Lake Kinneret, Israel. Freshw Biol 33:63–72
Hadas O, Pinkas R (1995b) Sulfate reduction processes in sediments at different sites in Lake Kinneret, Israel. Microb Ecol 30:55–66
Hadas O, Pinkas R (1997) Arylsulfatase and alkaline phosphatase (Apase) activity in sediments of Lake Kinneret, Israel. Water Air Soil Pollut 99:671–679
Hambright KD, Zohary T, Gude H (2007) Microzooplankton dominate carbon flow and nutrient cycling in a warm subtropical freshwater lake. Limnol Oceanogr 52:1018–1025
Hart DR, Berman T, Stone L (2000) Seasonal dynamics of the Lake Kinneret food web: the importance of the microbial loop. Limnol Oceanogr 45:350–361
Hepher B, Langer J (1969) Summary of the final research on the primary production in Lake Kinneret. Alon Techni (Mekorot) 4(2):32–35 (in Hebrew)
Houser JN, Bade DL, Cole JJ, Pace ML (2003) The dual influences of dissolved organic carbon on hypolimnetic metabolism: organic substrate and photosynthetic reduction. Biogeochemistry 64:247–269
Ingvorsen K, Jorgensen B (1984) Kinetics of sulfate uptake by freshwater and marine species of *Desulfovibrio*. Arch Microbiol 139:61–66
Jorgensen BB (1978) A comparison of methods for the quantification of bacterial sulfate-reduction in coastal marine sediments. Geomicrobiol J 1:11–27
Jumars PA, Penry DA, Baross JA, Perry MJ, Frost W (1989) Closing the microbial loop: dissolved carbon pathway to heterotrophic bacteria from incomplete ingestion, digestion and absorption in animals. Deep-Sea Res 36:483–495
King GM, Klug MJ (1982) Comparative aspects of sulfur mineralization in sediments of eutrophic lake basin. Appl Environ Microbiol 43:1406–1412
Kirchman DL, Knees E, Hodson RE (1985). Leucine incorporation and its potential as a measure of protein synthesis by bacteria in natural aquatic systems. App Environ Microbiol 49:599–607
Kuivila KM, Murray JW, Devol AH (1989) Methane production, sulfate reduction and competition for substrates in the sediments of Lake Washington. Geochim Cosmochim Acta 53:409–416
Landers DH, Mitchell MJ (1988) Incorporation of $^{35}SO_4$ into sediments of three New-York lakes. Hydrobiologia 160:85–95
Liu R, Hofmann A, Gulacer FO, Favarger PY, Dominik J (1996) Methane concentration profiles in a lake with permanently anoxic hypolimnion (Lake Lugano, Switzerland-Italy). Chem Geol 133:201–209
Lovley DR, Klug MJ (1983) Sulfate reducers can outcompete methanogens at freshwater sulfate levels. Appl Environ Microbiol 45:187–192
Lovley DR, Klug MJ (1986) Model for the distribution of sulfate reduction and methanogenesis in freshwater sediments. Geochim Cosmochim Acta 50:11–18
Luz B, Barkan E, Sagi Y, Yacobi YZ (2002) Evaluation of community respiratory mechanisms with oxygen isotopes: a case study in Lake Kinneret. Limnol Oceanogr 47(1):33–42
Nishri A, Zohary T, Gophen M, Wynne D (1998) Lake Kinneret dissolved oxygen regime reflects long term changes in ecosystem functioning. Biogeochemistry 42:253–283
Nüsslein B, Chin KJ, Eckert W, Conrad R (2001) Evidence for anaerobic synthrophic acetate oxidation during methane production in the profundal sediment of subtropical Lake Kinneret (Israel). Environ Microbiol 3:460–470
Nüsslein B, Eckert W, Conrad R (2003) Stable isotope biogeochemistry of methane formation in profundal sediments of Lake Kinneret (Israel). Limnol Oceanogr 48(4):1439–1446

Oremland RS, Polcin S (1982) Methanogenesis and sulfate reduction: competitive and noncompetitive substrates in estuarine sediments. Appl Environ Microbiol 44:1270–1276
Ostrovsky I (2003) Methane bubbles in Lake Kinneret: quantification, temporal, and spatial heterogeneity. Limnol Oceanogr 48:1030–1036
Ostrovsky I, McGinnis DF, Lapidus L, Eckert W (2008) Quantifying gas ebullition with echo sounder: the role of methane transport with bubbles in a medium-sized lake. Limnol Oceanogr Method 6:105–118
Ostrovsky I, Tegowski J (2010) Hydroacoustic analysis of spatial and temporal variability of bottom sediment characteristics in Lake Kinneret in relation to water level fluctuations. Geo-Mar Lett 30:261–269
Ostrovsky I, Yacobi YZ (2010) Sedimentation flux in a large subtropical lake: spatiotemporal variations and relation to primary productivity. Limnol Oceanogr 55(5):1918–1931
Pace ML, Prairie YT (2005) Respiration in lakes. In: del Giorgio P, Williams P (eds) Respiration in aquatic ecosystems. Oxford University Press, Oxford, pp 103–121, (324 pp)
Pinhassi J, Berman T (2003) Differential growth ersponse of colony-forming α- and γ-proteobacteria in dilution culture and nutrient addition experiments in Lake Kinneret, eastern Mediterranean and Gulf of Eilat. Appl Environ Microbiol 69:199–211
Plugge CM, Zhang W, Sholten JCM, Stams AJM (2011) Metabolic flexibility of sulfate-reducing bacteria. Front Microbiol. doi:10.3389/fmicb.2011.00081
Postgate JR (1984) The sulphate reducing bacteria, 2nd edn. Cambridge University Press, Cambridge
Pringault O, Tassas V, Rochelle-Newall E (2007) Consequences of light respiration on the determination of production in pelagic systems. Biogeosciences 4:105–114
Pringault O, Tesson S, Rochelle-Newall E (2009) Respiration in the light and bacteriophytoplankton coupling in a coastal environment. Microb Ecol 57:321–334
Riemann B, Fuhrman J, Azam F (1982) Bacterial secondary production in freshwater measured by 3 H-thymidine incorporation method. Microb Ecol 8:101–114
Robinson C (2008) Heterotrophic bacterial respiration. In: Kirchman DL (ed) Microbial ecology of the oceans, 2nd edn. Wiley, New York, pp 299–334
Rudd JWM, Taylor CD (1980) Methane cycling in aquatic environments. Adv Aquat Microbiol 2:77–150
Scavia D, Lang GA, Kitchel JF (1988) Dynamics of Lake Michigan plankton: a model evaluation of nutrient loading, competition, and predation. Can J Fish Aquat Sci 45(1):165–177
Schmidt U, Conrad R (1993) Hydrogen, carbon monoxide, and methane dynamics in lake constance. Limnol Oceanogr 38:1214–1226
Schwarz JIK, Eckert W, Conrad R (2007a) Community structure of Archaea and Bacteria in a profundal lake sediment, Lake Kinneret (Israel). Syst Appl Microbiol 30(3):239–254
Schwarz JIK, Lueders T, Eckert W, Conrad R (2007b) Identification of acetate-utilizing Bacteria and Archaea in methanogenic profundal sediments of Lake Kinneret (Israel) by stable-isotope probing of rRNA. Environ Microbiol 9:223–237
Schwarz JIK, Eckert W, Conrad R (2008) Response of the methanogenic microbial community of a profundal lake sediment (Lake Kinneret, Israel) to algal deposition. Limnol Oceanogr 53:113–121
Serruya C (1978) Water chemistry. In: Serruya C (ed) Lake Kinneret. W Junk, The Hague
Serruya C, Edelstein M, Pollingher U, Serruya S (1974) Lake Kinneret sediments: nutrient composition of the pore water and mud water exchanges. Limnol Oceanogr 19:489–508
Serruya C, Gophen M, Pollingher U (1980) Lake Kinneret: carbon flow patterns and ecosystem management. Arch Hydrobiol 88(3):265–302
Sherr BF, Sherr EB, Berman T (1982) Decomposition of organic detritus: a selective role for microflagellate protozoa. Limnol Oceanogr 27:765–769
Sinke AJC, Cornelese AA, Cappenberg TC, Zehnder AJB (1992) Seasonal variation in sulfate reduction and methanogenesis in peaty sediments of eutrophic Lake Loosdrecht, The Netherlands. Biogeochemistry 16:43–61

Sivan O, Adler M, Pearson A, Gelman F, Bar-Or I, John SG, Eckert W (2011) Geochemical evidence for iron-mediated anaerobic oxidation of methane. Limnol Oceanogr 56:1536–1544
Skyring GW (1988) Acetate as the main energy substrate for the sulfate reducing bacteria in Lake Eliza (South Australia) hypersaline sediments. FEMS Microbiol Lett 53:87–94
Smith RL, Klug MJ (1981) Electron donors utilized by sulfate reducing bacteria in eutrophic lake sediments. Appl Environ Microbiol 42:116–121
Smith RL, Oremland RS (1987) Big Soda Lake (Nevada) 2. Pelagic sulfate reduction. Limnol Oceanogr 32:794–803
Stiller M, Magaritz M (1974) Carbon-13 enriched carbonate in interstitial waters of Lake Kinneret. Limnol Oceanogr 19:849–853
Stone L, Berman T, Bonner R, Barry S, Weeks SW (1993) Lake Kinneret: a seasonal model for carbon flux through the planktonic biota. Limnol Oceanogr 38:1680–1695
Strayer D (1988) On the limits to secondary production. Limnol Oceanogr 33(5):1217–1220
Suttle CA (2007) Marine viruses—major players in the global ecosystem. Nat Rev Microbiol 5:801–812
Tessenow U, Frevert W, Hofgastner W, Moser A (1997) Ein simultanschliesender serienwasser-schopfer fur sedimentkontaktwasser mit fotoelektrischer selbstauslosung und fakultativem sedimentstecher. Arch Hydrobiol Suppl 48:438–452
Thebrath B, Rothfuss F, Whiticar MJ, Conrad R (1993) Methane production in littoral sediment of Lake Constance. FEMS Microbiol Lett 102:279–289
Trotsenko YA, Murrell JC (2008) Methabolic aspects of aerobic obligate methanotrophy. Adv Appl Microbiol 63:183–229
Valentine DL, Reeburgh WS (2000) New perspectives on anaerobic methane oxidation. Environ Microbiol 2(5):477–484
Westrich JT, Berner RA (1988) The effect of temperature on rates of sulfate reduction in marine sediments. Geomicrobiol J 6:99–117
Whitman WB, Bowen TL, Boone DR (1992) The methanogenic bacteria. In: Balowes A, Truper HG, Dwarkin M, Harder W, Schliefer KH (eds.) The Prokaryotes, 2nd edn. Springer, New York, pp 719–767
Williamson CE, Saros JE, Vincent WF, Smold JP (2009) Lakes and reservoirs as sentinels, integrators, and regulators of climate change. Limnol Oceanogr 54:2273–2282
Winberg GG (1960) Primary production of water bodies. The Academy of Sciences of BSSR, Minsk, 328 pp (in Russian)
Yacobi YZ (2006) Temporal and vertical variation of chlorophyll a concentration, phytoplankton photosynthetic activity and light attenuation in Lake Kinneret: possibilities and limitations for simulations by remote sensing. J Plankton Res 28:725–736
Zohary T, Hadas O, Pollingher U, Kaplan B, Pinkas R, Güde H (2000) The effect of nutrients (N, P) on the decomposition of *Peridinium gatunense* cells and thecae. Limnol Oceanogr 45:123–130
Zohary T, Ostrovsky I (2011) Ecological impacts of excessive water level fluctuations in stratified freshwater lake. Inland Waters 1:47–59
Zohary T, Nishri A, Sukenik A (2012) Present-absent: a chronicle of the dinoflagellate *Peridinium gatunense* from Lake Kinneret. Hydrobiologia 698:161–174