

III. Wissenschaftliches Programm Scientific Program

1. Ökomorphologische und ökophysiologische Anpassungen an den alpinen Raum Ecomorphological and ecophysiological adaptations to the alpine environment

**Adaptations to winter hypoxia in a shallow alpine lake.
Ecophysiological energetics of *Cyclops abyssorum* and rainbow
trout***

**Anpassungen an Winter-Hypoxie in einem kleinen alpinen See.
Ökophysiologische Energetik von *Cyclops abyssorum* und Regenbogen-
forellen***

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Summary

Aquatic hypoxia occurs naturally during winter in shallow alpine lakes at altitudes near the timber line. It is by far more severe than hypobaric hypoxia at extreme altitude. The cyclopoid copepod *Cyclops abyssorum* aggregated in the vertical oxygen gradient in the range of 0.5 to 2.5 kPa oxygen pressure during winter in lake Kalbelee (1650 m, Hochtannberg, Vorarlberg). Respiratory oxygen flux was a hyperbolic function of oxygen pressure, with a half maximal flux at 0.5 kPa and a critical oxygen pressure, p_c , of 1.6 kPa at which flux is 75% of maximum. By a combination of Twin-Flow respirometry and calorimetry it was shown that fluctuations of locomotor activity are maintained fully aerobic under hypoxia at <10% air saturation. The respiratory adaptation of *C. abyssorum* to hypoxia and low temperature ($Q_{10} = 2.3$), and the abundance of food near the anoxic boundary layer provide a basis for body

* Dedicated to Univ.-Prof. Dr. Roland Pechlaner at his 60th birthday

and reproductive growth, and the completion of a hypoxic winter generation. During spring stratification developing immediately after icebreak, the full range of anoxic and hyperoxic conditions was encountered up to 300% air saturation (46 kPa_{O₂}), indicating an active oxygen detoxification system even after months of hypoxic acclimation.

Complete winter kill of rainbow trout (*Oncorhynchus mykiss*) occurred and active *Daphnia* disappeared when maximum oxygen in the water column dropped to <3 kPa (ca. 60 μmol O₂ · dm⁻³). Positive growth and no mortality of rainbow trout were observed during less severely hypoxic winters at an average temperature of 1.7 °C. The fish behaved as a *diving trout*, periodically diving into depths of very low oxygen for scavenging food, as evidenced by stomach analyses.

Hypoxia in the environment and the cell

During half of the biological evolution, «normal» concentrations of molecular oxygen were less or much less than 10⁻³ the present atmospheric level, or <0.02 kPa (Kasting 1993), despite the occurrence of photoautotrophic prokaryotes as early as c. 3.5 billion years ago (Schopf 1993). When mitochondria associated with eukaryotic cells around 1.4 billion years ago (Margulis 1970, Schwartz and Dayhoff 1978), atmospheric O₂ pressure may still have been in this low range. The metazoan record starts when a rise in molecular oxygen in the earth's atmosphere is ascertained. However, the earliest benthic metazoan animals may have lived in an anoxic environment rich in H₂S (Giere 1992), although the energetic significance of very low levels of available oxygen (Gnaiger 1991, 1992) may have played a critical role in this period of evolution and mitochondrial function. Low oxygen continues to be important in many environments with extreme changes of oxygen in space and time (Boutilier 1990). Today, normoxia at sea level ($p_o = 1$ atmosphere = 101.3 kPa barometric pressure) corresponds to an oxygen pressure in water vapor saturated air of 19.9 kPa (at 37 °C) or 2.1 kPa (at 0 °C). The volume fraction of oxygen in dry air is 0.20946 and remains constant with altitude. Barometric pressure, p_b [kPa], however, changes with altitude above sea level, h [km], according to a power function (Forstner and Gnaiger 1983),

$$p_b = p_o (1 - h/44.3)^{5.25} \quad (1)$$

Concomitantly, the partial oxygen pressure, p_{O_2} , declines (Fig. 1A). Physiological performance of unacclimated humans may become impaired by hypoxia above 3000 m, corresponding to an O₂ pressure in the lungs of <13 kPa in air saturated with water vapor at 37 °C (Fig. 1A). No permanent human habitation is physiologically possible at altitudes above which oxygen is reduced to <50% of the concentration at sea level (Fig. 1A). Adaptations to hypobaric hypoxia in man are not genetically or developmentally fixed but are acquired (Hochachka 1993; Cerretelli 1993). The main feature is the avoidance of anaerobic lactate production and full exploitation of aerobic energy metabolism at maximum ATP stoichiometry. Finally, short-term survival in acclimated humans is limited to p_{O_2} levels of 25% of the oxygen pressure at sea level, at the risk of brain damage (p_{O_2} is 5.3 kPa at 8848 m; Fig. 1A).

Reduction of atmospheric oxygen pressure at extreme altitude is relatively mild when compared to severely hypoxic conditions in aquatic habitats (Fig. 1B and 1C). Moreover, oxygen concentrations in water at air saturation are less than 5% of the oxygen concentration in air. Therefore, it may be expected that adaptations to aquatic hypoxia in the alpine region are in general not different from those in lowland ponds and marine sediments, with environmental oxygen gradients spanning six orders of magnitude from the km (10³ m) to the mm range (10⁻³ m; Fig. 1A to 1C). Less is known about the oxygen gradients in the μm range (10⁻⁶ m) within cells towards the mitochondria, but the bioenergetic implications of the very low oxygen levels prevailing in the mitochondrial micro-environment may be profound (Gnaiger et al 1993). One of the most conspicuous adaptations described here for the planktonic copepod *Cyclops abyssorum* is the maintenance of fully aerobic functions under severe winter hypoxia.

The critical pO_2 is 1.6 kPa (see below), which may be compared to the critical pO_2 of 0.1 to 0.16 kPa in mitochondria isolated from rat liver (Gnaiger et al 1993) or cardiac myocytes (Rumsey et al 1990).

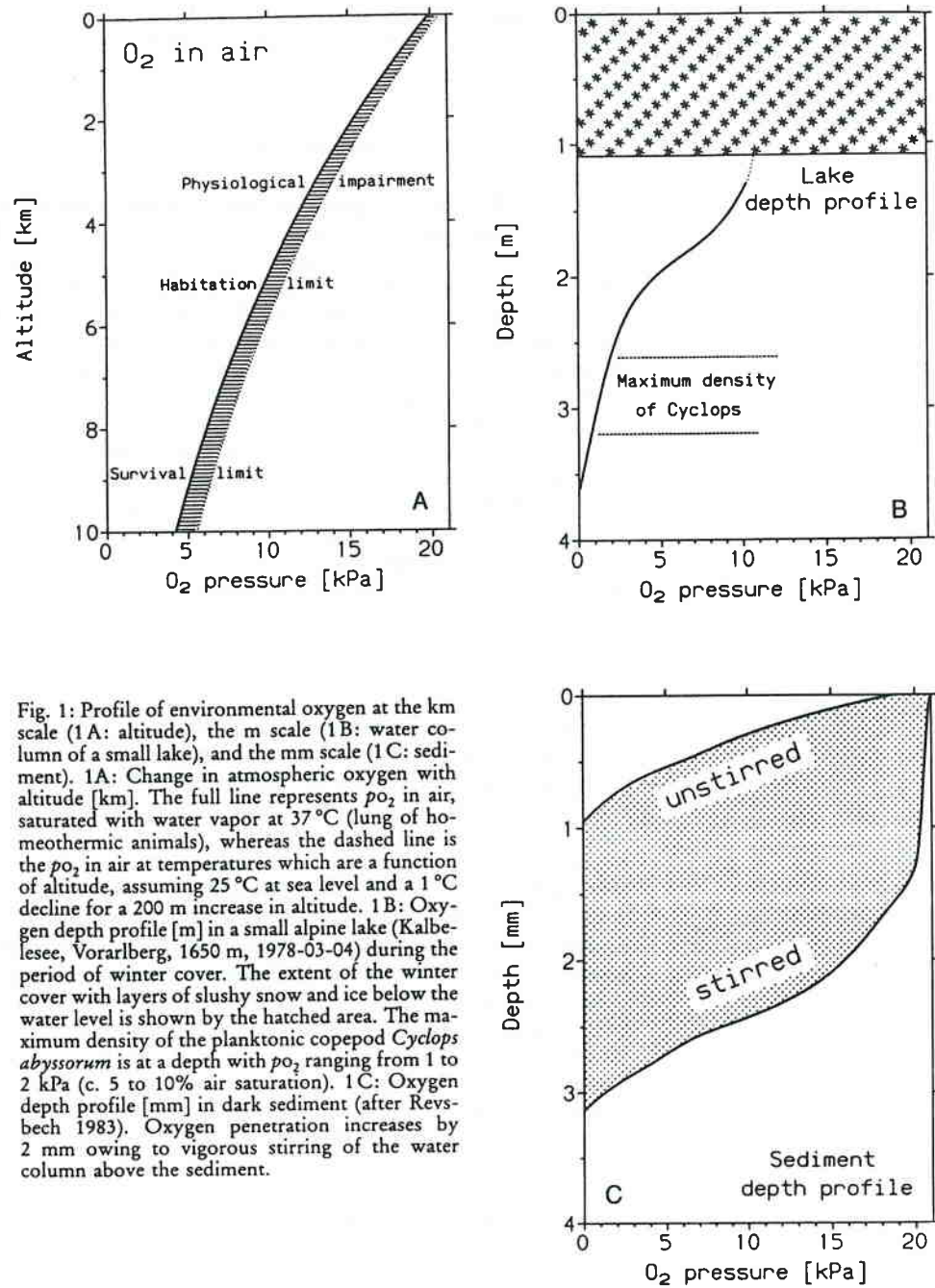


Fig. 1: Profile of environmental oxygen at the km scale (1A: altitude), the m scale (1B: water column of a small lake), and the mm scale (1C: sediment). 1A: Change in atmospheric oxygen with altitude [km]. The full line represents pO_2 in air, saturated with water vapor at 37°C (lung of homeothermic animals), whereas the dashed line is the pO_2 in air at temperatures which are a function of altitude, assuming 25°C at sea level and a 1°C decline for a 200 m increase in altitude. 1B: Oxygen depth profile [m] in a small alpine lake (Kalbelesee, Vorarlberg, 1650 m, 1978-03-04) during the period of winter cover. The extent of the winter cover with layers of slushy snow and ice below the water level is shown by the hatched area. The maximum density of the planktonic copepod *Cyclops abyssorum* is at a depth with pO_2 ranging from 1 to 2 kPa (c. 5 to 10% air saturation). 1C: Oxygen depth profile [mm] in dark sediment (after Revsbech 1983). Oxygen penetration increases by 2 mm owing to vigorous stirring of the water column above the sediment.

Winter anoxia in a small alpine lake

Hypoxic and anoxic conditions are common during summer stagnation in eutrophic ponds and lakes. Temperature stratification prevents vertical mixing and hence gas exchange below the thermocline (Finlay et al 1983). With increasing altitude of alpine lakes (alpine used in the sense of alpine region), winter stagnation is the more likely cause of hypoxia owing to the prolonged duration of the winter season and the massive winter cover which may convert the lake into a nearly isolated system (Fig. 1B; Greenbank, 1945; Gliwicz 1967; Pennak 1968; Schindler and Comita 1972; Ruttner-Kolisko 1975; Nagell and Brittain 1977). Exclusion of gas exchange between lake and atmosphere is practically complete. Nevertheless, 0.05 to 0.01% of the visible light penetrates through a winter cover of 1.5 m in high-alpine lakes (Pechlaner 1966, 1971). The low residual photosynthetic activity cannot compensate for the biological oxygen demand in the lake. However, prevalence of ultra-oligotrophic conditions in high-alpine lakes (above timberline) prevents large accumulation of degradable organic material and thus limits oxygen demand even during extended periods of winter enclosure in shallow lakes and ponds (Pechlaner 1966; Pechlaner et al 1972). Winter anoxia in lakes of the alpine region is intensified at moderate altitude near the timber line where winter cover is severe but organic production in the lake, and nutrient influx from the drainage area are not reduced to the high-alpine scarcity. Moreover, winter-anoxia is limited to shallow water bodies, illustrated by a comparison of two adjacent lakes with maximum depths of 4 and 7 m (Fig. 2).

Field and laboratory studies were carried out at lake Kalbelesee, a shallow productive lake encountering hypoxic and anoxic conditions during winter. The lake originated probably as a glacial ice-scour lake, situated at an altitude of 1650 m above sea level near the villages of Schröcken, Warth and Lech (Hochtannberg, Vorarlberg, Austria; Table 1). After deforestation in the 15th century, the drainage area of c. 1.5 km² consists of alpine meadows with a geologically predominant influence of calcareous sediments. The lake is separated into two basins

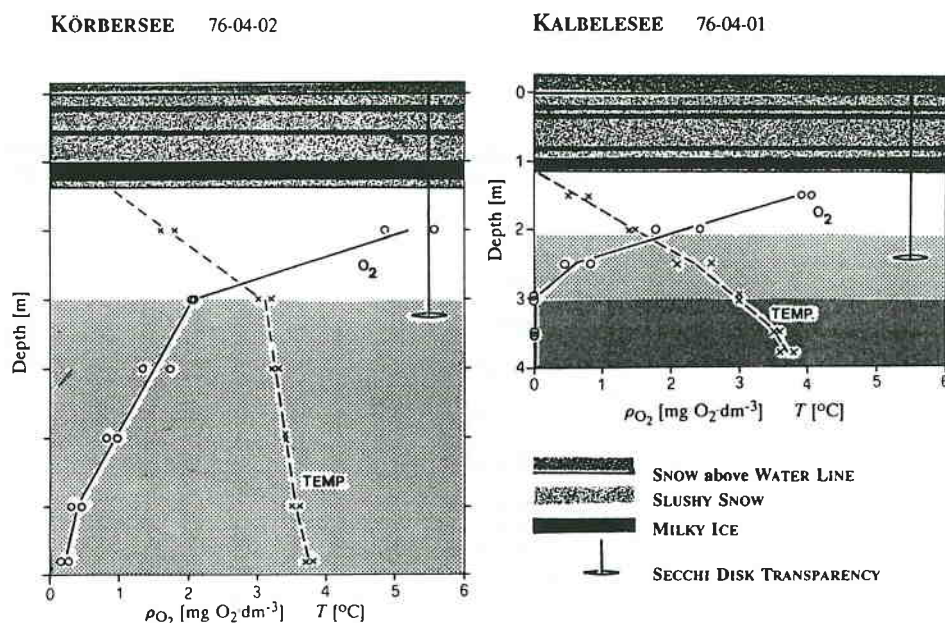


Fig. 2: Winter-hypoxia and anoxia in two adjacent lakes (Hochtannberg, Vorarlberg, Austria) of different maximum depth. Open circles: mass concentration of oxygen, ρ_{O_2} [mg · dm⁻³], determined by chemical Winkler analysis (Gnaiger 1983 a). Crosses: temperature measured in the 5 dm³ Schindler water sampler. The hatched area of the water column indicates the extent of the hypoxic zone at $\rho_{O_2} < 3$ kPa (63 μ mol O_2 · dm⁻³; 2 mg O_2 · dm⁻³). The anoxic zone is dark shaded. 1 mg O_2 · dm⁻³ = 31.215 μ mol · dm⁻³.

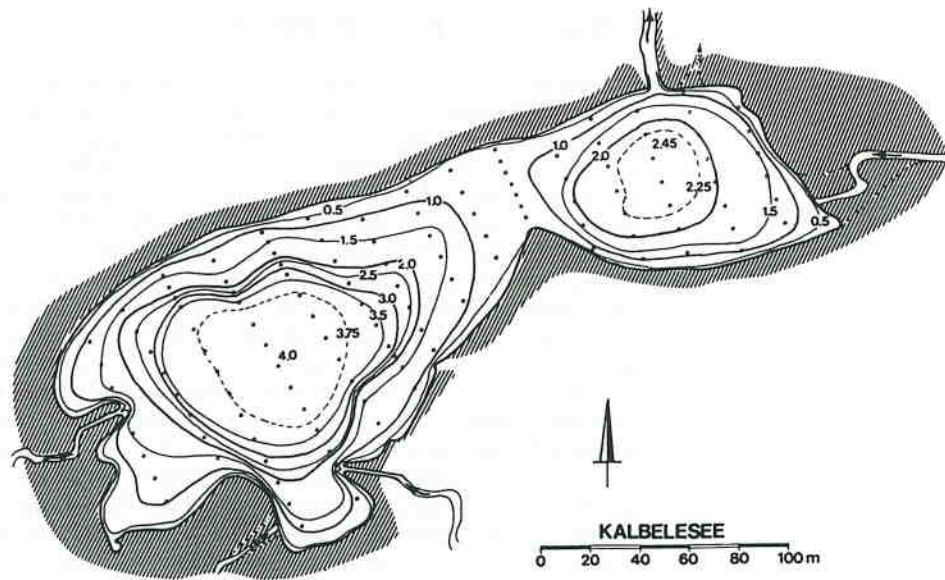


Fig. 3: Contour map of Kalbelesee with standard depths (numbers [m]). At the time of the record (August 1971), the water level was +0.3 m above standard zero, corresponding to a total maximum depth of 4.3 m. 155 depth soundings were taken (circles) in 15 horizontal profiles. The shore line within the *Carex* belt (shaded area) is at a standard water depth of 0.34 m.

Table 1. Morphometric parameters for the Western and Eastern basin of lake Kalbelesee (1650 m above sea level, latitude 47°16' N, longitude 10°08' E). After Gnaiger 1983 a and unpublished.

Parameter	Symbol	Western basin	Eastern basin
Maximum depth ^a	z_{\max}	4.0 m	2.45 m
Mean depth	$\bar{z} = V A^{-1}$	2.02 m	1.54 m
Relative depth	$z_r = 50 z_{\max} \sqrt{\pi} (\sqrt{A})^{-1}$	2.68%	2.63%
Length	l	210 m	130 m
Maximum breadth	b	130 m	70 m
Area ^b	A	$17.5 \cdot 10^3 \text{ m}^2$	$6.8 \cdot 10^3 \text{ m}^2$
Area at 1 m depth	A_1	$13.0 \cdot 10^3 \text{ m}^2$	$5.0 \cdot 10^3 \text{ m}^2$
Area at 2 m depth	A_2	$7.4 \cdot 10^3 \text{ m}^2$	$1.0 \cdot 10^3 \text{ m}^2$
Area at 3 m depth	A_3	$5.0 \cdot 10^3 \text{ m}^2$	
Volume ^a	V	$35.3 \cdot 10^3 \text{ m}^3$	$10.5 \cdot 10^3 \text{ m}^3$
Volume below 1 m	V_1	$19.0 \cdot 10^3 \text{ m}^3$	$4.3 \cdot 10^3 \text{ m}^3$
Volume below 2 m	V_2	$9.2 \cdot 10^3 \text{ m}^3$	$0.5 \cdot 10^3 \text{ m}^3$
Volume below 3 m	V_3	$3.2 \cdot 10^3 \text{ m}^3$	
Shore line ^b	L	660 m	340 m
Development of shore line	$D_L = L(2\sqrt{\pi A})^{-1}$	1.41 m^{-1}	1.16 m^{-1}

a All values are for a *standard* depth of 4.0 m (Fig. 3). The maximum *total* depth changes from 3.7 to 4.8 m during the year. For explanation of morphometric parameters see Hutchinson (1957).

b The shoreline is dominantly marked by *Carex* at a standard water depth of 0.34 ± 0.11 m when the maximum depth is 4.0 m. The area refers only to the open water not covered by stands of plants (Fig. 3 and 4).

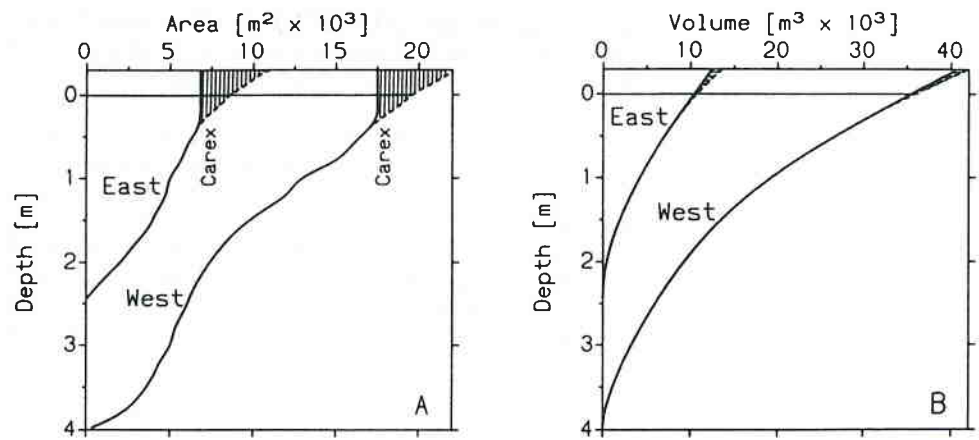


Fig. 4: Hypsographic relations of lake Kalbelesee, Eastern and Western basin. A: Area as a function of depth. B: Volume as a function of depth, obtained by integrating the area over depth (A). The area of the *Carex* shore belt is significant (A, hatched) but the corresponding volume is small (B). A winter cover extending to 1 m and 1.5 m depth reduces the free water volume to 30% and 50%, respectively.

by a shallow rim with a depth of 0.7 to 1.1 m, which is dominated by *Equisetum fluviatile* and *Carex sp.* as is the entire shoreline (Fig. 3 and 4A). The small inflow streams dry up particularly during winter. Light calcareous crusts, covering *Calliergon giganteum* in the South-eastern decline of the Western basin, indicate submerged inflows. In the region of maximum depth (>3.5 m; Fig. 3), the sediment is a homogenous mud of 70–76% water content; the carbonate content is 17–23% of the dry weight; the oxidizable carbon is 12–13 $mg C \cdot cm^{-3}$ (3–4% of the dry weight); and the grain size is 75–80% $<32 \mu m$, 15–17% 32–63 μm , and 3–10% 63 $>\mu m$ in the 0–10 cm layer (Gnaiger 1977). The pH of the water varies between 7.0 and 8.0 during winter.

The period of ice cover of up to 2.3 m thickness extends from October/November to mid May until early July (Amann and Gnaiger 1979). During this time the free water column at the maximum depth is regularly reduced to 2.5 m owing to the extent of the winter cover (Fig. 5). Then the available area is reduced to half (Fig. 4A) and the volume of the pelagial even to a third of the extent during summer, effectively concentrating the active zooplankton and fish population (Fig. 4B). In addition, a steep oxygen gradient develops during winter stagnation. The anoxic zone increases gradually 0.5 m (Fig. 5), up to 1.5 m from the bottom, thus reducing further the habitat volume of anoxia-intolerant species.

Mortality or growth of rainbow trout under winter hypoxia

Effect of hypoxia and low temperature

A complete winter kill of *Oncorhynchus mykiss* (previously *Salmo gairdneri*) was observed several times in Kalbelesee, such as in 1976 when oxygen concentrations under the ice dropped to $<30 \mu mol O_2 \cdot dm^{-3}$ ($pO_2 < 1.5$ kPa) during March. Rainbow trout were restocked from a local fishery in May 1976 (II⁺; 340 g average fresh body mass). Winter hypoxia was less severe in 1977, when fish of an average mass of 500 g were sampled monthly in gill nets exposed under the ice. No dead fish were observed during this season nor after ice break, in agreement with the complete survival of rainbow trout in a Tyrolean high-alpine pond with $pO_2 < 5$ kPa over a period of 2.5 months (Pechlaner 1966). Moreover, a positive growth was recorded in terms of length and body mass (Fig. 6), despite the low oxygen in the lake and the low temperature, averaging 1.65 °C and not exceeding 2.9 °C in the euoxic zone (Fig. 5; un-

shaded area: $>60 \mu\text{mol O}_2 \cdot \text{dm}^{-3}$; $p\text{O}_2 > 3 \text{ kPa}$). Growth under winter hypoxia could be corroborated during the following year when ice-break occurred on the 10th of June and 4 days afterwards rainbow trout of 940 g average body mass were captured, compared to 880 g in November (Fig. 6) just prior to the formation of the winter cover (see Fig. 1C and 14 for oxygen conditions in March, May and June, 1978). This field observation of low oxygen requirements of rainbow trout agrees with the physiological indices of the critical $p\text{O}_2$ of 2.8 kPa (p_c , below which respiration declines steeply with ambient oxygen levels; Ott et al 1980), and blood O_2 affinity. The half-saturation pressure, p_{50} , is 2.6 and 3.1 kPa in rainbow trout acclimated to hypoxia and normoxia at 15°C (Bushnell et al 1984) and is independent of acclimation temperature (Weber et al 1976). As reviewed by Kramer (1987), there is evidence in general of reduced feeding of fish with reduced environmental oxygen availability. A correlation between angling success for rainbow trout and oxygen concentrations over the range 75–190 μmol

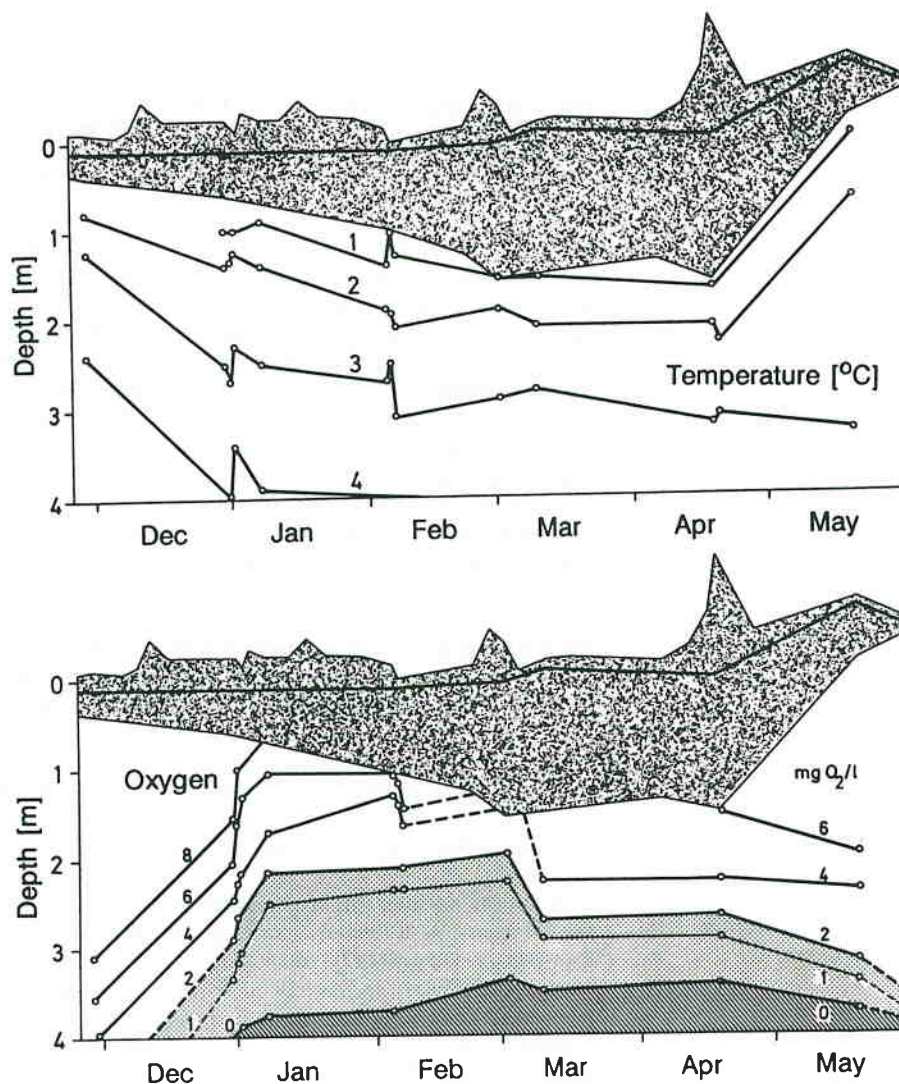


Fig. 5: Dynamics of temperature (top) and oxygen (bottom) during winter in lake Kalbelesee (1976/77; isopleths). The hatched area shows the extent of the winter cover, interpolated between periods of measurement. The shaded area indicates the zone of severe hypoxia ($<60 \mu\text{mol O}_2 \cdot \text{dm}^{-3}$; $<3 \text{ kPa } p\text{O}_2$).

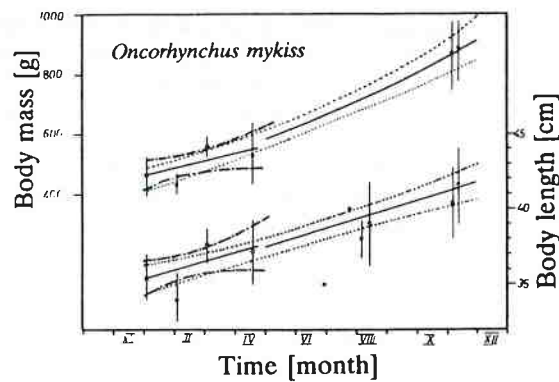


Fig. 6: Growth in terms of body mass [g fresh weight], and length [cm], of rainbow trout, *Oncorhynchus mykiss* (previously *Salmo gairdneri*), stocked into Kalbelese. The regression lines and their 95% confidence limits are shown for the winter catches (linear regressions; 25 individuals or 11% of the stocked population; $P < 0.05$) and for the entire year (exponential regressions; 49 individuals; $0.21 \pm 0.034\%$ body mass per day; 95% C.L.). The vertical bars are the standard deviations of the mean for each catch. The relation between mass and length was identical during winter and summer, $mass = 0.011 \cdot length^{3.01}$, despite a lower degree of gut filling during the period of hypoxia from February to April.

$O_2 \cdot dm^{-3}$ ($2.4-6.0 \text{ mg } O_2 \cdot dm^{-3}$) indicates reduced feeding at low oxygen which may be more pronounced at higher temperature, although the p_c of the standard metabolic rate is remarkably independent of temperature (Ott et al 1980). The low oxygen level sufficient for homeostasis and slow growth of rainbow trout (Fig. 6) contrasts with the incipient oxygen response thresholds of $>10 \text{ kPa}$ reviewed by Davis (1975).

Between January and April, 80 to 100% of the prey of rainbow trout consisted of benthic invertebrates (mainly trichoptera; Amann and Gnaiger 1979). Oxygen levels declined to zero towards the bottom of the lake during that period (Fig. 5). Therefore, *O. mykiss* appears to behave as a 'diving trout': For scavenging food, these fish dive temporarily into layers of very low oxygen levels which cannot be tolerated over extended periods of time. The swimming and feeding behavior under severe hypoxia is indicative of metabolic adaptations in skeletal muscle of rainbow trout (Johnston 1975; Boutilier et al 1988). The swimming performance at high speed of hypoxia-acclimated fish is not improved in comparison to normoxic controls (Bushnell et al 1984). Metabolic downregulation and reduction of heart rate under hypoxia, such as cardiac hypometabolism observed in diving turtles, does not seem to be invoked by fish (Driedzic 1992), although the remarkable survival of complete winter hypoxia up to six months in crucian carp involves adaptations to anoxia even at the level of glycolytic ethanol production (Holopainen and Hyvärinen 1985).

The growth potential of salmonids at low temperatures has generally been underestimated until recently. Rainbow trout is able to grow even at 0.3°C (Brännäs und Wiklund 1992). Therefore, models including the assumption that growth ceases during winter (Elliott 1975) may not be valid. Over the entire year, the average temperature in lake Kalbelese estimated for the trout population was 6°C (see also Fig. 16 and 17). The mass-specific exponential growth rate calculated from Fig. 6 was 0.21% per day (116% per year). When extrapolating the relationship between temperature, size and specific growth rate of 10 to 300 g brook trout fed on maximum ration (Elliott 1975) to rainbow trout of 500 to 880 g, a growth rate of 0.09% per day is obtained for 6°C (compared to $0.21\% \cdot d^{-1}$). This comparison is indicative of the larger potential for growth in rainbow trout and the optimum food conditions in the lake.

Fish stocking and cladoceran survival

During the ice-free period, 30% of the gut contents of rainbow trout consists of *Rivulogammarus lacustris*, which was stocked from another lake in the region in 1967 (Amann and

Gnaiger 1979). Zooplankton (mainly *Daphnia* sp.; some *Cyclops abyssorum*) amounts on average to 8% of the gut contents of the rainbow trout over the year (Amann and Gnaiger 1979). Up to 5,000 *Daphnia* are found in the gut of an individual fish. Nevertheless, the cladoceran population survived the stocking of the lake with rainbow trout as documented since 1967 (fingerlings, one and two year old fish), with scarce information from earlier years (Amann 1972). *Phoxinus phoxinus* is abundant in the lake but is partially decimated during winter kill conditions. The shallow depth, periodic winter kill, and the correlated abundance of benthic food explain the persistence of a strong population of *Daphnia* after fish stocking (compare Pennack 1968; Taylor and Gerking 1980), in contrast to the extinction of cladocerans in oligotrophic lakes after the introduction of planktivorous salmonids (Gliwicz and Rowan 1984; Gliwicz 1986).

Daphnia sp. reaches maximum abundance in Kalbelesee during August to October (Amann 1972; personal observations). There may be a higher abundance in the water column during the night than day. In September 1977, for instance, we observed in four vertical sample series an average of 324 individuals · dm⁻² during the day (± 65 S.D.; maximum density at 1.5 to 2.5 m depth) versus 1378 individuals · dm⁻² during the night (± 369 S.D.; even vertical distribution; 20 dm³ water samples at 7 depth positions, taken with a 5 dm³ Schindler sampler; Benzer 1978). During the day, near-bottom strata were over-proportionally favored by egg-carrying females. These amounted to $9 \pm 3\%$ of the population in the water column during the day but $22 \pm 3\%$ during the night ($N = 4$), possibly reflecting the effect of planktivorous fish. However, such behavior was not always apparent during summer and absent during winter. The cladocerans disappeared gradually from the water column during winter and survived winter kill conditions exclusively in the ephippial stage. Only when oxygen conditions supported survival of the trout (e.g. Fig. 5), then a proportion of active *Daphnia* remained in the water column throughout the winter season.

Adaptations of *Cyclops abyssorum* to environmental hypoxia

Population dynamics during winter hypoxia

In contrast to the cladocerans, *Cyclops abyssorum* (copepodites and adults but not nauplii) remained active under severe winter hypoxia, did not even select the more oxygenated water layers near the ice, and continued development with the completion of a hypoxic winter generation (Fig. 7). Whereas *Daphnia* was more abundant than the copepods during summer, the population maximum of *C. abyssorum* increased to >100 individuals per dm³ during January/February (Fig. 7). During the following winter months there was an exponential decline of the population, which was not due to planktivorous fish in this year of complete winter kill. Only 1% of the copepodite maximum early in February (mainly CIII and CIV) reached the adult stage at the beginning of May (Fig. 7). There was no diapause stage. Adults of the winter generation appeared in April and were significantly smaller than the adults found in January. The magnitude of this change resembles the long-term size-transition observed in populations of lakes which were originally oligotrophic (with small *C. abyssorum*) and became eutrophic (Einsle 1975; Nilssen 1979). Morphometric and genetic characteristics of the Kalbelesee population are described by Einsle (1969).

In Kalbelesee, the population dynamics is synchronized by the effect of the rapid temperature rise at the time of icebreak on the rate of egg development (Gnaiger 1980). *C. abyssorum* in high-alpine lakes is monocyclic without diapause (Eppacher 1968; Praptokardiyo 1979). In Northern lowland lakes, synchronization of population dynamics of this species is effected by periodic cessation of development in the copepodite V stage. The entire population may pass the winter in diapause in the bottom sediment under anoxia (Nilssen and Elgmork 1977). Aggregations of diapausing marine copepods are known at depths near the aerobic/anoxic boundary (Alldredge et al 1984). The physiological mechanisms in these resting stages are still

obscure, whereas anoxia is well known to induce a state of dormancy in embryonic brine shrimp (Hand and Gnaiger 1988).

Vertical distribution, winter hypoxia and respiration as a function of oxygen

During winter hypoxia, *C. abyssorum* aggregated near the anoxic boundary layer identically during day and night (Fig. 8C to 8E; see also Fig. 1B). In monthly samples taken during January to May, the maximum density of adults and copepodites occurred at a pO_2 of 1.5 ± 1.0 kPa (8.6% air saturation; $31 \mu\text{mol O}_2 \cdot \text{dm}^{-3}$; $0.98 \text{ mg O}_2 \cdot \text{dm}^{-3}$) and at an average temperature of 2.2°C . 52 to 85% of the population were clustered at the preferred depths, in the

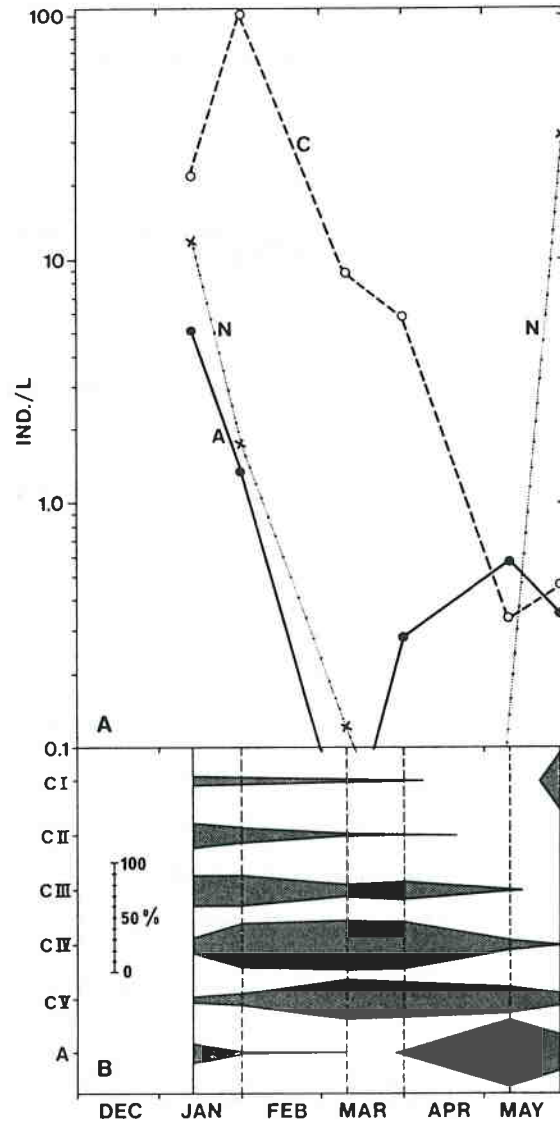


Fig. 7: Population dynamics of *Cyclops abyssorum* during winter hypoxia. A: Population density on a logarithmic scale [individuals per dm^3]; A – adults; N – nauplii; C – copepodites. B: Relative abundance of copepodite stages I to V and adults. Each data point is the average of 2 (day) or 4 (day and night) parallel samples of 10 dm^3 (2 dm^3 Ruttner sampler) taken at 1 m depth intervals (see Fig. 8).

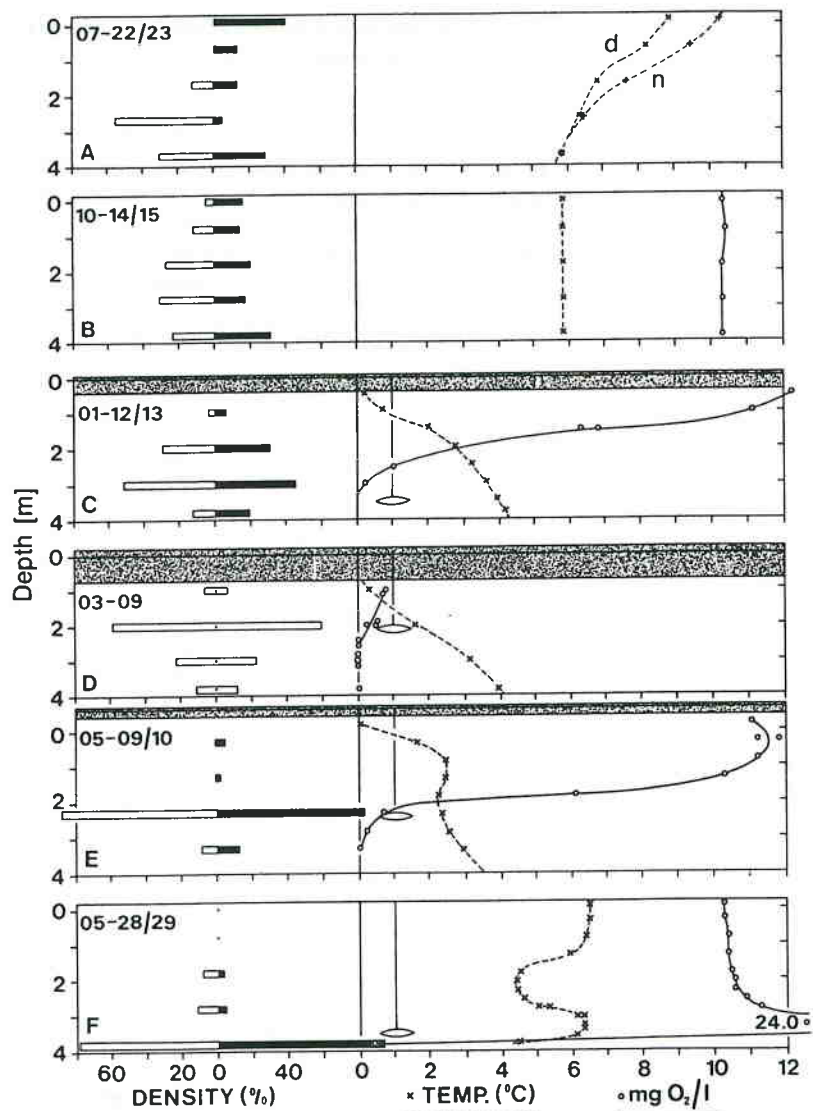


Fig. 8: Depth distribution of *Cyclops abyssorum* (copepodites and adults), temperature profiles (crosses [$^{\circ}\text{C}$]) and O_2 profiles (circles [$\text{mg} \cdot \text{dm}^{-3}$; $1 \text{ mg O}_2 = 31.251 \mu\text{mol O}_2$]) in lake Kalbelesee in 1975/76, during summer stratification (A; d and n indicate the temperature profiles during the day and subsequent night following a sunny day), fall circulation (B), winter stratification (C to E) and spring stratification (F; see also Fig. 12). The depth [m] is given as measured from the standard water line with a fixed position to the bottom rather than the dynamically changing surface level. The relative density [%] is shown for day (open bars; 14:00–16:00) and night (dark bars; 01:00–04:00). Only samples taken in 1 m-intervals are considered for comparison (contrast with Tab. 2). The Secchi disk transparency is indicated when the visibility did not reach to the bottom (see also Fig. 2).

sharp oxygen gradient just 0.75 m above the anoxic boundary layer (Fig. 8). The maximum density of nauplii was above that of the larger instars, at oxygen concentrations of 110 to 150 $\mu\text{mol} \cdot \text{dm}^{-3}$ (3.7 to 4.8 $\text{mg} \cdot \text{dm}^{-3}$). The aggregation of zooplankton near the anoxic boundary layer raises the physiological and energetic issue of the dependence of respiration on oxygen pressure and the possibility of a reliance on anaerobic sources of energy under hypoxic conditions (see also Ruttner-Kolisko 1975).

Respiratory oxygen flux was measured as a function of experimental oxygen pressure in groups of 40 individuals at 6 °C in the CYCLOBIOS Twin-Flow respirometer (Gnaiger 1983 b). Measurements of oxygen flux at various steady state levels of oxygen were combined with quantification of locomotory activity (Flöry 1980) and with direct calorimetry (Gnaiger 1983 b; 1991). Animals (copepodite V and adult females) were transported to the laboratory and acclimated to the experimental temperature for at least one day prior to the experiments. In the Twin-Flow respirometer, the p_{O_2} of the inflow water is kept constant by equilibration with air or gas mixtures controlled by a Wösthoff pump. The inflow water passes a polarographic oxygen sensor for determination of the sensor's calibration factor. An identical sensor is connected to the outlet of the animal chamber. The medium in contact with the sensors is rigorously stirred in two minimum-volume measuring chambers. These are switched into either the measuring or calibration position by means of two 4-way microvalves. With this Twin-Flow principle (Gnaiger 1983 b), one sensor operates always in the outflow position giving the respiratory signal, while the other sensor is calibrated. Switching the two 4-way valves does not change the direction of flow through the animal chamber or connected microcalorimeter. With calibrations made at 2 to 12 hour intervals, the accuracy of p_{O_2} measurements is better than 0.2% in long term experiments over several days. The precision of the measurement of oxygen flow is $<1 \text{ pmol O}_2 \cdot \text{s}^{-1}$ (Gnaiger 1983 b; Gnaiger et al 1989).

The copepods showed an oxygen flux/pressure relation typical of oxyregulators (Fig. 9). In a hyperbolic fit, the p_{50} is the oxygen pressure at which 50% of the maximum oxygen flux is obtained. This is mathematically identical to the K_m of Michaelis-Menten kinetics, but an enzyme kinetic interpretation is meaningless on the level of organismic respiration. At three times the p_{50} , oxygen flux is 75% of the maximum value of the hyperbolic curve, and this may be defined as the critical oxygen pressure, p_c . This separates a relatively oxygen-independent homeostatic region $>p_c$, from a hypoxic region $<p_c$ where oxygen flux declines steeply with

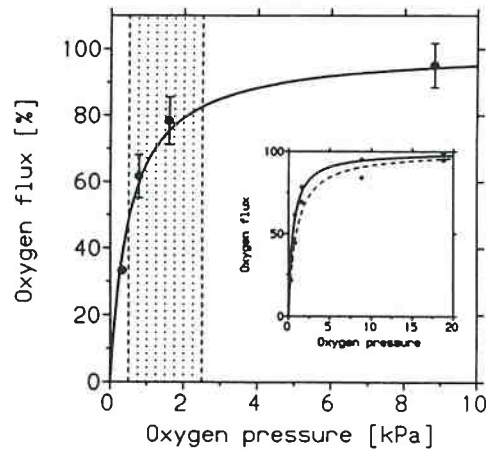


Fig. 9: Oxygen flux [% of maximum] of *Cyclops abyssorum* as a function of oxygen pressure, p_{O_2} [kPa], measured at 6 °C at steady state in the CYCLOBIOS Twin-Flow Respirometer. The full line shows the hyperbolic fit, vertical bars are \pm S.D. of oxygen flux at constant oxygen pressure (within the size of the symbol at the lowest p_{O_2}); three experiments initiated one to two days after sampling the copepods from lake Kalbelesee in April and beginning of May (Gnaiger 1938 b and Flöry 1980). The vertical dotted lines indicate the p_{O_2} range encountered by the population maximum in the vertical oxygen gradient during winter hypoxia (Fig. 8). Inset: Full line, closed circles – as in main figure, but showing the full oxygen range up to air saturation; $p_{50} = 0.53 \text{ kPa}$; $p_c = 1.6 \text{ kPa}$; maximum oxygen flux was $23.5 \text{ nmol} \cdot \text{s}^{-1} \cdot \text{g}^{-1}$ dry mass (average $35 \text{ } \mu\text{g}$ per individual; copepodite V and females). Dashed line, open circles – original data uncorrected for the decline of oxygen flux with time of starvation in the respirometer chamber. Without correction the curve is shifted to the right, and an erroneous higher p_c is calculated at 2.8 kPa (for details see Gnaiger 1983 b).

oxygen pressure (Gnaiger 1991). The p_c of *C. abyssorum* was 1.6 kPa (Fig. 9) which extends into the low oxygen range prevailing in the natural habitat during winter hypoxia (1.5 kPa; Fig. 8). Homeostatic oxygen regulation rather than hypoxic down-regulation is an important physiological adaptation in zooplankton for maintaining an active mode of life in the water column and for supporting the energy demands of growth and development (Fig. 7). Therefore, there is strong evidence that routine respiration is virtually unaffected down to the severely hypoxic conditions of 1.5 kPa encountered by the maximum of the population during winter over a period of 5 to 6 months.

In correspondence with the field observations the oxygen requirements of the less hypoxia tolerant *Daphnia pulex* are higher, with a p_c of approximately 2.3 to 4.6 kPa in various clones acclimated to low and high pO_2 (20 °C; Weider and Lampert 1985). The p_c and the minimum environmental oxygen pressure of marine crustacean plankton in the oxygen minimum layer correspond closely. The lowest critical oxygen pressures are in the range of 0.5 to 2 kPa, indicating that these species are fully aerobic in their hypoxic environment (Childress 1975). There are possible exceptions, such as the midwater copepod *Gaussia princeps* which migrates into the oxygen minimum of 0.8 kPa during the night but has a p_c of 1.3 kPa (Childress 1977). Similarly, *C. abyssorum* aggregates occasionally at oxygen levels slightly below the critical oxygen pressure. In such cases, an energetically costly anaerobic component of energy metabolism (Gnaiger and Staudigl 1987) cannot be ruled out.

Heat dissipation, locomotory activity and respiration under hypoxia

To test the possibility that spontaneous activity of the planktonic copepods may invoke anoxic contributions at the low oxygen levels of the environment, simultaneous calorimetric and respirometric experiments were carried out (Gnaiger 1983 b; 1991). By calorimetry, activation of anaerobic pathways of energy metabolism (Gnaiger 1991) is detected as an increase of directly measured heat flux above that calculated on the basis of respirometry (indirect calorimetry; Gnaiger 1983 c). In such calorimetric experiments, spontaneous activity fluctuations occurred with simultaneous changes of heat flux and oxygen flux (Fig. 10). The slope between heat flux and oxygen flux yielded a calorimetric-respirometric ratio (C/R ratio) of the activity component of -430 to -470 kJ · mol⁻¹ O₂, identical at 100 and 10% air saturation. By comparison, the oxycaloric equivalent calculated for the fully dissipative oxidation of carbohydrate, lipid and protein ranges from -430 to -480 kJ · mol⁻¹ O₂ (Gnaiger 1983 c). This agreement between the experimental C/R ratio and the theoretical oxycaloric equivalent of aerobic respiration indicates that spontaneous activity levels were fully supported by aerobic metabolism (Gnaiger 1983 c; Gnaiger and Kemp 1990).

The relation between oxygen flux, hypoxia and locomotory activity of *C. abyssorum* is shown in Fig. 11. In the confinement of the respirometer chamber, a number of active animals moved freely in the water column, N_c , whereas a number of inactive specimens rested motionless at the bottom, N_b . There was an oxygen-dependent tendency to attach to the walls of the animal chamber and the corresponding number of individuals, N_w , was inactive for comparatively short periods of time. The distribution of animals in these positions in the respirometer chamber was observed with a video recorder (Flöry 1980). The simultaneously recorded oxygen flux was then related to the index of relative activity (Gnaiger 1983 b),

$$\text{Relative activity} = \frac{N_c + f_w N_w}{N_c + N_w + N_b} \quad (2)$$

where f_w is a weighing factor for the relative activity of animals attaching shortly to the wall. At $f_w = 1$, the activity of copepods attached to the wall is rated identical to those swimming in the water column, whereas at $f_w = 0$ their activity is graded as zero. At $f_w = 0.33$, the relation was linear between oxygen flux and relative activity measured at various degrees of hypoxia in animals after various periods of partial starvation in the laboratory (Fig. 11). Interpretation of the slope is complex, since it combines the aerobic cost of locomotion and the effect of de-

creasing pO_2 on the basal energy metabolism. Anaerobic metabolism may be invoked when environmental oxygen declines below the *critical* oxygen level (Childress 1977). However, this must be examined in each case by direct calorimetry or biochemical methods, since adaptation to environmental hypoxia may involve a partial reduction of metabolic activity before the onset of anaerobic mechanisms (Gnaiger 1991, 1992). Then, only below the *limiting* pO_2 , at oxy-

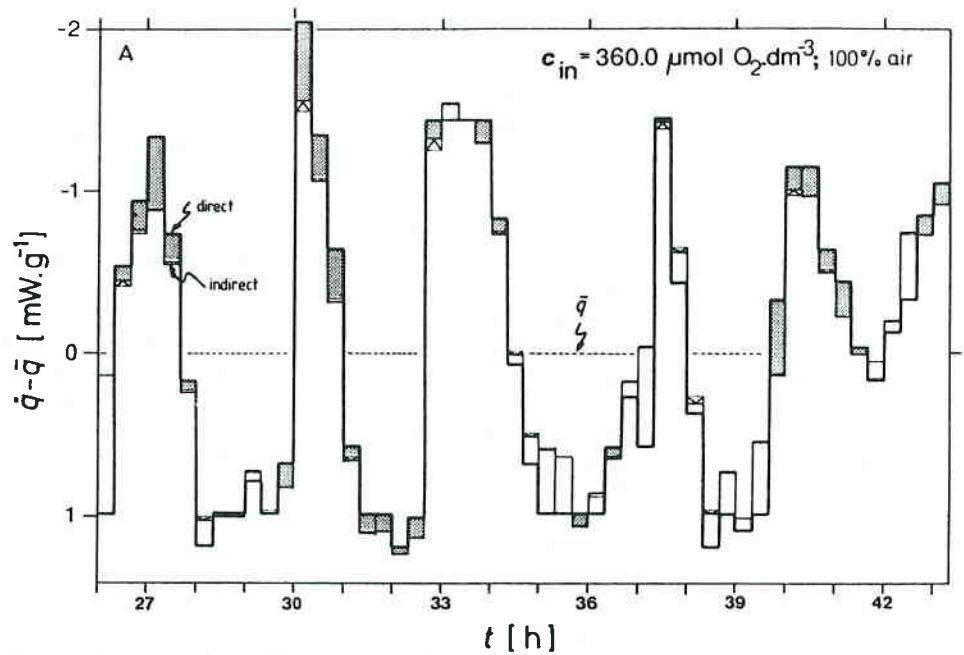


Fig. 10: Fluctuations of heat flux and oxygen flux of a group of 40 *Cyclops abyssorum* (copepodite V and females), measured simultaneously by CaloRespirometry under aerobic conditions, and expressed as deviations from the average value, \bar{q} , during the period of the experiment (26 to 43 hours at aerobic steady state). Thick line: heat flux (direct calorimetry). Thin line: oxygen flux converted to energy units by the theoretical oxycaloric equivalent of $0.45 \text{ mW}/(\text{nmol O}_2 \cdot \text{s}^{-1})$. The mean oxygen consumption was $14.3 \text{ nmol} \cdot \text{s}^{-1} \cdot \text{g}^{-1}$ in the starved copepods (calculated $\bar{q} = -6.41 \text{ mW} \cdot \text{g}^{-1}$). The dark areas show 20 min periods where measured heat flux is more exothermic than calculated (after Gnaiger 1983b).

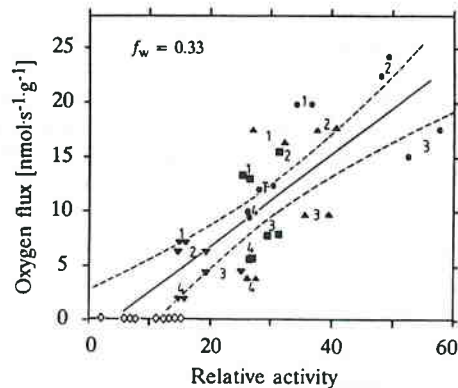


Fig. 11: Oxygen flux and swimming activity of *Cyclops abyssorum* at various steady state pO_2 levels (● 19 kPa; ▲ 1.6 kPa; ■ 0.8 kPa; ▼ 0.3 kPa; ◇ 0.0 kPa). The numbers 1 to 4 indicate experiments at progressing levels of starvation (6 °C; 40 individuals in the CYCLIBIOS Twin-Flow respirometer). Full and dashed lines: Linear regression and the 95% C.L., using a constant weighing factor for the wall effect, $f_w = 0.33$ (Eq. 2; for further details see Flöry 1980 and Gnaiger 1983b).

gen levels $\ll p_c$, anaerobic metabolism contributes to the basal and activity component of the energy budget. The intercept of the linear relation with the ordinate agreed well with the relative activity observed under anoxic conditions (Fig. 11, open symbols). Heat flux under anoxia was c. 10% of the aerobic level.

Anoxia in Cyclops abyssorum

Despite the sharp maximum density in a confined hypoxic layer, copepodites and adults were invariably found in the anoxic zone (Fig. 8). Zooplankton may be carried over into the anoxic depths by the descending water sampler. While such an artifact is not entirely excluded by comparison of temperature measurements in the sampler and *in situ* (Gnaiger 1983 a), an anoxic occurrence of the copepods was corroborated by several observations. 1) Chemical oxygen analyses were performed on water samples obtained by the same sampling procedure and corresponded with *in situ* polarographic oxygen analyses (Gnaiger 1983 a). 2) Swimming *C. abyssorum* were observed in the anoxic zone directly by SCUBA diving under the winter cover. 3) Schindler water samplers (5 dm³) were lowered into the anoxic layer at 3.5 m depth and left *in situ* for up to 8 days. During this period the enclosed copepods were prevented from periodic migrations into oxygen containing layers. In addition, copepods enclosed in Winkler flasks with anoxic water (300 cm³) were exposed in the anoxic zone. After recovering the water samplers and flasks, the copepods were active in their anoxic environment. The mortality after 8 days of 77% is a maximum figure owing to the handling stress, as evidenced by the 43% mortality observed after only 2 days of exposure (compare the high population mortality rate without anoxic confinement; Fig. 7). 4) In addition to these field observations, feeding experiments with *C. abyssorum* reveal a predatory behavior on *Paramecium* under strictly anoxic conditions (Steinlechner 1979). Feeding rates are lower under anoxic than aerobic conditions which corresponds to observations on the aquatic oligochaete *Lumbriculus variegatus* (Gnaiger and Staudigl 1987). Anoxic tolerance experiments without adequate food supply are relatively meaningless owing to the high substrate demand of anaerobic metabolism and the possibility that mortality may be caused by starvation rather than anoxic cell injury. Starving *C. abyssorum* tolerated anoxia at 12 °C for only 15–16 hours, and the Lt_{50} (time of 50% mortality) was 8–9 hours at 20 °C (compare Chaston 1969).

The capacity to withstand anoxia in an active planktonic mode of life is also known in rotifers, particularly *Filinia terminalis* occurring under similar limnological conditions near the anoxic boundary layer (Ruttner-Kolisko 1975, 1980). In contrast, the anoxic capacity is low in most marine zooplankton accumulating in the oxygen minimum layer (Childress 1975; but see Childress 1977). The difference in ecophysiological adaptations can be rationalized by the absence of an anoxic environment for the marine midwater crustaceans occurring in the oxygen minimum or by the vertical scale of the low oxygen region providing a large safety margin from the anoxic waters. Owing to the comparatively steeper oxygen gradient in lakes and ponds, hypoxia in the freshwater zooplankton is closely associated with a high probability of encountering the lack of oxygen at or below the anoxic boundary layer (Fig. 8). Oxygen gradients are even steeper in sediments (Fig. 1c), correlated with a high anoxic tolerance of meiofauna living in the sulfide system some mm or cm below the sediment surface (Wieser et al 1974; Giere 1992).

Hyperoxia during spring stratification

Despite the importance of anoxic tolerance, the physiological studies revealed the aerobic mechanism underlying the active lifestyle and growth of a winter generation of *C. abyssorum* under severe hypoxia. The close correlation of the depth of maximum density of *C. abyssorum* and hypoxia in the range of 0.5 to 2.5 kPa during winter stratification (Fig. 8C–E) may suggest a preference of the copepods for low oxygen levels. However, care must be taken not to incorrectly interpret the observed correlation in terms of a causal relationship between low oxygen and maximum abundance. In fact, this hypothesis was immediately rejected in view

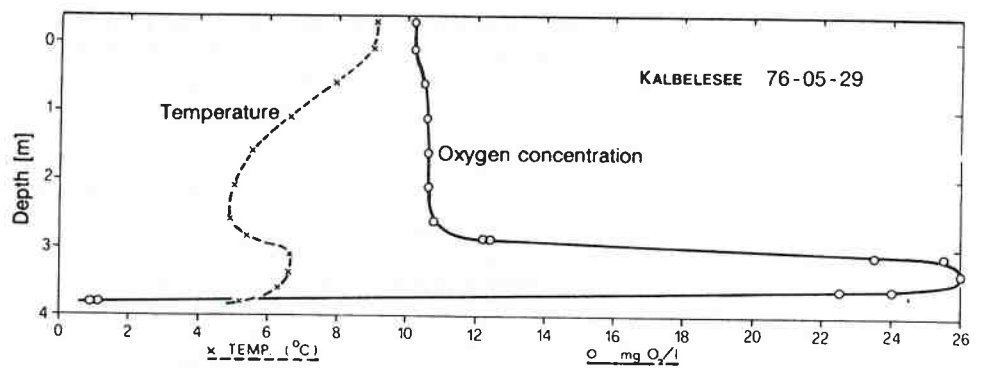


Fig. 12: Oxygen profile during spring stratification (1976-05-29, 16:00). The symbols indicate the *in situ* measurements of oxygen (circles) and temperature (crosses).

of the invariant depth distribution of *C. abyssorum* between anoxic, hypoxic and hyperoxic conditions up to 300% air saturation during a remarkable 'spring stratification' observed immediately after ice break (Fig. 8F and 12; Table 2).

Within two weeks after ice break, an oxygen maximum developed at 3.3 to 3.5 m depth owing to *in situ* photosynthetic oxygen production (Fig. 13 and 14). Oxygen levels approached absolute saturation such that bubbles of oxygen gas developed when water samples were brought to the surface and the hydrostatic pressure was released (Gnaiger 1983 a). High inorganic nutrient concentrations accumulate in the dark during winter anoxia in a zone extending up to 1.5 m from the bottom. The chemical stabilization of this water body prevents an immediate spring circulation, leading to temporal meromictic conditions and autochthonous oxygen maxima characterizing the spring stratification (Fig. 14). The chemical stabilization was quantified by the conductivity (κ_{20}) which increased from 150 μS at the surface to 250–400 μS at 3.5 m depth and 500–600 μS towards the bottom before icebreak (Gnaiger 1983 a). The density effect of ion concentration was sufficient to stabilize a temperature mini-

Table 2. Correlation of relative population density of *Cyclops abyssorum* in the vertical profile of lake Kalbelessee (average densities of two replicate 10 dm³ samples, each during the day and night), and relative density of algae during spring stratification, c. 10 days after ice break (76-05-28/29; see also Fig. 8F and 12).

Depth ^a [m]	Density of algae ^b			Density of <i>Cyclops abyssorum</i> [Individuals · dm ⁻³]		
	Unicellular flagellate algae	<i>Dynobryon</i> colonies	<i>Volvox</i> colonies	Nauplii	Copepodites & day	adults night
+0.2	–	–	–	–	0.00	0.00
0.8	–	–	–	–	0.00	0.00
1.8	–	–	–	–	0.15	0.10
2.8	X	–	–	X	0.25	0.15
3.3	XXX	XX	X	XXX	1.30	2.65
3.8	XXX	–	X	XX	1.65	3.40

^a Standard depth with a maximum of 4.0 m. The actual depth was +0.2 m above standard zero.

^b The symbols –, X, XX and XXX indicate relative densities ranging from zero or negligible to extremely high biomass concentrations, reflected in a sharp boundary of the Secchi disk transparency at 3.5 m.

imum where warming by solar radiation was prevented owing to the inflow of melt water forming a cold layer at intermediate depth (Fig. 15). With progressing photosynthetic nutrient assimilation the conductivity declined gradually, the chemical stabilization of the spring stratification diminished, and spring circulation mixed the entire water column three to four weeks after ice break (Fig. 13).

During spring stratification, a large part of the population of *C. abyssorum* was found at hyperoxic pressures up to 46 kPa ($900 \mu\text{mol} \cdot \text{dm}^{-3}$; c. 270% air saturation; Fig. 12 and 14). These elevated oxygen levels require an effective defense system against the toxic effects of molecular oxygen (Dyken and Shick 1982). Therefore, high superoxide dismutase activity either was maintained under hypoxia over months or was induced during the short period of a few days (Fig. 13 and 14). The two-fold increase of population density during the night in the water column one meter above the bottom (Tab. 2) indicates that during the day 50% of the population was anoxic at the water-sediment boundary layer. Oxygen does not determine the vertical distribution of *C. abyssorum*. The close correlation between density of algae and copepods points to food concentration as a direct cause for the depth preference of *C. abyssorum* (Fig. 8; Tab. 2).

Vertical aggregation of bacteria, algae and zooplankton in an oxygen gradient at depths near zero oxygen is a common phenomenon (Ruttner-Kolisko 1975; 1980; Laybourn-Parry and Strachan 1980; Finlay et al 1983; Baker et al 1985). Vertical differences in oxygen pressures are the direct signal on the basis of which the ciliated protozoan *Loxodes* congregates at very low oxygen (Fenchel and Finlay 1984). This ciliate is capable of nitrate respiration under anoxic

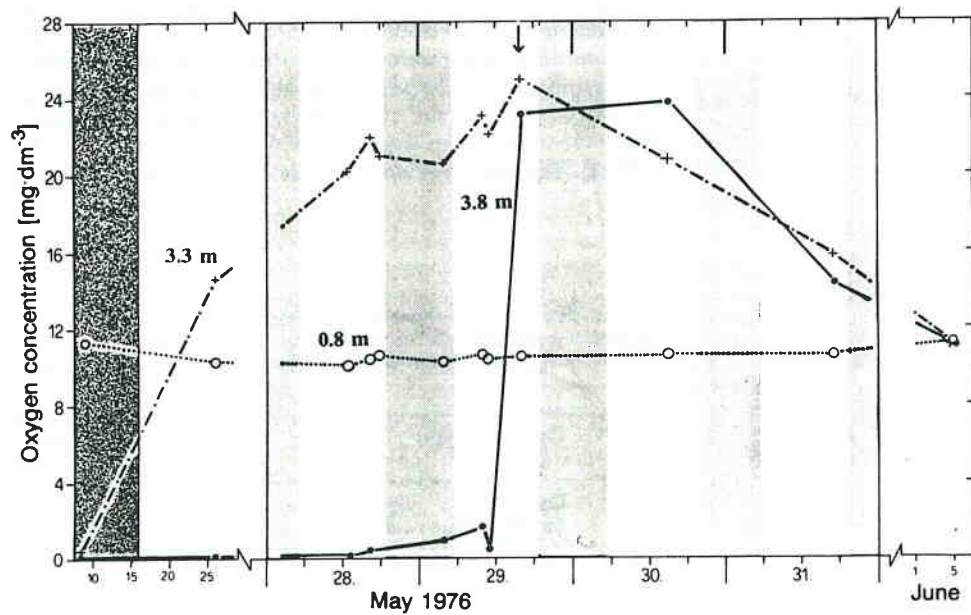


Fig. 13: Oxygen dynamics during spring stratification (1976). Oxygen concentration is shown for 0.8 m (○), 3.3 m (+), and 3.8 m standard depth (●), whereas total water level varied +0.2 to +0.7 m above standard zero. The dark area (left) shows the period of winter cover (compare Fig. 8E). The shaded areas indicate the periods between sunset and sunrise during May 28 to 31 (expanded time scale). Note the surprisingly small decline of oxygen in 3.3 m before sunrise on May 29. The arrow points to the vertical profile shown in Fig. 12. Full circulation occurred on June 5.

and microoxic conditions (Finlay et al 1983). Higher up in the food chain, there is evidence that rotifers and copepods orient themselves according to food concentration. The energetic benefits of life in the anoxic-aerobic boundary layer in sediments (Giere 1992) and of mitochondrial oxidative phosphorylation under extremely hypoxic conditions (Gnaiger et al 1993) may also sustain a rich biocoenosis in the microoxic boundary of lakes and ponds. On the other hand, the energetic disadvantages of oxygen limitation are compensated for by the abundance of food and the correspondingly high availability of energy.

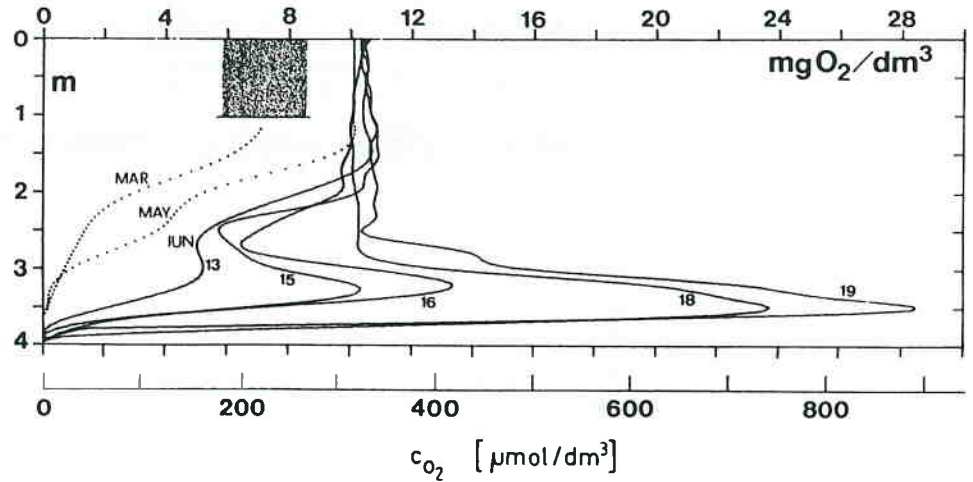


Fig. 14: Oxygen profiles during spring stratification (1978). In March and May (dotted profiles), the winter cover extended to about 1 m depth as indicated by the shaded column. After icebreak (June 11), an oxygen maximum developed at 3.5 m standard depth. The numbers indicate the dates in June (from Gnaiger 1983 a).

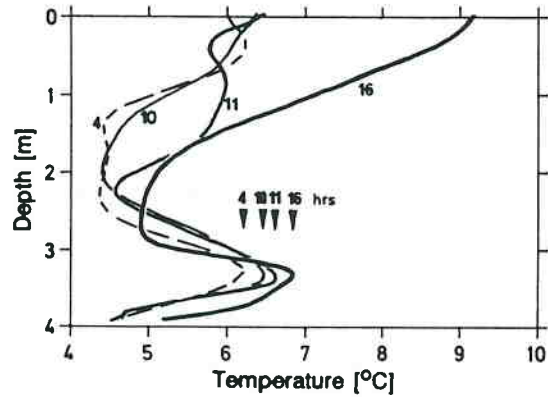


Fig. 15: Temperature/depth profiles in Kalbelesee during spring stratification (1976-05-29). The numbers indicate the time of measurement of the depth profile, using the thermistor of an *in situ* oxygen and temperature monitoring system (Gnaiger 1983 a). Sun rise was at 05:20. The warming up of the surface water, of the intermediary temperature minimum and the temperature maximum at 3.3 m depth arrows clearly evident.

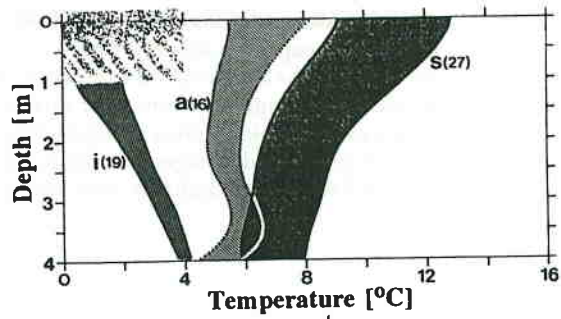


Fig. 16: Patterns of temperature stratification in lake Kalbelesee. s – summer stratification; i – inverse winter stratification, under ice cover; a – anomalous spring stratification. The ranges are the 99% confidence limits of the means of temperature/depth profiles taken over the years 1975 to 1978. The number of profiles taken under each condition is given in parentheses.

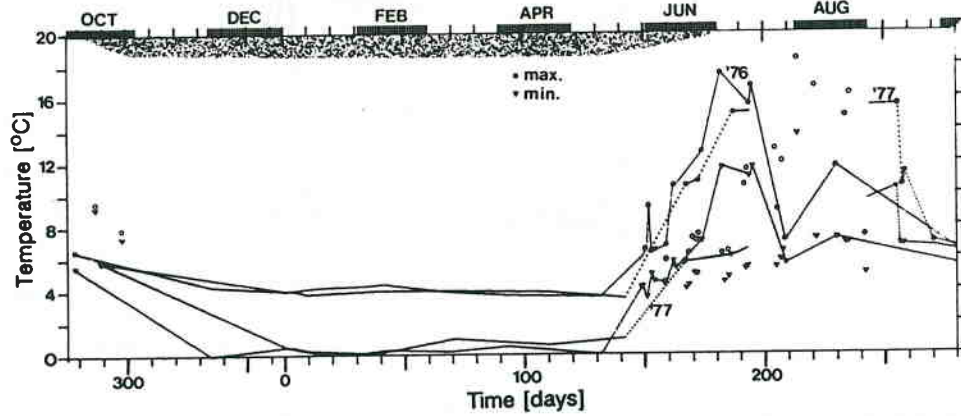


Fig. 17: Annual dynamics of minimum (circles) and maximum temperatures (triangles) in lake Kalbelesee. The temperature minima and maxima are interpolated for the years 1976 (full line) and 1977 (dotted line).

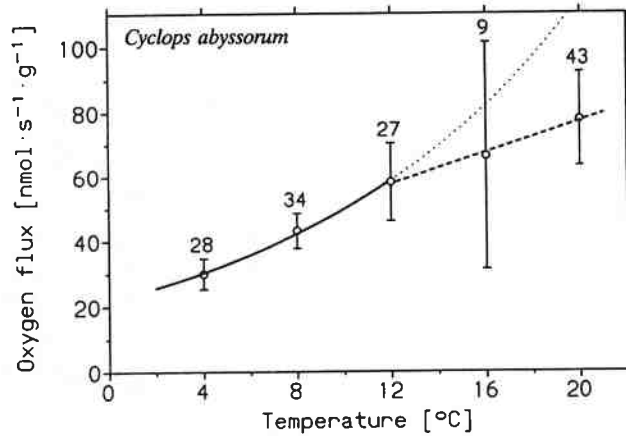


Fig. 18: Respiration of *Cyclops abyssorum* [$\text{nmol O}_2 \cdot \text{s}^{-1} \cdot \text{g}^{-1}$ dry mass] as a function of experimental temperature. Oxygen uptake was measured with 10 individuals (32 to 42 μg dry mass per individual; copepodites and females) enclosed in 5 cm^3 glass syringes during 5 to 10 h. Oxygen was measured by the chemical Winkler determination with amperometric endpoint titration (Benzer, 1978). The number of experiments at each temperature is given by numbers. The expected exponential temperature relation is shown by the full line for temperatures between 4 and 12 $^\circ\text{C}$, extrapolated by the dotted line corresponding to a Q_{10} of 2.3. Respiration above 12 $^\circ\text{C}$ drops significantly compared to the exponential relation (dashed line). The vertical bars indicate the 95% confidence intervals.

Oxygen is not considered to be a prominent factor in the control of vertical migration of zooplankton (Haney 1993). Vertical migrations were absent during winter hypoxia (Fig. 8C and 8E for January and May; similar in February and April). During summer stratification, oxygen concentration in Kalbeleesee was near air saturation at all depths (Fig. 8A). Development of an oxygen deficit towards the sediment was rare (Gnaiger 1983 a). Nocturnal migration during summer was evident from the vertical distribution pattern (Fig. 8A) and from changes of the abundance in the water column. Absolute densities increased in the water samples taken at night as compared to the day, indicating a nocturnal vertical migration from the sediment boundary, even when the relative distribution patterns did not change during fall circulation (Fig. 8B) or spring stratification (Fig. 8F; Tab. 2). Under these diverse conditions without winter cover, only 36% (± 23 S.D.; $N = 8$) of the population density (adults and copepodites) were caught in the water column during the day relative to the night. In contrast, the densities during day and night were not different under winter cover ($91\% \pm 13$ S.D.; $N = 4$; copepodites and adults). Vertical migration of the nauplii was not apparent which may be expected since immature individuals often do not migrate (Haney 1993). The absence of diurnal migration under winter hypoxia, in contrast to the typical diurnal migrations of *C. abyssorum* in Kalbeleesee during summer stagnation is difficult to reconcile with a simple fish predation hypothesis (Gliwicz 1986).

Despite the shallow depth, the temperature stratification in Kalbeleesee was stable throughout the summer, except for rare weather conditions. Compared to the large annual temperature variation, the water temperatures during any season were predictable within narrow ranges, particularly at the bottom and with an increasing range at the surface (Fig. 16). Occasionally, there were conditions during warm periods in July and August, when the temperature at the bottom of the lake increased to $>12^{\circ}\text{C}$. However, the probability to encounter higher temperatures in the water column over extended periods of time is low even during summer (Fig. 17).

The effect of temperature on respiration of *C. abyssorum* is shown in Fig. 18. Temperature acclimation was without significant effect on oxygen flux (Benzer 1978). Up to 12°C the Q_{10} was 2.3, indicative of the expected exponential increase of respiration with temperature. However, above 12°C the measured oxygen flux increased less steeply relative to the extrapolated exponential oxygen flux/temperature relation (Fig. 18). Respiration declines $>8^{\circ}\text{C}$ in the cold adapted *Cyclops bicuspidatus* (Laybourn-Parry and Strachan 1980). *C. abyssorum* has been considered as cold-stenothermal but was later classified as eurythermal on the basis of its ecological distribution (Nilssen and Elgmork 1977) which is supported by the respiratory results (Fig. 18). Large temperature and oxygen variations are well tolerated by *Cyclops abyssorum* which is a physiological basis for the success of this species in alpine lakes at various altitudes and of different trophic status.

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