Plankton - going down slowly - always *

Richard Müller†

Ecological field station YH Sorpesee, Am Sorpesee 7, 59846 Sundern, Germany

Fitness prolongs life

Most planktonic organisms have a density greater than that of the surrounding water. As a consequence, they sink down through the water. In standing waters of a certain depth, sinking means death for planktonic algae because of the lack of light for photosynthesis below the compensational depth. Organisms which sink slowly or even avoid sinking altogether have a great evolutionary advantage. To escape certain death from sedimenting, several strategies are conceivable, e.g.:

- Planktonic organisms can move actively in order to attain their optimal depth
- Planktonic organisms are able to regulate their density and accordingly their depth
- Planktonic organisms have mechanisms to slow down their sinking

Evolution has followed all these paths. For each of these strategies many examples exist. In the experiment shown here, we will investigate strategy no. 3.

Light: not too much and not too little

The simple rule 'the more the better' does not apply for the relationship between the intensity of light and photosynthetical production. With low light intensities the correlation with production is linear, but at intensities greater than ca. 100 μE m^{-2} s (the published numbers vary between 20 and 300 μE m^{-2} s) the production rises less steeply and even becomes negative with very high intensities (200-1000 μE m^{-2} s). The reason for the so called light inhibition lies in the damage caused to plastids by ultraviolet radiation and the higher photorespiration. ([3], cf. fig. 1) Especially during summer lesser chlorophyll concentrations are measured at the surface compared to some meters deeper, but higher pheopytin concentrations. Having a density lower than the

*Download in english and german, together with worksheets at `http://www.phytoplankton.info/download/sedimentation.zip`

†r.mueller@oeko-sorpe.de

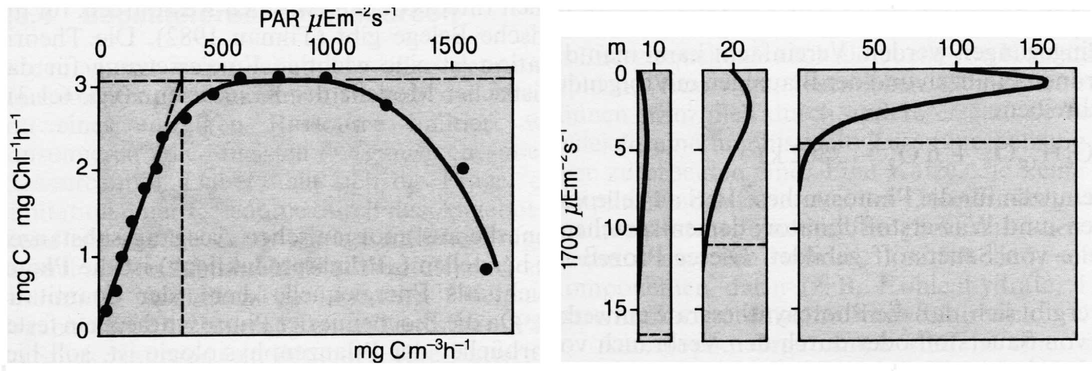

Figure 1:

Impact of surface radiation on the vertical profile of photosynthesis. Left: lightintensity (photosynthethic active radiation = PAR, measured in μEinstein per m^2 and s) against production (measured in mg chlorophyll/hour). Right: production (measured in mg carbon per m^2 and hour) against depth (in m) at 1700 μE m^{-2} s and with different densities of biomass (1, 10 and 50 mg chlorophyll per m^3). From [3]

surrounding waters would prevent the algae from sedimenting, but would also expose them to more of the deadly ultraviolet radiation (algae, which live at or near the surface, e.g. in very shallow waters, have specific protecting mechanisms). An alga should stratify in the layer where its optimal light conditions prevail. But this mechanism is impossible for non-motile algae or those lacking the ability to regulate their density. Even motile species are subject to turbulence in the water. Even windspeeds of 3 m/s (2 . . . 3 Bft) dislocate layers in the epilimnion. Even motile algae underlie this fate [1]. Because in late summer the epilimnion can reach into the tropholytical zone, even motile plankic organisms can not evade their destiny.

Who brakes wins [4]

The sedimentation velocity of a body in water depends on three variables: its density ρ (or more exactly the difference between its density and the density of the water), its surface area A, and the viscosity of the water η.

Let us first have a look at the influence of the surface area A. Sedimentation is influenced by frictional resistance, and this is a function of surface area: *the greater the area, the greater the frictional resistance.* For a sphere, the surface-volume ratio is inversely proportional to the radius: $A/V = 3r^{-1}$. A sphere with a radius of 1000 μmhas a *specific* surface[2] in relation to the radius in μm) of 3 μ $10^{-3} \times m^{-1}$, with a radius of 1 μmthe specific surface for a sphere is 3 $\times m^{-1}$ and therefore 1000 times larger and it will sink much more slowly: That is one evolutionary reason why planktonic organisms are

[1]Because of this these algae are included in the plankton despite their motility.

[2]Dimension of specific surface: $\frac{A}{V} \rightarrow \frac{\mu m^{-2}}{\mu m^{-3}} = \mu m^{-1}$

so small. The time they have for photosynthesis and reproduction, before they sink to a deadly depth, is therefore greater than that for larger organisms.

The sinking velocity of a sphere shaped planktonic organism is, according to STOKES' law:

$$v_{sink-sphere} = \frac{4gr^3\pi(\rho_{sphere} - \rho_{water})}{3 \times 6\pi\eta r} = \frac{2gr^2(\rho_{sphere} - \rho_{water})}{9\eta}$$

A sphere shaped planktonic organism ($\rho = 1{,}05 \times 10^3$ kg m^{-3}) of $r = 10$ μmin water of 20 ℃ ($\rho = 0{,}998 \times 10^3$ kg m^{-3}) sinks 98 cm per day.

Investigating plankton with a microscope reveals that most such organisms differ greatly from simple spherical shapes (Fig. 2). .

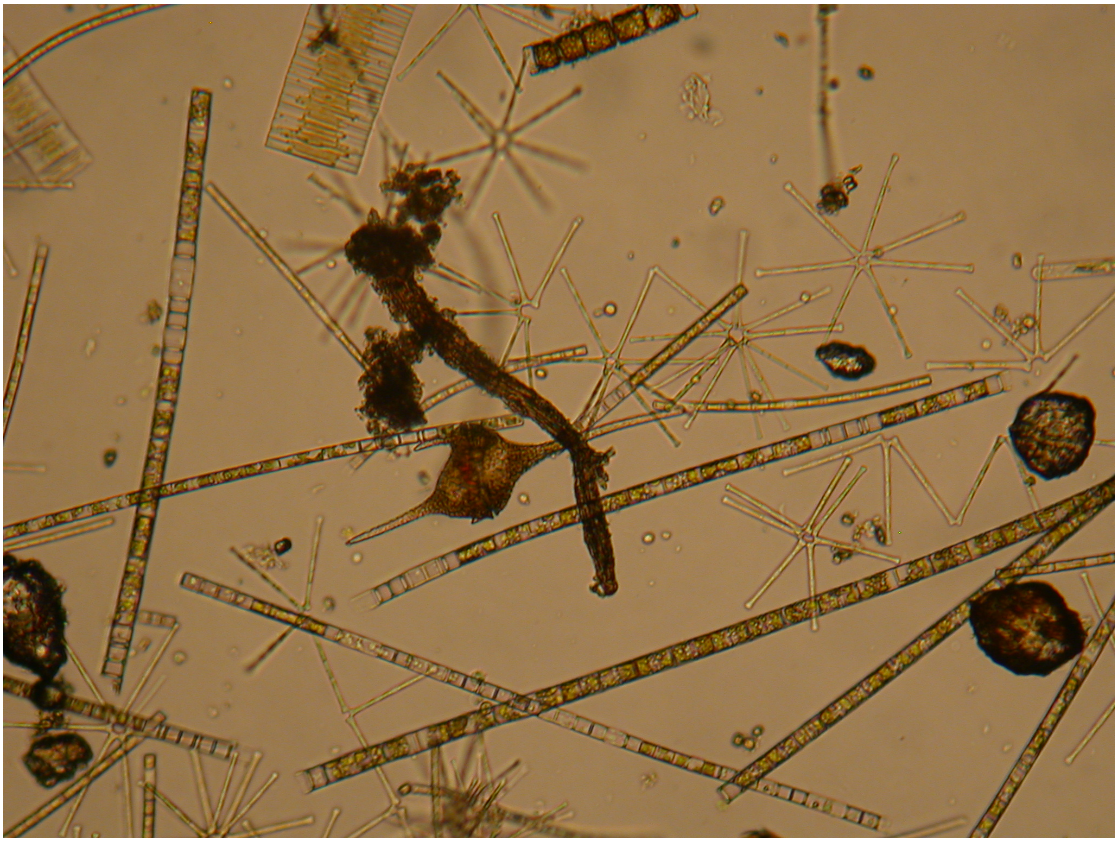

Figure 2:

Plankton from Sorpe Reservoir (main basin), april 2005: *Fragilaria crotonensis, Asterionella formosa, Melosira italica, Ceratium hirundinella*

Spheres are the geometric objects whose surface is the smallest for a given radius; all other objects have a greater specific surface. Partly the increase of the surface is extreme (Tab. 1, data after [7]). For non-spherical objects, a correction coefficient c (the sinking quotient) has to be introduced:

	Organism					Sphere	
	No. of cells	Length (max.) (μm)	Surface (A) (μm^2)	Volume (V) (μm^3)	A/V (μm^{-1})	A/V (μm^{-1})	$\frac{A/V_{organism}}{A/V_{sphere}}$
Cyclotella	1	15	780	1600	0,49	0,41	1,18
Synedra	1	110	4100	7900	0,52	0,24	2,14
Mallomonas	1	40	3490	4200	0,83	0,3	2,77
Chlorella	1	4	50	33	1,52	1,51	1
Ceratium	1	201	9600	43740	0,22	0,14	1,6
Dinobryon	10	145	5350	7000	0,76	0,25	3,02
Asterionella	8	130	6690	5160	1,3	0,28	4,63
Fragilaria	10	70	9190	6230	1,48	0,26	5,61
Fragilaria	100	300	91900	62300	1,48	0,12	12,09
Pediastrum	32	100	18200	16000	1,14	0,19	5,93
Melosira	10	240	4350	5930	0,73	0,27	2,75
Sphaerocystis		46	6650	5100	1,3	0,28	4,64
Sphere		1	3,14	0,52	6	6	1

Table 1:
Dimensions, surface areas and volumes of different planktonic organisms, calculated with data from [7]

$$v_{sink-organism} = \frac{v_{sink-sphere}}{c_{organism}}$$

This sinking quotient depends on the frictional resistance, which is a function of the specific surface. Algae with a greater *specific* surface sink more slowly.

We can take as an example *Asterionella formosa*: a typical 8-celled colony has a mean volume of $V = 5160\ \mu m^3$and a density of 1130 kg/m^3 [7]. Water of 20 ℃has a density of 998 kg/m^3. Its viscosity is about $\eta = 0.001$ kg/ms. The gravity constant is $g = 9.81 m/s^2$. A spherical body with the same volume as this *Asterionella* colony would have a radius of 10.4 μm. These values inserted into the formula for sinking velocity, converted to the distance per day, gives $v = 2.69$ m/d for a sphere with the density and volume of an *Asterionella* colony. Considering the non-sphericality of *Asterionella*, and using a corresponding sinking quotient of $c = 4.63$ (cf. table 1), one obtains a sinking velocity of $v = 0.58$ m/d, which corresponds well with the values observed. By experimental investigation values of 0.59 m/d have been measured for dead *Asterionella* colonies (Smayda 1974 in [7])[3]. Thus, the special shape reduces *Asterionella*'s sinking velocity to about one fifth!

[3]It is noticeable, that the sinking velocity of algae is depending from the physiological state of the organisms.

And the same in larger objects?

To demonstrate the relationship between shape and sinking velocity, the use of a model experiment is readily to hand. It is no surprise that a number of school textbooks describe such model tests(fig. 3). Conducting these experiments as mostly described reveals a non satisfying outcome.

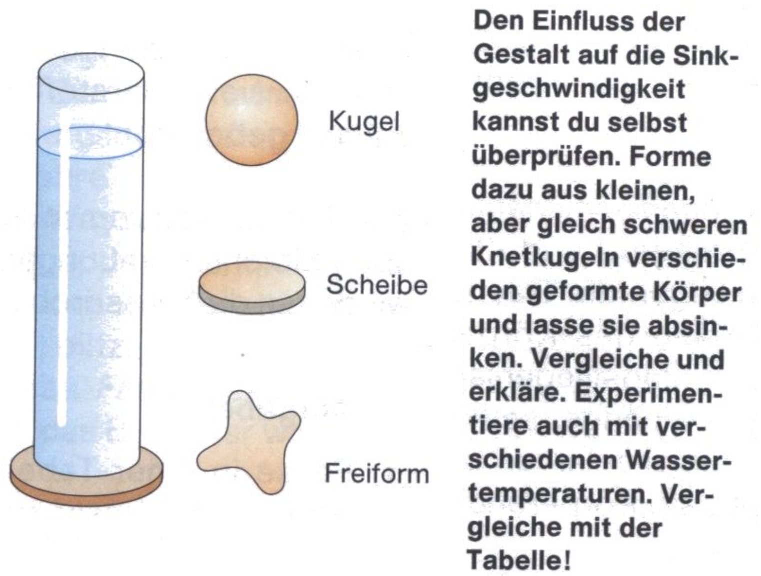

Figure 3:
Sinking experiments in a schoolbook, from [1]. Text: The influence of shape on sinking velocity you can findout yourself. Model different shaped objects from small lumps of plasticine with identical weight and let them sink. Compare and explain! Use also different water temperatures!

When conducting these experiments, the outcome is often not satisfactory. The results differ only by fractions of a second. The influence of the shape on the sinking velocity is only barely measurable.

To test the published protocol model bodies were made, each from 2.2 g of plasticine (ρ = 1600 kg/m^3): a sphere (14 mm $\varnothing$) and a model of *Ceratium hirundinella*. The measuring distance in a 250 ml cylinder was 18 cm. 10 experiments yielded the following results:

	sphere	*Ceratium*
sinking time (median) $\bar{t}$ (s)	0,673	0,914
standard deviation s	0,119	0,095
$\Rightarrow$ sinking velocity $\bar{v}$ (m/s)	0,627	0,197

These small times are nearly unmeasurable with a manual stopwatch, accordingly the values are quite unsafe. Even with larger cylinders and longer distance the values differ

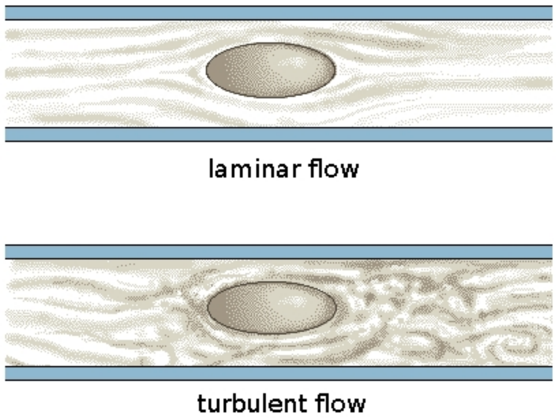

Figure 4: Laminar und turbulent flow, from [5]

only by fractions of a second. The influence of the shape on the sinking velocity is only very limited measurable.

These protocols ignore that objects cannot be larger without altering their hydrodynamics. With very small objects we must imagine a 'creeping' streamline flow around the object; this means that the flow lines merge behind the object the same way they have opened in front of it. With larger objects, flow separation and the formation of eddies appear, so that the influence of surface friction become less important. (Fig. 4).

To describe the nature of the flow, REYNOLD's number Re is used. It is definded as follows:

$$Re = v \times l \times \nu^{-1},$$

with sinking velocity v measured in m/s, l is the reference length in m, e.g diameter or maximum length and ν is the kinematic viscosity in m^2/s¸[4]. For water at 20 ℃ ν is 1.01 $\times$ 10^{-6} m^2/s.

At $Re \leq 1$ only laminar flow occurs, from $Re = 1$ and larger, the portion of turbulent flow is growing with Re. A plasticine spherical body ($l = 14 \times 10^{-3}$m) put in water ($\nu = 1{,}01 \times 10^{-6}$ m^2/s), with an observed sinking velocity of $v = 0{,}267$ m/s gives a REYNOLDS number of

$$Re = \frac{0,267\frac{m}{s} \times 14 \times 10^{-3}m}{1,01 \times 10^{-6}\frac{m^2}{s}} = 3701,$$

which is far above the mentioned limit 1. These high REYNOLDS number describes turbulent flow, which is nearly non-existent for small organisms. To achieve smaller REYNOLDS numbers, one has to make the object smaller, but it is only working with large objects that makes sense in this model experiment. The alternative is to increase the viscosity of the medium.

[4]kinematic viscosity ν is dynamic viscosity η divided by density ρ

Figure 5: Media for model experiments: sugar, motor oil, raspberry syrup

An example of a liquid with higher viscosity is glycerol (w = 98.5 %) [2], [6], which has a kinematic viscosity of $\nu = 768{,}6 \times 10^{-6}$ m^2/s and a density of $\rho = 1256$ kg/m^3. In this liquid, our plasticine model alga needed about 2.5 min for a sinking distance of 18 cm. That means a sinking velocity of about $v = 0.0012$ m/ and aREYNOLDS number of $Re = 0.02$ and therefore the model is in the range of laminar flow. The use of glycerol instead of water delivers two advantages: the sinking velocity becomes so low that it is readily measurable and only laminar flow has to be considered. PADISÁK et al. [6] point out the importance of the size of the used containers. To avoid interferences with turbulescence generated at the walls of the cylinder, it has to be as large as possible. For reasons of economy we used 1000 ml-measuring cylinders and put up with the error of turbulescence. The results show, that this is tolerable.

On the other hand, the use of glycerol has two drawbacks: First, one needs a non-trivial volume to fill larger cylinders, which means a certain challenge for some schools' budgets. Second, glycerol is very hygroscopic and even small amounts of water absorption have considerable effects on its viscosity. But there are alternatives. In principle every liquid is usable, as long as it is viscous enough. Concentrated saccharose solution or motor oil are recommended (Fig. 5) .

Saccharose solution (w = 66 % (w/v)) has a kinematic viscosity of $\nu = 165{,}3 \times 10^{-6}$ m^2/s and a density of $\rho \approx 1300$ kg/m^3. For our model algae (Fig. 7) that means a Reynold's number of $Re \approx 705$, meaning a certain part of turbulent flow, but it is three to four times less than water and therefore the sinking velocity becomes more easily measurable. Results of experiments with this solution are shown in table 2 and fig. 6

Experiments with motor oil (Calpam Multifleet SAE15W40) gave even better results (table 4). This oil (20 ℃) ν is about 230×10^{-6} m^2/s and the density ρ measures circa 883

shape:	sphere	small disk	star	cone
sinking times t (s)	1,07	4,58	3,69	1,05
	1,17	2,00	3,06	1,00
	1,12	4,38	4,07	1,31
	1,01	4,62	3,75	1,24
	1,13	4,80	3,69	1,14
	1,15	5,08	3,06	1,2
	1,24	5,17	3,55	1,33
	1,26	1,82	3,57	1,24
	1,07	4,89	2,56	1,00
	1,08	3,38	3,57	1,18
median $\bar{t}$ (s)	1,13	4,07	3,46	1,17
sinking velocity v (m/s)	0,27	0,07	0,09	0,26
sinking quotient c	1	3,6	3,06	1,02

Table 2:
Sinking experiments with plankton models in concentrated saccharose solution, measuring distance 30 cm

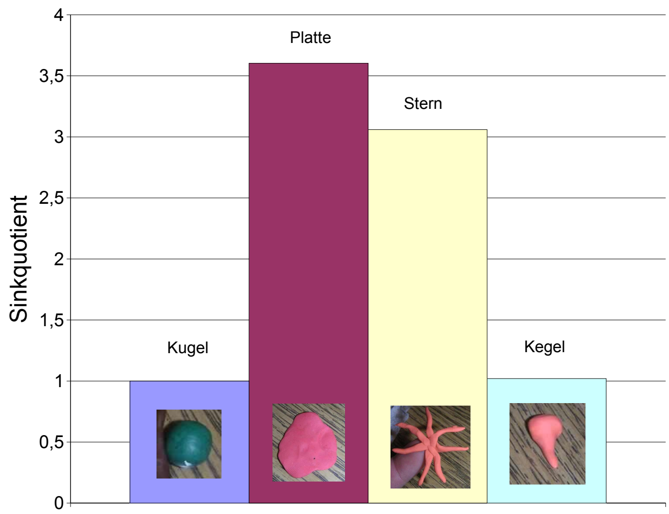

Figure 6: Correlation of sinking quotient c and shape

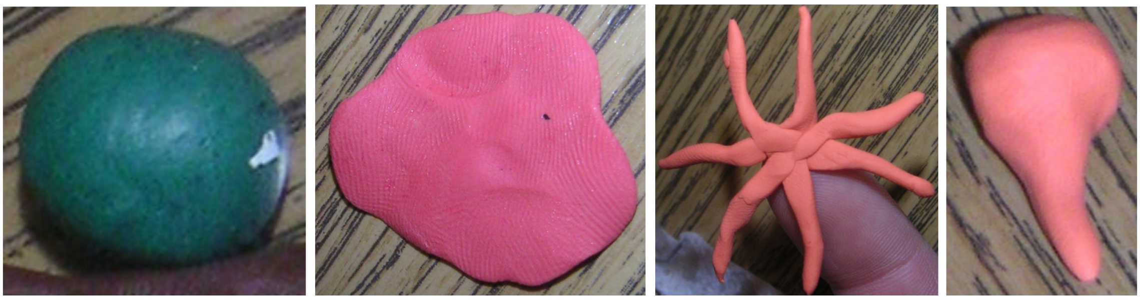

Figure 7: Plankton models of plasticine

Temperature (℃)	ρ_{water} (kg/m^3)	$\rho_{plankton}$ (kg/m^3)	η_{water} (kg/ms)	v_{sink} (m/s)	v_{sink} (m/d)
0	999,87	1130	0,0018	$3{,}96 \times 10^{-6}$	0,34
20	998,2	1130	0,001	$7{,}18 \times 10^{-6}$	0,62
40	992,1	1130	0,0007	$11{,}5 \times 10^{-6}$	0,99

Table 3: Influence of temperature on sinking velocity of plankton

kg/m^3. Using the same sphere as with the experiments in saccharose results a Reynolds number *Re* of only 9.1; with a model of *Asterionella Re* rises to 43.7. These values are still not perfect, but nearer to the values which are decisive with real plankton in water.

Warm and cold

The temperature of the water not only influences its density, but also its viscosity [5]. The warmer the water, the more readily it flows. We don't sense this effect while swimming in colder or warmer water, because we are much larger than a planktonic alga. The Reynolds number for a swimming man would be about 2 million, so the surface friction is of no importance. While swimming, we only have to overcome the resistance of the water. For a planktonic alga the challenge is different; it sinks in water of 20 ℃ about twice as fast than in water of 0 ℃. For a sphere shaped organism of 10 μm diameter the values can be found in table 3.

The influence of temperature on sinking velocity can be demonstrated in a model experiment. Our viscose medium is heated to about 45 ℃. For safety reasons, temperature should not rise higher. Besides that, plasticine is becoming too weak with higher temperatures. The results of experiments with motor oil are shown in table 4.

The warming from 20 to 45 ℃ results in a 2.2-fold increase of sinking velocity.

During summer, some lakes show maxima or minima of oxygen at the beginning of the metalimnion. In cases where the euphotic zone reaches the metalimnion, a maximum of oxygen will be found there, otherwise, if the metalimnion is in the dark, a minimum. The

[5] There is no 'viscosity anomaly'

		sphere	*Asterionella* 8 cells	*Asterionella* 4 cells
20 ℃	v (m/s)	0,12	0,033	0,049
	c	1	3,64	2,45
45 ℃	v (m/s)	0,256	0,079	0,112
	c	1	3,24	2,23
velocity factor		2,13	2,39	2,28

Table 4:
Sinking velocity v and sinking quotient c at different temperatures in motor oil SAE15W40

reason is that, in the cold metalimnion, the sinking velocity of the plankton is reduced and a planktonic 'traffic jam' arises. If the light intensity is sufficient in the zone of the 'jam', net photosynthesis is positive, otherwise respiration is the dominant factor.

The Sorpe reservoir regularly shows each summer maxima or minima in its oxygen profile in the depths of the metalimnion. In early summer, when the euphotic zone reaches into the metalimnion, an oxygen maximum can be found there. The sinking velocity of algae is reduced due to the colder water. They accumulate there, and a 'traffic jam' is resulting. This higher amount of algae effectuates a higher production of oxygen. In the course of the summer the lower boundary of the epilimnion moves more to greater depth, so in late summer the metalimnion lies in the dark, in the tropholytic zone. So also the 'plankton jam' lies in the dark depth. The value of net photosynthesis becomes negative, oxygn is not produced but consumpted, which shows as minimum in the oxygen curve (fig. 8).

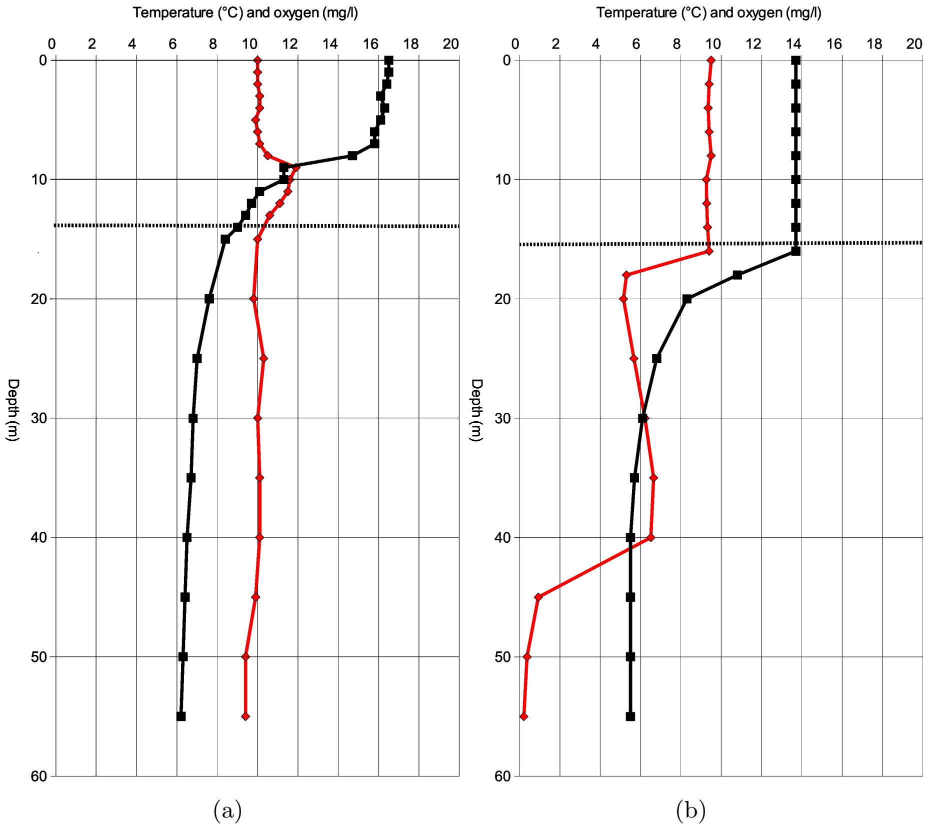

Figure 8:

Oxygen concentration and temperature of Sorpe Reservoir at 3 June 2002 (a) and 24 October 2005 (b). Squares: temperature, diamonds: oxygen, horizontally dotted: depth of euphotic zone

References

[1] Haala, G.; Wichert, G.; Zohren, D. (2004): Natura. Biologie für Gymnasien. Nordrhein-Westfalen. 8. und 9. Schuljahr. Klett

[2] Lagergren, R.; Lord, H.; Stenson, J.A.E. (2000): Influence of temperature on hydrodynamic costs of morphological defences in zooplankton. Functional Ecology **14**(3), S. 380–387

[3] Lampert, W.; Sommer, U. (1993): Limnoökologie. Stuttgart

[4] Nachtigall, W. (1999): Warum sinken kleine Plankter so langsam ab? Mikrokosmos **88**(3), S. 157–166

[5] N.N. (o.J.): Hydrodynamic principles (`http://library.thinkquest.org/18033/hydrodyn.html`)

[6] Padisák, J.; Soróczki-Pintér, E.; Rezner, Z. (2003): Sinking properties of some phytoplankton shapes and the relation of form resistance to morphological diversity of plankton - an experimental study. Hydrobiologia **500**, S. 243–257

[7] Reynolds, S.C. (1994): The ecology of freshwater phytoplankton. Cambridge

Abbreviations and units

μE	mikro-Einstein	6.02×10^{17} photons
Bft	Beaufort	windspeed
ρ	density	kg/m^3
A	surface	m^2
η	dynamiche viscosity	often also μ; Pa s = kg/m s
Pa	pressure	Pa = kg/m s^2
V	volume	m^3
g	gravity constant	$g = 9.81$ m/s^2
r	radius	m
v	velocity	m/s
c	sinking quotient	dimensionless; sinking velocity of an object in relation to sinking velocity of a sphere of same volume, at identical conditions
Re	Reynolds numberl	dimensionless; gives information of nature of flow (laminar/turbulent)
ν	kinematic viscosity	$\nu = \eta/\rho$