

## The edibility of *Staurastrum chaetoceras* and *Cosmarium abbreviatum* (desmidiaceae) for *Daphnia galeata/hyalina* and the role of desmids in the aquatic food web

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### Abstract

A laboratory clone of *Daphnia galeata/hyalina* was fed with two different planktic desmid taxa: *Staurastrum chaetoceras* and *Cosmarium abbreviatum* var. *planctonicum*, being about equal in cell size. Whereas *Staurastrum chaetoceras* was readily ingested and assimilated to a high degree, *Cosmarium* was hardly incorporated. This could be partly due to the presence of an extracellular mucilaginous envelope in the latter species. When decapsulated by mild sonification, *Cosmarium* cells were significantly better ingested but digestion was still inferior to that of *Staurastrum*, presumably because of the more compact cell shape of *Cosmarium*.

From literature it appears that small-sized planktic desmid species occasionally may constitute a main food source for zooplankton, especially in eutrophic lakes. Most likely however, desmids, particularly large-sized species, play a much more important role in the food chain in the benthic compartment of shallow, oligotrophic water bodies where they serve as a food source for various macro-invertebrate taxa.

### Introduction

In the large body of literature on grazing of plankton algae the specific role of desmids as a food source in the aquatic food web is only briefly described (Brook, 1981). No doubt, this has to do with the generally low contribution by desmids to the phytoplankton biomass. Traditionally, desmids are associated with oligotrophic freshwaters (Hutchinson, 1967). However, although the number of desmid species in algal samples from oligotrophic softwater bodies often exceeds that of other taxonomic groups (Thunmark, 1945) in terms of biomass, desmids play a minor role in the composition of the phytoplankton (Järnefelt, 1952; Rawson, 1956; Rosén, 1981). Another reason why desmids are seldom observed in studies on grazing may be their generally large cell size, often additionally extended by a copious extracellular mucous envelope. Large-sized algal cells are hard to handle for most zooplankters and, when supplied with an additional tough mucilaginous sheath, ingestion and digestion appear to be hampered even more (Porter, 1973, 1976; Sommer, 1981).

The present paper aims at providing more insight into the significance of two planktonic desmid species, one with and one without extracellular mucous envelopes, as a potential food source for the *Daphnia galeata/hyalina* group, commonly occurring in deep, temperate lakes. In addition the possible role of desmids in the aquatic food web in general, as indicated from literature, will be considered.

### Materials and methods

Grazing experiments were performed with a laboratory clone of the probable hybrid between *Daphnia galeata* and *Daphnia hyalina* isolated from Lake Maarsseveen (Spaak & Hoekstra, 1993). The clone was pre-cultured in filtered (0.2  $\mu\text{m}$ ) lake water with the chlorococcalean green alga *Scenedesmus acuminatus* as a food source. For the experiment proper two desmid clones were used: *Staurastrum chaetoceras*, isolated from the plankton of the alkaline, eutrophic Lake IJmeer, and *Cosmarium abbreviatum* var. *planctonicum*, isolated

from the likewise alkaline, but oligo-mesotrophic Lake Maarsseveen (both lakes are situated in the centre of The Netherlands). The desmid clones under discussion were grown in Woods Hole medium (Nichols, 1973) in which TRIS buffer was substituted by 2 mmol l<sup>-1</sup> HEPES and pH was set at 7.0–7.2. Cultures were aerated, kept at 20 °C and an incident irradiance of ca. 50 μmol m<sup>-2</sup> s<sup>-1</sup> at a daily regime of 16 h light: 8 h darkness. Cell volumes of both taxa are roughly comparable, i.e., 3000–5000 μm<sup>3</sup> (Coesel & Wardenaar, 1990). However, *C. abbreviatum* cells are devoid provided with a copious, sharply outlined mucilaginous envelope whereas *S. chaetoceras* cells are destitute of such an extracellular mucous configuration (Coesel & Wardenaar, 1994, Figure 4). The presence of the spherical mucous cell envelope in *C. abbreviatum* implies an increase of its particle volume with a factor of 20 to 100.

Concentrated (by sedimentation) culture suspensions of *S. chaetoceras* and *C. abbreviatum* occurring in the exponential growth phase were added to filtered lake water to a final concentration of ca. 1000 cells ml<sup>-1</sup> (checked by coulter counter), corresponding with a carbon content of ca. 1 μg C ml<sup>-1</sup> which is amply above the incipient limiting level as mentioned for the related species *Daphnia longispina* (Lampert, 1987). Next to the suspensions of complete desmid cells a variant was prepared in which *C. abbreviatum* cells were trimmed of their mucous envelope. The extracellular envelope, with a thickness of 12–18 μm, can be completely removed by centrifugation and successive mild sonification of the pellet.

Adult *Daphnia* individuals (size range 1.4–1.8 mm), starved for a period of 12 h, were transferred to 250 ml beakers. Each beaker contained 200 ml of one of the above-mentioned desmid suspensions and ten *Daphnia* individuals. Grazing (at room temperature in subdued daylight) was allowed for a period of 1 h, during which the beaker was periodically stirred to prevent algal sedimentation. After that, *Daphnia* individuals were anaesthetised by adding carbonated mineral water and microscopically examined for their gut content. In each set-up (differentiated to the three desmid suspension variants) thirty *Daphnia* individuals were examined. The conducted experiment was done in October 1993 and repeated a month later.

## Results

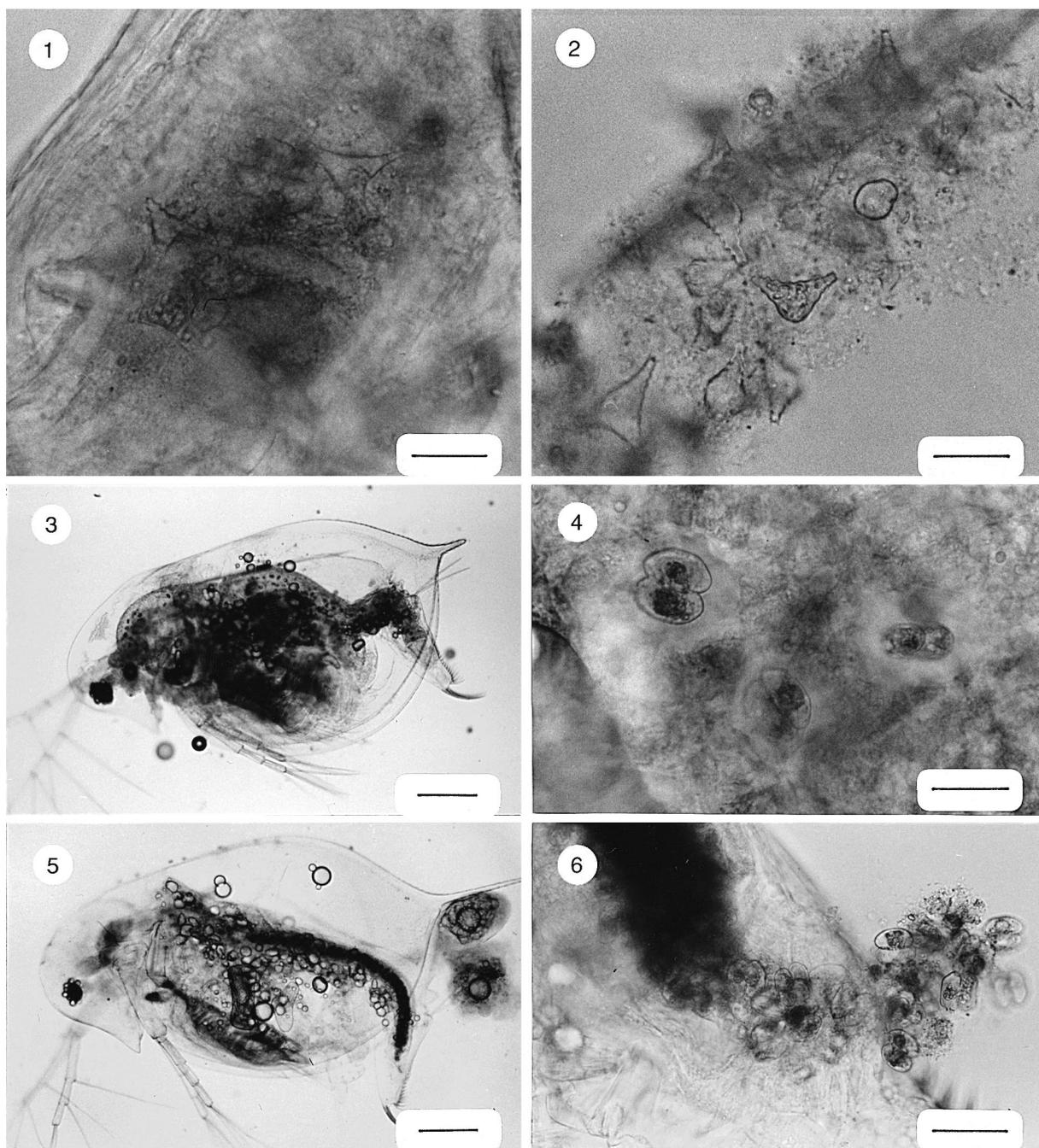
Both in the October and the November experiment all of the *Daphnia* individuals fed *Staurastrum chaetoceras* appeared to have their gut filled up with numerous empty semicells. Only incidentally a few intact *Staurastrum* cells were encountered in the beginning of the intestinal tract. Empty semicells were closely packed and mixed up with discoloured cell contents in such a way that counting was impossible (Figures 1 and 2). The number of digested cells per *Daphnia* was estimated to be around 300.

In distinct contrast to that, in suspension of *Cosmarium abbreviatum* (untreated cells), no remnants of digested cells could be detected. Intact cells of *Cosmarium* (with green chloroplast and enveloped by a mucilage layer), on the contrary, were present in the *Daphnia* guts, passing the anal opening apparently undamaged (Figures 3 and 4). The number of *Cosmarium* cells counted per *Daphnia* gut ranged from 4 to 38 (mean = 16, SD = 9, n = 60).

When decapsulated *Cosmarium* cells were offered as a food source, the numbers of recognisable cells in the intestinal tract were much higher. Actually, in many cases the gut was completely stuffed with a compact mass of cells (Figure 5). A rough calculation, generally by extrapolation, resulted in a mean cell number per *Daphnia* gut of 186 (SD = 67, n = 60). Remarkably enough, although a protective extracellular mucilaginous envelope was wanting, when leaving the anus most of the cells (ca. 60%) still had their chloroplasts and were thus not mechanically damaged to any extent (Figure 6).

## Discussion

The observed high degree of ingestibility of *Staurastrum chaetoceras* by adult *Daphnia galeata/hyalina* is in agreement with that found by Infante (1973) for *Staurastrum spec.* as food for *Daphnia pulex* and *Daphnia longispina*. Judging from a micrograph provided (Infante, l.c., Figure 23) the unspecified *Staurastrum* concerns *S. pingue*, a species whose morphology and dimensions are comparable with those of *S. chaetoceras* (Coesel & Wardenaar, 1990, Figure 1). Infante (l.c.) noticed that *Staurastrum* was assimilated more easily than other algal species with cellulose walls, like *Scenedesmus*, because its cells, passing the gut, readily break at the narrow junction of the two semicells and free their content. Indeed, also in



Figures 1–6. (1) Part of the gut of a *Daphnia galeata/hyalina* individual fed with *Staurastrum chaetoceras*, containing disconnected, empty semicells. Scale bar = 25 $\mu$ m. (2) Faeces of a *Daphnia galeata/hyalina* individual fed with *Staurastrum chaetoceras*, showing empty semicells. Scale bar = 25 $\mu$ m. (3) A *Daphnia galeata/hyalina* individual fed with *Cosmarium abbreviatum* having in its gut a relatively low number of scattered *Cosmarium* cells. Scale bar = 200 $\mu$ m. (4) Detail of the gut of a *Daphnia galeata/hyalina* individual fed with *Cosmarium abbreviatum*. Note the mucilaginous layer enveloping each individual algal cell. Scale bar = 25 $\mu$ m. (5) A *Daphnia galeata/hyalina* individual fed with decapsulated cells of *Cosmarium abbreviatum*, having in its gut a dense mass of closely packed *Cosmarium* cells. Scale bar = 200 $\mu$ m. (6) Faeces of a *Daphnia galeata/hyalina* individual fed with decapsulated cells of *Cosmarium abbreviatum*. Note that the majority of the algal cells are still unbroken. Scale bar = 50 $\mu$ m.

our experiment almost all *Staurastrum* cells ingested appeared to be broken at their isthmus. What does matter is algal cell size in relation to *Daphnia* body size. Infante (l.c.) found *Daphnia pulex* to incorporate ten times more of *Staurastrum pingue* than the somewhat smaller-sized *Daphnia longispina* (1.5–1.7 versus 1.9–2.1 mm). Obviously, in our experiment, *Staurastrum chaetoceras* cells, including processes that measured roughly  $30 \times 30 \mu\text{m}$ , were within the algal size range readily ingestible by *Daphnia galeata/hyalina* (a 'species' closely related to *Daphnia longispina*). However, *Staurastrum pingue*, slightly larger-sized than *Staurastrum chaetoceras* may cause some ingestion problems to the smaller daphnids and this is, of course, even more true for still larger planktic desmid species, *Staurastrum planctonicum*. Accordingly, clones of last-mentioned species with an average particle volume of  $40\,000 \mu\text{m}^3$  proved to be poorly ingestible even by the relatively large-sized *Daphnia pulex* (Geller, 1975; Lampert, 1975).

In view of this critical particle size, the low ingestibility of *Cosmarium abbreviatum* var. *planctonicum* found by us for *Daphnia galeata/hyalina* is not surprising. Though proper cell volume of this taxon is comparable to that of *Staurastrum chaetoceras* and its cell diameter is even smaller, the presence of an extensive extracellular mucous envelope, increasing the particle volume to (far) over  $100\,000 \mu\text{m}^3$ , hampers ingestibility by *Daphnia* considerably. This is demonstrated by the much higher cell numbers ingested when mucous envelopes were detached and removed beforehand. However, in contrast to *Staurastrum chaetoceras*, most of the ingested, decapsulated cells of *Cosmarium abbreviatum* remained intact during their passage through the intestinal tract. Most probably this has to do with the compact, rounded cell shape of *Cosmarium*. *Staurastrum chaetoceras* is characterised by semicells, which are mutually largely separated by a wide gap (sinus) and whose angles are extended into long, hollow processes. This makes the cells extremely vulnerable to breakage when closely packed in a peristaltically pulsing *Daphnia* gut. As only a few intact *Staurastrum* cells were encountered in the beginning of the intestinal tract it is even likely that most of the cells were already cracked by movements of the mandibles. Large-sized, capsulated phytoplankton species benefit from conditions of high grazing pressure, particularly if grazers are predominated by large zooplankters, such as daphnids. Not only that the algal cells in question are hardly ingested, but they take advantage of enhanced nutrient recycling rates, caused by grazing of small

phytoplankters (Porter, 1976; Bergquist & Carpenter, 1986).

Given the experimental data, small-sized desmid species may constitute a suitable food source for zooplankton. Moreover, desmids probably may be considered high-quality food. Infante (1973) found in large grazers (*Daphnia pulex*, *Eudiaptomus gracilis*, *Sida crystallina*) a higher carbon assimilation rate when fed with *Staurastrum* than when fed with *Asterionella formosa*, *Nitzschia actinastrioides*, *Cryptomonas ovata* or *Scenedesmus acuminatus*. As to the ecological relevance of this finding, however, it has to be recalled that planktic desmids only rarely occur in high cell densities. This is particularly true of species characteristic of oligotrophic lakes in temperate and cold climatic regions. Of more significance are the (relatively few) desmid species present in eutrophic lakes. They may occur in considerable cell numbers and occasionally even cause blooms (Reynolds & Butterwick, 1979; Sommer, 1981; Bailey-Watts, 1987; Takamura et al., 1988). Moreover, extracellular mucous cell envelopes, which drastically increase particle size and consequently significantly reduce the ingestibility by zooplankters, are unknown of desmid species characteristic of eutrophic waters (Coesel, 1994). Reinertsen et al. (1990) found that, in a Norwegian eutrophic lake, *Anabaena flos-aquae* and *Staurastrum luetkemuelleri* (the latter is related, if not identical with *Staurastrum pingue*) accounted for more than 95% of the total algal biomass in summer. They also signalled a sharp decline in algal biomass as a result of increased grazing pressure by daphnids after total elimination of the fish population. The clone of *Staurastrum pingue* demonstrated by Infante (1973) to be one of the best algal food sources for daphnids originated from the German lake Titisee. It was found in a high percentage in the guts of zooplankton (*Daphnia longispina*, *Bosmina longirostris*, *Holopedium gibberum*, *Polyphemus pediculus* and *Cyclops vicinus*), collected from Titisee (Infante l.c.). Nevertheless, it seems that high abundances of planktic desmids in cold and temperate climatic regions occur only incidentally. There are indications that this is different from the situation in (sub)tropical parts of the world. Desmids are more widely distributed in tropical than in temperate regions (Coesel, 1996) and although quantitative data of tropical freshwater plankton assemblies are relatively scarce, quite a lot of them show a predominance of desmids (e.g., Braun, 1952; Hegewald et al., 1976; Biswas, 1984; Khan & Ejike, 1984; Biswas, 1992; Anton, 1994). Most of the references in question concern oligotrophic soft water

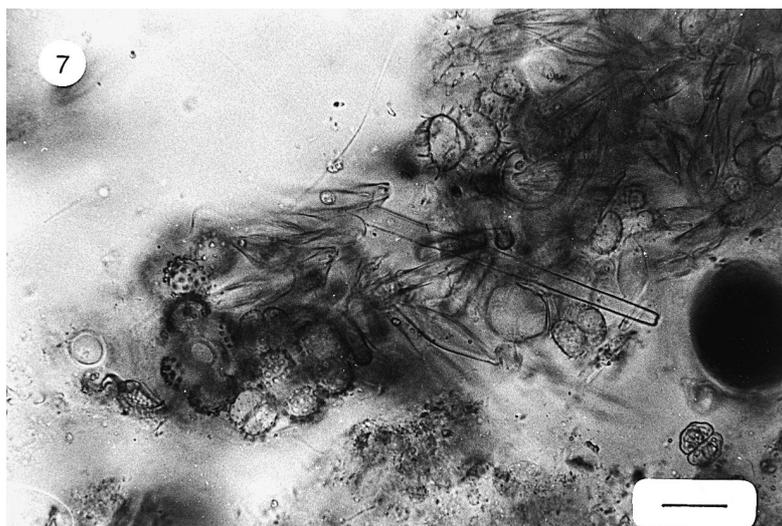


Figure 7. Faecal pellet of an unknown consumer largely consisting of empty desmid cells (originating from a shallow, oligotrophic pool in French Guiana). Scale bar = 25  $\mu\text{m}$ .

systems, well-known for their richness in large-sized desmid species which, as we have shown, are unattractive to zooplankters. However, it is noted that in tropical waters both zooplankton individuals and population size are small and many fish are herbivorous (Fernando, 1994). Consequently, it is hypothesized that in tropical, oligotrophic waters planktic desmid species may be an important food source for herbivorous fish. Olurin and Awolesi (1991) found that the fish species *Tilapia mariae* and *Chromidotilapia guntheri*, in a Nigerian stream, fed mainly on phytoplankton largely consisting of the desmid genera *Closterium* and *Cosmarium*.

Most likely, however, it is in the benthic compartment of oligotrophic systems that desmids play their most important role as a link in food chains. Cells of most desmid species are so big that they cannot circulate in a stagnant water column for a prolonged period. They are encountered at the bottom of shallow water bodies or in the periphyton of submerged plants (Brook, 1981). I observed that the substrate of shallow fen and bog hollows to be frequently covered by a green film, mainly consisting of desmid cells. Unfortunately, those habitats are not as easy to sample in a quantitative way as a relatively homogeneous column of open water. The few quantitative studies on non-planktic microalgal assemblies involving desmids are those by Woelkerling (1976) and Gough and Woelkerling (1976). With respect to oligotrophic soft waters, they assessed desmid cells to account for up to 30%

of the algal periphyton population (mean 11%). It has to be noted that these figures are based on cell numbers, not on biovolumes. In view of the overall remarkably large cell size of benthic desmid species the proportional share in biomass is supposed to be higher. When desmid cells constitute a substantial, if not predominant proportion of the benthic algal population in stagnant, oligotrophic waters, they presumably act as an important food source for various macrofauna elements. Although studies in this field are lacking circumstantial indirect evidence exists. In Canter-Lund and Lund (1995, Figure 538) part of an oligochaete gut is shown, which contains a fair number of clearly recognisable, large desmid cells (genera *Closterium* and *Euastrum*). As for chironomid larvae, Botts and Cowell (1992) and Botts (1993) found a marked feeding selectivity for the desmid species *Cosmarium impressulum* as opposed to various species of diatoms and other green algae. Gupta et al. (1994) reported desmids to belong to the dominant food material for mayfly nymphs in an Indian lake. Also my own observations have shown faecal pellets largely consisting of empty desmid cells (Figure 7). So it would not be surprising if benthic desmids turned out to be one of the major food sources for macro-invertebrates in the euphotic zone of lentic, oligotrophic water bodies.

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## References

- Anton A (1994) Long-term phytoplankton changes in a tropical reservoir. *Mitt int Verein Limnol* 24: 243–249
- Bailey-Watts AE (1987) Coldingham Loch, S.E. Scotland (UK): II. Phytoplankton succession and ecology in the year prior to mixer installation. *Freshwater Biol* 17: 419–428
- Bergquist AM and Carpenter SR (1986) Limnetic herbivory: effects on phytoplankton populations and primary production. *Ecology* 67: 1351–1360
- Biswas S (1984) Phytoplankton of Opi Lake, Anambra State, Nigeria. *Verh int Verein Limnol* 22: 1180–1184
- Biswas S (1992) Phytoplankton periodicity in Ogelube Lake, Anambra State, Nigeria during 1979–1980. *Hydrobiologia* 246: 169–172
- Botts PS (1993) The impact of small chironomid grazers on epiphytic algal abundance and dispersion. *Freshwater Biol* 30: 25–33
- Botts PS and Cowell BC (1992) Feeding electivity of two epiphytic chironomids in a subtropical lake. *Oecologia (Heidelb.)* 89: 331–337
- Braun R (1952) Limnologische Untersuchungen an einigen Seen im Amazonasgebiet. *Schweiz Z Hydrol* 14: 1–128
- Brook AJ (1981) The biology of desmids. Blackwell Scientific Publications, Oxford
- Canter-Lund H and Lund JWG (1995) Freshwater algae: their microscopic world explored. Biopress Ltd, Bristol
- Coesel PFM (1994) On the ecological significance of a cellular mucilaginous envelope in planktic desmids. *Algol Stud* 73: 65–74
- Coesel PFM (1996) Biogeography of desmids. *Hydrobiologia* 336: 41–53
- Coesel PFM and Wardenaar K (1990) Growth responses of planktonic desmid species in a temperature-light gradient. *Freshwater Biol* 23: 551–560
- Coesel PFM and Wardenaar K (1994) Light-limited growth and photosynthesis characteristics of two planktonic desmid species. *Freshwater Biol* 31: 221–226
- Fernando CH (1994) Zooplankton, fish and fisheries in tropical freshwaters. *Hydrobiologia* 272: 105–123
- Geller W (1975) Die Nahrungsaufnahme von *Daphnia pulex* in Abhängigkeit von der Futterkonzentration, der Temperatur, der Körpergröße und dem Hungerzustand der Tiere. *Arch Hydrobiol Suppl* 48: 47–107
- Gough B and Woelkerling WJ (1976) Wisconsin desmids. II. Aufwuchs and plankton communities of selected soft water lakes, hard water lakes and calcareous spring ponds. *Hydrobiologia* 49: 3–25
- Gupta A, Gupta S and Michael RG (1994) Seasonal abundance and diet of *Cloeon* sp. (Ephemeroptera: Baetidae) in a northeast Indian lake. *Arch Hydrobiol* 130: 349–357
- Hegewald EA, Aldave A and Hakuli T (1976) Investigations on the lakes of Peru and their phytoplankton. 1. Review of literature, description of the investigated waters and chemical data. *Arch Hydrobiol* 78: 494–506
- Hutchinson GE (1967) A treatise on limnology. Vol. 2, 1115 pp. Wiley, New York
- Infante A (1973) Untersuchungen über die Ausnutzbarkeit verschiedener Algen durch das Zooplankton. *Arch Hydrobiol Suppl* 42: 340–405
- Järnefelt H (1952) Plankton als indicator der Trophiegruppen der Seen. *Ann Acad Sci Fenn, Ser A, IV, Biol* 18: 1–29
- Khan MA and Ejike C (1984) Limnological aspects of plankton variation and water characteristics of a tropical West African reservoir. *Verh Intern Verein Limnol* 22: 1584–1589
- Lampert W (1975) Studies on the carbon balance of *Daphnia pulex* as related to environmental conditions. II. The dependence of carbon assimilation on animal size, temperature food concentration and diet species. *Arch Hydrobiol Suppl* 48: 310–335
- Lampert W (1987) Feeding and nutrition in *Daphnia*. *Mem Ist Ital Idrobiol* 45: 143–192
- Nichols HW (1973) Growth media: freshwater. In: Stein JR (ed.) *Handbook of Phycological Methods: Culture Methods and Growth Measurements* (pp. 7–24). Cambridge University Press, Cambridge
- Olurin KB and Awolosi OO (1991) Food of some fishes of Owa Stream, south-western Nigeria. *Arch Hydrobiol* 122: 95–104
- Porter KG (1973) Selective grazing and differential digestion of algae by zooplankton. *Nature* 244: 179–180
- Porter KG (1976) Enhancement of algal growth and productivity by grazing zooplankton. *Science* 192: 1332–1333
- Rawson DS (1956) Algal indicators of trophic lake types. *Limnol Oceanogr* 1: 18–25
- Reinertsen H, Jensen A, Koksvik JI, Langeland A and Olsen Y (1990) Effects of fish removal on the limnetic ecosystem of a eutrophic lake. *Can J Fish aquat Sci* 47: 166–173
- Reynolds CS (1984) The ecology of freshwater phytoplankton. Cambridge University Press, Cambridge
- Reynolds CS and Butterwick C (1979) Algal bioassay of unfertilized and artificially fertilized lake water, maintained in Lund Tubes. *Arch Hydrobiol Suppl* 56: 166–183
- Rosén G (1981) Phytoplankton indicators and their relations to certain chemical and physical factors. *Limnologica* 13: 263–290
- Sommer U (1981) The role of r- and K-selection in the succession of phytoplankton in Lake Constance. *Acta Oecol/Oecol Gen* 2: 327–342
- Spaak P and Hoekstra JR (1993) Clonal structure of the *Daphnia* population in Lake Maarssen: its implications for diel vertical migration. *Arch Hydrobiol Beih* 39: 157–165
- Takamura N, Iwakuma T and Yasuno M (1988) Primary production in Lake Kasumigaura (Japan), 1981–1985. *Jap J Limnol* 48: S13–S38
- Thunmark S (1945) Zur Soziologie des Süßwasserplanktons. Eine methodologisch-ökologische Studie. *Folia Limnol Scand* 3: 1–66
- Woelkerling WJ (1976) Wisconsin desmids. I. Aufwuchs and plankton communities of selected acid bogs, alkaline bogs, and closed bogs. *Hydrobiologia* 48: 209–232