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SYNERGISTIC EFFECTS OF FOOD CHAIN DYNAMICS AND INDUCED BEHAVIORAL RESPONSES IN AQUATIC ECOSYSTEMS

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Abstract. The aim of the present study was to test the hypothesis that temporal differences in food chain composition affect lower trophic levels not only directly, by predation and grazing, but also indirectly, by inducing avoidance behavior. In a field study, the recruitment rate from the sediments to water of two algal species (*Gonyostomum semen* and *Peridinium* sp.) was higher at low than at high biomass of herbivorous zooplankton. In complementary laboratory experiments, where abiotic conditions were standardized, the presence of live, as well as dead, herbivores reduced the recruitment rate of both *Gonyostomum semen* and *Peridinium* sp. These results suggest that some algal species are able to adjust their recruitment behavior in response to the likely risk of being grazed. Together with morphological adaptations (e.g., spines and large size) common among many algal species, such an induced behavioral response is an important adaptation to reduce cell mortality. As shown in this study, this behavioral response may have a profound impact on dominance and succession patterns in algal communities. The high zooplankton biomass observed during the first year of the field study was caused by failed reproduction of the dominant fish species in the lake (roach, *Rutilus rutilus*). Hence, food chain interactions (low predation on zooplankton, leading to high biomass of herbivorous zooplankton) may act in concert with more indirect, predator-avoidance behavior in structuring the phytoplankton community.

Key words: algae; aquatic ecosystems; food chain; food web; Gonyostomum semen; *grazing; herbivory; induced behavior;* Peridinium *sp.; phytoplankton; predation; Sweden; zooplankton.*

INTRODUCTION

In combination with abiotic features of an ecosystem, direct interactions such as predation, grazing, and competition explain a major part of the variation in abundance, biomass, and succession of organisms. Accordingly, these processes have long been the focus of ecological research, including competition, food web, and optimal foraging theories, as well as succession models such as the PEG model for aquatic ecosystems (Sommer et al. 1986). However, during recent years several studies performed in terrestrial as well as in aquatic systems have shown that many organisms gather information from their environment by being receptive to chemical signals exuded not only by conspecifics, but also by potential predators and grazers. Waterborne chemicals are known to elicit morphological adjustments in prey organisms that reduce their predation rates. Examples are higher body shape in crucian carp (*Carassius carassius*; Brönmark and Miner [1992]), spine formation in rotifers (Stemberger and Gilbert 1987), helmet and neck teeth formation in many cladoceran zooplankton species (Tollrian 1995), and colony formation in the green alga *Scenedesmus* (van Donk and Hessen 1993, Lampert et al. 1994, Lürling and van Donk 1997). Furthermore, behavioral responses have been demonstrated in flagellated algae, which

avoid entering the water column when grazing zooplankton are abundant (Hansson 1996*a, b,* Rengefors et al. 1998). Unfortunately, our knowledge of the "chemical network" that transfers information from predators to their prey is still negligible. However, such signals are likely to affect the outcome of predator–prey interactions, as well as successional patterns in aquatic ecosystems.

If the use of a "chemical network," invisible to the human eye and to traditional sampling devices, is widespread among organisms, knowledge of this system may be of crucial importance for our understanding of natural ecosystems. When quantifying abiotic effects and direct interactions among organisms, we may have described only one dimension of the ecosystem, whereas another dimension of interactions—the chemical network—has been neglected. This may have serious consequences since chemically mediated behavioral adjustments are likely to affect the outcome of direct interactions: a prey that can detect a predator before they meet will most probably avoid the predators presence. In such a situation, simple predator–prey theory will have reduced explanatory power. Moreover, food web analyses, such as assessments of interaction strength among organisms at different trophic levels, potentially will lead to spurious conclusions if certain actors use chemical information to adjust their own behavior. It may then be of crucial importance to combine direct food chain links with induced behavioral

responses in order to properly understand the functioning of natural ecosystems.

Many algal species spend part of their life cycle at the sediment surface, either as vegetative cells or in resting stages. Individuals are then recruited to the pelagic (open water) part of the population. Our knowledge of which factors that trigger these recruitments is negligible, although several physical factors such as light and temperature (Trimbee and Harris 1984, Hansson 1993) and chemical factors (oxygen; Trimbee and Prepas [1988], Hansson et al. [1994]) have been suggested to be important. Recently, biological factors, such as the presence of large herbivores, have also been proposed to affect the recruitment of certain algal species (Hansson 1996, Rengefors et al. 1998), indicating that succession patterns in the phytoplankton assemblage may be affected by chemical signals derived from herbivores.

The aim of the present study was to test the hypothesis that temporal differences in food chain composition affect lower trophic levels not only directly via predation, grazing, and competition, but also indirectly by inducing behavioral adjustments among algae. Consequently, my study aims at combining traditional food chain components with the dimension of induced avoidance behavior. The study was performed as a field study where algal recruitment from sediment to water was quantified simultaneously with measurements of physical and chemical variables as well as the biomass of herbivores. In a series of complementary laboratory experiments, where physical and chemical variables were held constant, I tested the effects of herbivores on recruitment of algae from the sediment.

MATERIAL AND METHODS

Field study

This study was performed in a south Swedish lake, Dagstorpssjön (55°52′ N, 13°32′ E), a mesotrophic, slightly humic lake in which flagellated algae often dominate (usually *Peridinium* sp. or *Gonyostomum semen*). Water samples were taken eight times in 1996 (10 July to 16 October) and nine times in 1997 (4 July to 23 September), at 3.5 m depth. I took water from 0, 0.5, 1, 1.5, 2, 2.5, and 3 m depths with a Ruttner sampler (diameter 70 mm). These discrete samples were then pooled and mixed, and subsamples for analyses of nutrients (total phosphorus and total nitrogen), chlorophyll *a,* phytoplankton, and zooplankton were taken from the pooled sample. Total phosphorus and total nitrogen samples were frozen and later analyzed on a Technicon AutoAnalyzer II. Air temperature was automatically registered eight times per day during 1996 and 1997 at a nearby weather station (Hörby, ~15 km from the lake). Daily mean values for temperature were calculated and summarized as accumulated temperature from 1 January to 31 October each year.

Algal chlorophyll *a* was retrieved on a GF/C filter

and frozen within 2 h, to be later extracted with ethanol and measured spectrophotometrically according to Marker et al. (1980). Five liters of water were filtered through a 55-μm net and fixed with Lugols solution for quantification and determination of zooplankton. Phytoplankton samples were fixed with Lugols solution and later filtered through membrane filters (Millipore), mounted on glass slides with HPMA (2-hydroxypropyl methacrylate (Crumpton 1987), and counted at 200× magnification. Temperature (in degrees Celsius) was measured at the surface (0.1 m) and close to the bottom (3 m), and the Secchi depth was determined.

Traps to catch algae migrating between the sediment and the water were made from 120-mL glass jars each filled with GF/C (Whatman)-filtered lake water (i.e., no algae were present in the trap at the start), with a funnel mounted through the lid (funnel diameter 0.14 m). Traps were attached to a metal pyramid frame, which was carefully lowered to the sediment surface (Hansson et al. 1994). Three traps, attached to three different frames, were rigged 0.4 m above the sediment surface at 3-m depth for 48 h with the funnels facing down to collect algae recruited from the sediment (Hansson 1996*b*). The traps were set within 20 m from the sampling site of chemical and physical data. Funnel openings were covered with a 300-μm nylon net to reduce grazing on trapped algae. Algae caught in the traps were treated in the same way as phytoplankton samples.

The species composition and size distribution of fish in Dagstorpssjön was determined in September 1997, using three benthic gill nets consisting of eight segments 7 m long and 1.5 m high with different mesh sizes. Mesh sizes were: 9.5, 14.5, 18.0, 24.0, 29.5, 33.0, 38.0, and 46.0 mm. The nets were set for 24 h. Scales along the lateral line of fish were chosen, and year-rings on the scales were analyzed to assess age distribution of the fish. The fishing in 1997 was compared to data collected during 1980, when the procedure was the same except that only two nets were used (Gelin et al. 1983). Morover, in order to assess if the fish size distribution and, especially, the young-of-the-year recruitment in Dagstorpssjön was similar to that in other lakes, fish data from three further lakes similar to Dagstorpssjön were analyzed (Lessmark 1983). These reference lakes were Lake Kalvsjön, Lake Fegen, and Lake Flaten, in southern Sweden (Lessmark 1983)

Laboratory experiment

Simultaneously with the water sampling, twelve sediment cores (inner diameter 68 mm, length 300 mm) were taken at 3-m depth within the same area as the other samples. To reduce exposure to light during transport to the laboratory, the cores were covered with black plastic. Within 2 h, cores were put into a growth cabinet at temperatures corresponding to that of the lake and with a 14:10 light:dark cycle at a light intensity (photosynthetic photon flux density) of 1.1
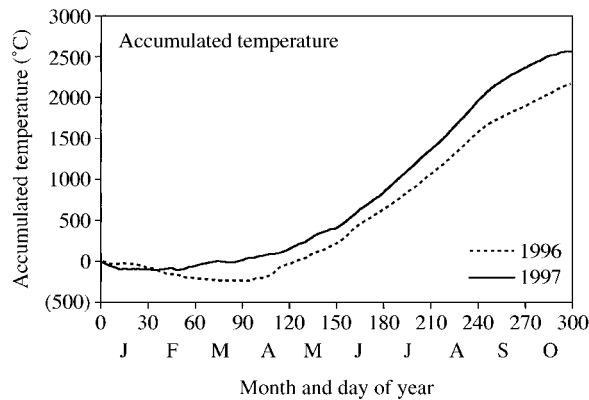
Fig. 1. Accumulated air temperature from January to October 1996 and 1997 near Dagstorpssjön in Sweden. The figure shows that the increase in temperature was faster in the spring of 1997 than in 1996.

$\mu mol \cdot m^{-2} \cdot s^{-1}$ at the sediment surface. Cores were lightly and evenly aerated by letting air pass through an expansion bottle before being distributed through cannulas to the cores. Aeration kept the oxygen concentration >19 mg/L in all cores. In each core, I placed miniature recruitment traps (diameter 55 mm), similar to the ones used in the lakes, ~15 mm above the sediment surface. Four of the cores were used as grazer-free controls. Another four cores each contained 20 living *Daphnia magna* enclosed in a 100-μm mesh cage (Z treatment). The *Daphnia* were caged to exclude them from the sediment surface and the recruitment traps. Prior to the experiment, the *Daphnia* were kept for 1 h in filtered lake water to empty their guts, thereby reducing the input of algae and nutrients to the experiment. In each of the last four cores, between 25 and 40 (corresponding to a fresh mass of between 0.1 and 0.2 g) heat-killed (4 h at 60°C) *D. magna* were put in

cages with 100-μm mesh size (ZD treatment). In order to eliminate the possibility that the material used as cages for zooplankters in treatments Z and ZD affected the algae, or that the cages reduced light penetration to the sediment surface, pieces of net were also hung in the C treatment. The experiment lasted for 5 d. At the end of the experiment, the water in the traps was fixed with Lugols solution and treated in the same way as algal samples from the field study.

Data analysis

Between-year differences in the descriptive lake data on chemical, physical, and biological variables were analyzed with Wilcoxons signed-ranks test. This non-parametric test was used since the lake data, by definition, lack replication (and therefore measureable variance). Samplings were performed on about the same day of the year during both years and no sampling differed by >9 d between the years. Repeated-measures ANOVA was used to test for differences between years with respect to algal recruitment from sediment to water in the field study, as well as in the laboratory study. In the laboratory study, a Kruskal-Wallis one-way ANOVA was also used to test differences in pH and phosphorus among treatments.

RESULTS

Field study

The accumulated air temperature curves illustrate that the spring period (February to April) was cooler in 1996 than in 1997 (Fig. 1). This difference was reflected in a lower seasonal mean temperature in the lake water in 1996 than in 1997 (Table 1). Both total phosphorus and total nitrogen also showed a tendency towards lower seasonal mean values in 1996 compared to 1997, although these differences were not statisti-

TABLE 1. Seasonal mean values for abiotic variables, phytoplankton, and zooplankton in Dagstorpssjön during the summers of 1996 and 1997.

Variable	Mean, 1996	Mean, 1997	Z	P
Abiotic variables				
Temperature (°C)	16.5	19.1	−2.366	0.018
Total phosphorus (μg/L)	33	38	−1.120	NS
Total nitrogen (μg/L)	916	1 035	−1.820	NS
Secchi depth (m)	2.1	1.7	−1.400	NS
Phytoplankton				
Chlorophyll *a* (μg/L)	10	39	−2.521	0.012
Gonyostomum (no./L)	4 350	52 370	−2.521	0.012
Peridinium (no./L)	801	1 545	−0.734	NS
Anabaena (no./L)	114	79 499	−2.521	0.012
Zooplankton				
Daphnia (μg/L)	44	4	−2.521	0.012
Copepods (μg/L)	274	94	−2.521	0.012
Total macrozooplankton (μg/L)	348	148	−2.521	0.012

Notes: Differences between years were tested with Wilcoxon's signed-ranks test on paired observations ($n = 8$ pairs of sampling dates). NS indicates that differences were not significant at the 5% level.
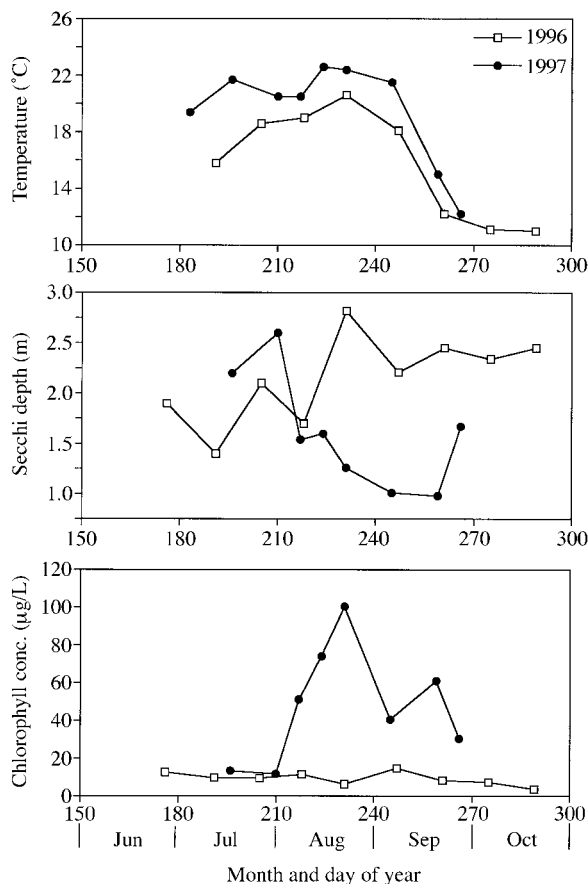
FIG. 2. Temperature, Secchi depth, and the concentration of chlorophyll *a* in Dagstorpssjön lake during 1996 and 1997.

cally significant (Table 1). Mean Secchi depths tended to be higher in 1996 than in 1997 (Fig. 2), but these differences also were not statistically significant (Table 1).

Chlorophyll *a* values differed considerably between years, with almost ten times higher maxima in 1997 than in 1996 (Fig. 2, Table 1). *Gonyostomum* sp. and *Anabaena* sp. both occurred at lower abundances in 1996 than in 1997, whereas the abundances of *Peridinium* sp. were similar between years (Table 1). Recruitment rates from the sediment to the water of *Gonyostomum, Peridinium,* and *Anabaena* were significantly lower in 1996 than in 1997 (Fig. 3; $F_{1,7}$ = 3.47, 19.70, and 358.5, respectively; P < 0.008, repeated-measures ANOVA).

Biomasses of *Daphnia* sp. and copepods were higher in 1996 than in 1997 (Table 1, Fig. 4), which was also generally the case with *Bosmina* sp. and rotifers. However, while *Diaphanosoma* sp. occurred in biomasses of up to 67 μg/L in 1997, it was not present in the lake at all in 1996. The mean total biomass of macrozooplankton was more than twice as high in 1996 as it was in 1997 (Table 1, Fig. 4).

The dominant planktivorous fish in Dagstorpssjön is

roach (*Rutilus rutilus*) and fish population analyses were therefore focused on this species. The size [presumably age] distribution of roach was similar in the reference lakes and in Dagstorpssjön in 1980 (the only available data on fish in the lake), suggesting that such a pattern may be viewed as "normal" in lakes of this type (Lessmark 1983, Fig. 5). However, the size distribution of roach in 1997 differed considerably from this "normal" pattern. The maximum frequency in 1980, as well as in the reference lakes, was at 90 mm, a size class that occurred only in low abundances in Dagstorpssjön 1997. Scale analyses showed that the maximum size for the 1+ age class in 1997 (fish born in 1996) was 98 mm. Hence, the border between 1+ and 2+ roach is between 90 and 100 mm in this lake. The 1+ size class occurred in very low abundances in 1997 compared to in 1980 and in the reference lakes (Fig. 5). Actually, 1+ constituted only 3% of the total catch of roach in 1997, compared to 22% in 1980, suggesting that the roach reproduction failed in 1996.

Laboratory experiment

In the laboratory experiment, light was held constant at 1.1 μmol·m^{-2}·s^{-1} in all treatments throughout the
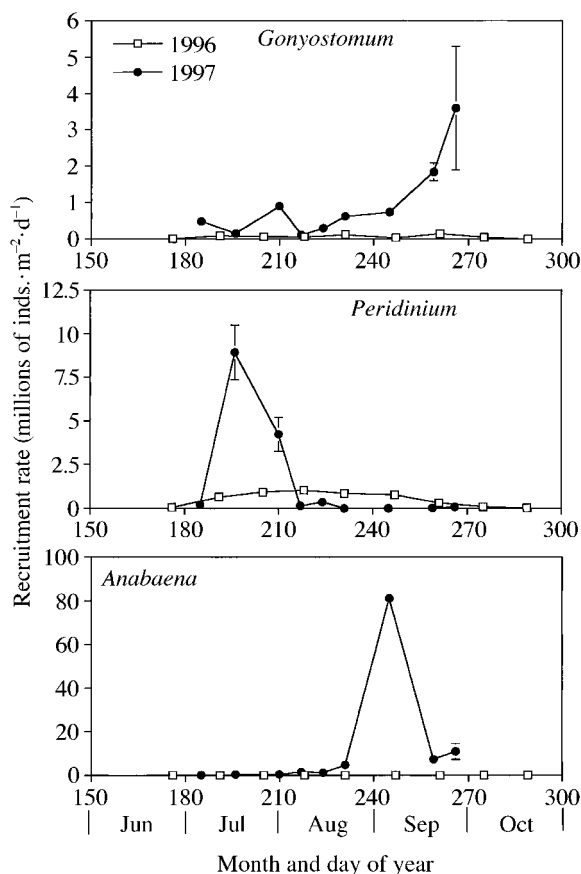

FIG. 3. Recruitment rate of *Gonyostomum semen, Peridinium* sp., and *Anabaena* sp. in Dagstorpssjön in 1996 and 1997. Data are presented as mean values ± 1 SE (*n* = 3 traps).
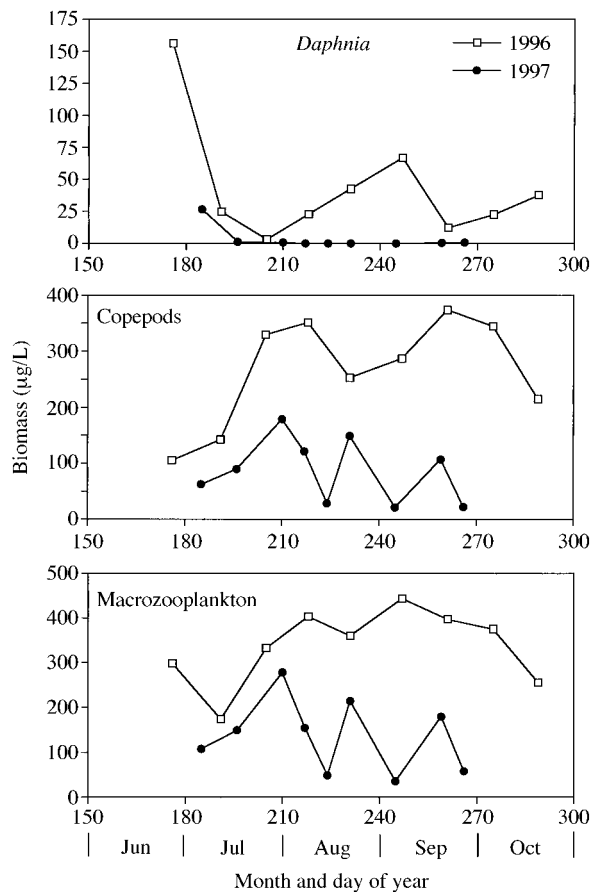
Fig. 4. Biomass of *Daphnia,* copepods, and total macrozooplankton in Dagstorpssjön in 1996 and 1997.

higher in 1997 than in 1996 (Figs. 6 and 7). With only two exceptions (24 July 1996 and 29 July 1997), mean recruitment was highest in the controls and lowest in the treatment with caged, but live *Daphnia* (Fig. 7). Differences among treatments were only significant in 1997 ($F_{2,16} = 2.789$, $P < 0.002$, repeated-measures ANOVA). *Peridinium* sp. never occurred in the laboratory experiment in 1996. In 1997, *Peridinium* was never detected in treatments with live *Daphnia,* but it was recruited in controls (C) and in the treatment with dead zooplankton (ZD; Fig. 7). There was no difference in recruitment between C and ZD treatments (repeated-measures ANOVA, $P > 0.36$). The recruitment of *Anabaena* differed considerably among treatments in the laboratory experiment (Fig. 7; repeated-measures ANOVA, $F_{2,16} = 17.240$, $P < 0.001$). However, in contrast to *Gonyostomum, Anabaena* generally showed highest abundance in the Z-treatment traps.

In the laboratory experiment, recruitment of *Gonyostomum* in the treatment with live zooplankton (Z) was generally <20% of the recruitment in the control (C) and only at one occasion >50% of that in the control (Fig. 8). Actually, in 1997 recruitment in Z was never >10% of that in the controls. The recruitment in ZD was generally somewhat higher and was >50% of that in C at four occasions (Fig. 8). During three of these, recruitment was similar to or higher than that in the controls. On all occasions when recruitment in Z or ZD was >50% of that in the controls, the temperature was between 18 and 23°C (Fig. 8). At temperatures below 18°C, recruitment in Z or ZD was never >40% of that in the controls.

DISCUSSION

Among animals, predator-avoidance behavior is an obvious adaptation to reduce the risk of being eaten. Although terrestrial as well as aquatic primary producers are known to exhibit many sophisticated morphological adaptations to reduce grazing pressure, including poisons, spines, and thorns, they are generally viewed as being unable either to detect or to respond behaviorally to the presence of grazers. Here I have shown that some algal species avoided entering the

study. Moreover, oxygen saturation was always >100% due to continous aeration of the water and pH did not differ between treatments (Kruskal-Wallis $H = 0.477$, $P > 0.7$). At the end of the experiment the total phosphorus concentration was higher in the Z treatment (83.3 ± 12.9 μg/L) than in the C (39.5 ± 15.9 μg/L) and ZD treatments (53.5 ± 9.3 μg/L; $H = 7.883$, $P < 0.020$, Kruskal-Wallis test).

The recruitment of *Gonyostomum semen* was ~100×

Fig. 5. The proportion of different size classes of the dominant planktivorous fish (*Rutilus rutilus* [roach]) in Dagstorpssjön 1980 and 1997. For comparison, the mean size class distribution of roach is also given for three other south Swedish lakes similar to Dagstorpssjön ("reference lakes"). The dashed vertical line shows the boundary (based on scale analysis) between fish 1-yr-old or younger (≤1+) and fish 2-yr-old or older (≥2+). The figure illustrates that in 1997 the size (age) class 1+ (born in 1996), constituted a minor proportion of the roach population in comparison to 1980, as well as to the "reference lakes."

FIG. 6. Recruitment rate from sediment to water in 1996 of *Gonyostomum semen* in the control (C; white bars), the treatment with caged, live *Daphnia* (Z; black bars), and the treatment with dead *Daphnia* (ZD; grey bars). Bars show mean values ± 1 SE (*n* = 4 traps). Neither *Peridinium* sp. nor *Anabaena* sp. was recorded in the recruitment traps in 1996.
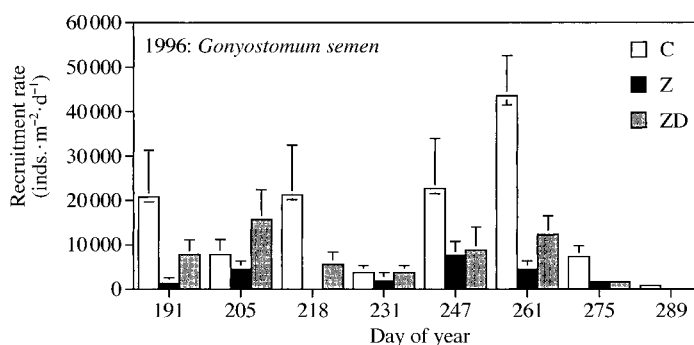
water column from their resting stage at the sediment surface when grazing zooplankton were present.

Many flagellated algae are known to undergo diel vertical migrations. This is the case with *Gonyostomum semen,* which has been shown to migrate upwards at dawn and downwards at dusk, both in laboratory experiments (Cowles and Brambel 1936, Eloranta and Räike 1995) and in natural systems (Cronberg et al. 1988, Pithart et al. 1997). However, the upward migration seems to stop at light intensities of ~80 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (LeCohu et al. 1989, Eloranta and Räike 1995), suggesting that light availability is an important factor in determining migratory patterns in *Gonyostomum.* In addition to diel vertical migration, many algal groups spend part of their life cycle at the sediment surface either as resting cysts, such as *Gonyostomum* and *Peridinium,* or as vegatative cells, such as the blue-green alga *Microcystis.* However, our knowledge of the ecological significance of such complex life cycles is negligible. We have, for example, poor understanding of the triggering factors for habitat shifts, and their importance for succession patterns in the phytoplankton community, although dormant life-cycle stages have been suggested to provide the key to understanding fluctuations in the abundance of planktonic species (Eppley 1986). A possible reason for such a complex life cycle is "risk spreading", i.e., always having part of the population resting in case of catastrophes, as has been suggested with respect to zooplankton "egg-banks" (Hairston et al. 1995, Lampert 1995). Moreover, resting stages also afford species a temporal refugium from adverse conditions (Marcus and Boero 1998).

In the field study in Dagstorpssjön, recruitment of both *Gonyostomum semen* and *Peridinium* sp. was lower when zooplankton biomass was high (1996) than when it was low (1997). In addition to zooplankton biomass, several other variables differed between years that potentially may have affected recruitment, including temperature and light conditions (expressed as chlorophyll *a* concentration; Table 1, Fig. 1). Although light conditions expressed as Secchi depth differed during the later part of the summer (Fig. 2), differences over the whole season were not significant (Table 1). The level of recruitment also differed between years

in the controlled laboratory experiment, where the recruitment of *Gonyostomum semen* in 1996 was <5% of that in 1997, and no *Peridinium* sp. was ever recorded in the recruitment traps in 1996. Since the light climate in the culture room was identical in the two years, light may not be the ultimate variable in determining the recruitment rates of *Gonyostomum semen* and *Peridinium* sp.

In contrast to light, temperature in the laboratory was adjusted to mimic that in the lake, which rules out excluding between-year differences in temperature as a factor behind the level of recruitment of *Gonyostomum semen* and *Peridinium* sp. However, since temperature was identical among treatments in the laboratory experiment, this variable cannot explain the lower recruitment of either *Gonyostomum semen* or *Peridinium* sp. in treatments having zooplankton than in those without zooplankton. Temperature appears to have only a minor impact on the recruitment rate of *Gonyostomum* in the control treatment, since recruitment was still high in September 1997 (day 261), when the temperature was only 12°C. However, recruitment rates observed in both the Z and the ZD treatments were always < 40% of that in the controls at temperatures < 18°C (Z/C and ZD/C < 0.40, Fig. 8). This stronger effect of zooplankton on recruitment rate at low than at high temperatures suggests that it may be worth the risk of leaving the sediment refuge when temperature is optimal for growth, but not at suboptimal temperatures when growth is slower (Rengefors et al. 1998).

It thus may be concluded that neither temperature nor light alone can explain differences in recruitment rates of algae in the laboratory experiments since both variables were held constant across each experimental treatment. The large differences in recruitment rates of both *Peridinium* sp. and *Gonyostomum semen* between controls (C) and treatments containing live zooplankton (Z) suggests instead that the presence of herbivores was the primary factor that depressed recruitment of these two algal species from the sediment into water. The recruitment traps were attached only ~15 mm above the sediment surface (that is, below the zooplankton cages) and covered 65% of the sediment surface (diameter 55 mm). In addition, zooplankters in the Z treatment were caged and therefore could not have
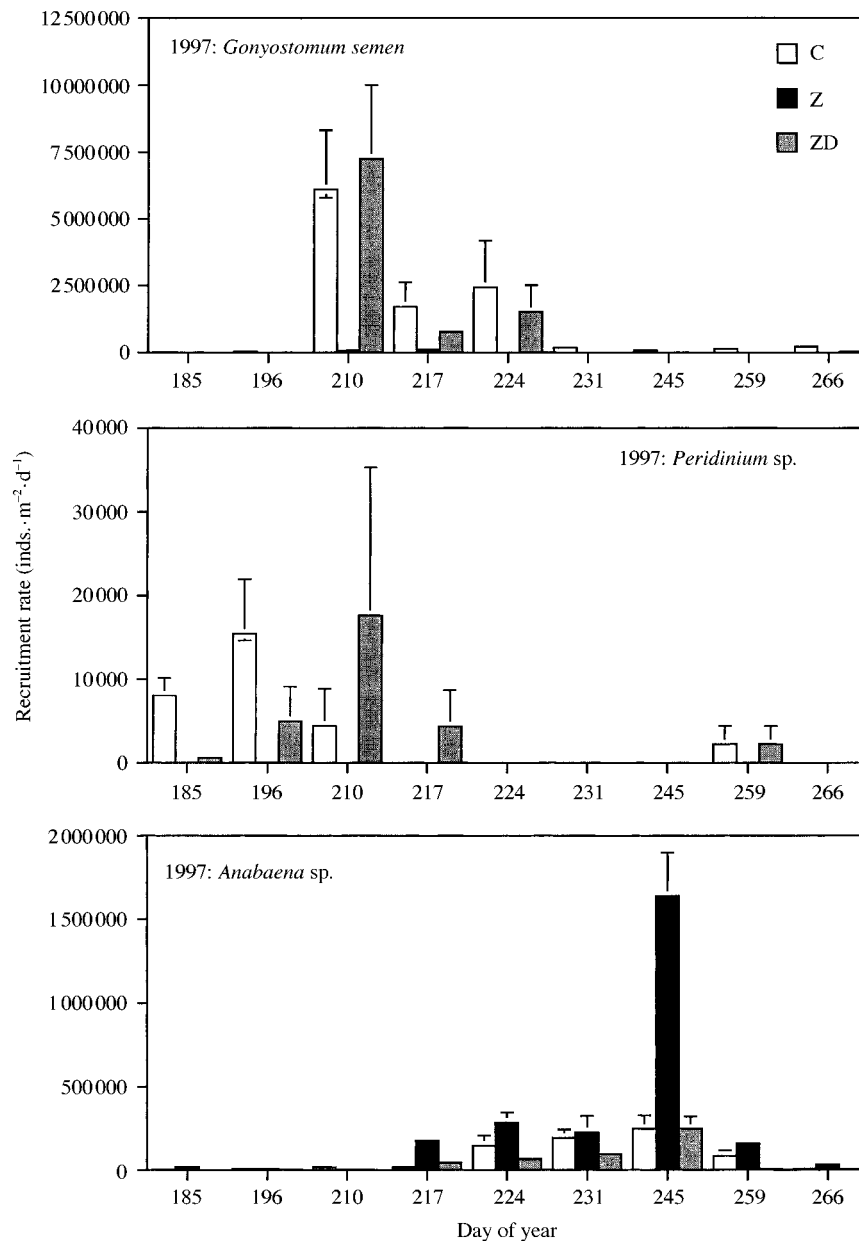
FIG. 7. Recruitment rate from sediment to water in 1997 of *Gonyostomum semen, Peridinium* sp., and *Anabaena* sp. in the control (C; white bars), the treatment with caged, live *Daphnia* (Z; black bars), and the treatment with dead *Daphnia* (ZD; grey bars). Bars show mean value ± 1 SE ($n = 4$ traps).

grazed upon algae recruited from the sediment surface not covered by the traps. Hence, the possibility of direct grazing on recruited algal cells causing the difference can be outruled. Moreover, in the majority of experiments, the recruitment rate of *Gonyostomum semen* was lower than of the controls even in the treatment with dead zooplankton (ZD). Accordingly, the presence of herbivores strongly reduced recruitment of both *Gonyostomum semen* and *Peridinium* sp. even without direct feeding on the algae.

It may be argued that algal species with long generation times (low "birth rates") should be more sensitive to mortality factors, such as grazing, than species with short generation times, and that adaptations to reduce the impact of mortality factors may therefore be expected to be more common among these species. Although both *Gonyostomum* and *Peridinium* in Dagstorpssjön are relatively large (greatest axial linear dimension 50.8 ± 4.6 and 48.0 ± 4.3 μm, respectively [means $\pm$ 1 SD], $n = 20$ cells measured), grazing pressure may be substantial, both from macrozooplankton and large rotifers, such as *Asplanchna* (Cronberg et al.
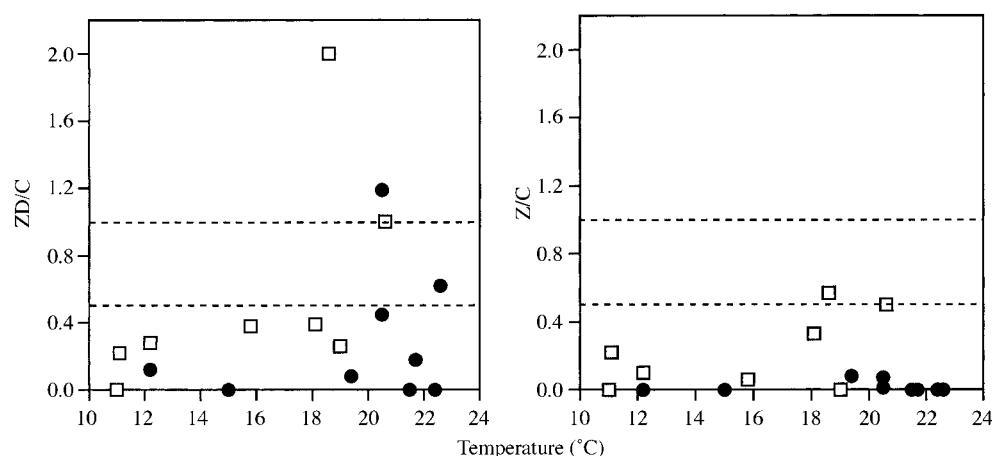
FIG. 8. The ratio between the recruitment rate of *Gonyostomum semen* in the ZD and Z treatments, respectively, and the control (C) plotted against temperature at each experiment in 1996 (open symbols) and 1997 (solid symbols). The plots show that on only three occasions, when temperature was between 18° and 20°C, the recruitment rate in the ZD treatment higher than in the control (i.e., ZD/C > 1), whereas recruitment rate was never higher in the Z treatment than in the control (Z/C > 1).

1988). One sophisticated adaptation to reduce mortality by grazing is to simply avoid encounters with high densities of herbivores, a behavior that appears to be practiced by both *Gonyostomum* and *Peridinium* in my laboratory study, as well as in Dagstorpssjön. Accordingly, we would expect these algae to have long generation times compared to algal groups without the adaptation, which also seems to be the case (Table 2). All other common algal genera in Dagstorpssjön have generation times <0.9 d, whereas *Gonyostomum* have generation times of 1.5–5 d and *Peridinium* ~11 d (Table 2). It may be argued that in order to become dominant in an algal assemblage it is necessary either to have a short generation time and thereby ''grow away'' from the grazer; to have a morphological adaptation to reduce grazing, such as spines; or to be able to detect and avoid grazers, as is the case suggested for *Peridinium* and *Gonyostomum* in this study. In line with this notion, rapidly growing *Anabaena* sp. (generation time of <1 d) showed no reduction in recruitment rate in response to herbivores in the laboratory study (Fig. 7). Instead, the abundance of *Anabaena* in the Z-treatment traps was generally higher than in other

treatments. This may possibly be a result of stimulation of recruitment by zooplankters or by the higher phosphorus concentrations in the Z compared to the other treatments. However, due to the short generation time (<1 d), the relatively long experimental period (5 d), and the higher nutrient availablility in the Z treatment, this positive response may have been a result of higher growth rate of *Anabaena* within the Z traps compared to in the other treatments. Hence, an artifact cannot be outruled as having affected the laboratory results of *Anabaena,* although it may be concluded that its recruitment rate is less affected by grazers than *Gonyostomum* and *Peridinium.*

The level of *Gonyostomum* recruitment in the Z treatment of the laboratory experiment was similar the two years, illustrating that algal recruitment at high zooplankton abundances was low independent of the ambient temperature. Hence, it is likely that the interannual difference in recruitment of *Gonyostomum* and *Peridinium* recorded in the field component of this study was similarly due to the differences in zooplankton biomass rather than to differences in temperature. A relevant question to ask is then: what caused the

TABLE 2. Generation time for some algal groups occurring in Dagstorpssjön, illustrating that both *Gonyostomum semen* and *Peridinium* sp. have long generation times compared to most other algae.

Algal taxon	Generation time (days)	Temperature (°C)	Reference
Gonyostomum semen	1.5–3	17	LeCohu et al. (1989)
Gonyostomum semen	3–5	18	Cronberg et al. (1988)
Peridinium	>11	22	Pollinger and Zemel (1981)
Cryptomonas	0.8	23.5	Morgan and Kalff (1979)
Anabaena flos aquae	0.9	20	Foy et al. (1976)
Asterionella	0.4	20	Lund (1949)
Scenedesmus	0.2	25	Reynolds (1984)

major zooplankton groups to show lower biomasses in 1997 than in 1996?

The primary clue to the answer of this question is the observation that very few eggs of the dominant planktivorous fish species roach (*Rutilus rutilus*) appeared in the spring of 1996 (P. Romare, *personal communication*), suggesting that few young-of-the-year (YOY) roach entered the lake that year. It is well known that YOY fish can have considerable impact as predators on zooplankton (Romare and Bergman 1999), and in a study of biomanipulated lakes, high abundances of YOY were shown to be correlated with low abundances of large body size zooplankters (Hansson et al. 1998). The net-fishing data from 1997 corroborated the hypothesis that YOY roach in 1996 occurred in very low frequency both compared to earlier studies in Dagstorpssjön and to several other lakes of similar type (Fig. 5). In 1997, 1+ roach (born in 1996) only constituted ~3% of the caught fish, compared to a generally occurring proportion of between 20 and 30% in the reference lakes. Hence, a failed reproduction in the dominant fish species in 1996 can be inferred; this failure allowed high biomasses of macrozooplankton, in turn leading to high grazing pressure on algae. Some algal species, however, including *Gonyostomum semen* and *Peridinium* sp., avoided entering the water column, which most probably would have resulted in a considerable reduction of the population size due to grazing, and instead prolonged their resting period. During the next year (1997), when fish reproduction was more normal, zooplankton biomass was lower and, accordingly, the recruitment of *Peridinium* sp. and *Gonyostomum semen* was higher.

Consequently, the data presented here suggest that succession and dominance patterns in the algal community may differ between years as an indirect result of the composition of the food web. Although the fact that planktivorous fish can affect algal succession directly by altering zooplankton grazing pressure is well known, the proposed causal chain from fish predation, to zooplankton to algal avoidance behavior has not been previously demonstrated. Since both *Gonyostomum semen* and *Peridinium* sp. often form high-density "blooms" and are viewed as nuisance algae, this finding may be of importance as a predictive tool in lakes where such blooms are common. A knowledge of fish reproductive success allows predictions about zooplankton development during the coming season. This knowledge, in turn, may help provide a valuable tool to predict the recruitment of common bloom-forming algae, including *Gonyostomum semen* and *Peridinium* sp. The distribution of *Gonyostomum* blooms has increased during recent years mainly in humic, acidified lakes (Lepistö et al. 1994). This expansion is, however, not directly associated with the acidification process (lowering of pH) that many lakes in Scandinavia are suffering from (Cronberg et al. 1988, Lepistö et al. 1994). Since the acidification process negatively affects reproduction of many efficient zooplankton species (Stenson et al. 1993), a possible explanation may instead be that the recruitment of *Gonyostomum* increases as a secondary effect of acidification. Noxious blooms are an increasingly important problem also in eutrophicated freshwaters, where mainly blue-green algae (cyanoprokaryota) form nuisance, and often toxic, blooms. Many of these algae form resting stages and may rapidly enter the water column at suitable growth conditions. Similar problems also occur in marine systems, where mass developments of mainly flagellates cause severe problems in coastal areas, e.g., by producing toxins (Burkholder et al. 1992). Hence, most noxious bloom-forming algae, both in freshwater and marine environments, seem to have a "cyst bank" at the sediment from which recruitment to the water column occurs. Moreover, environmental problems induced by humans, such as eutrophication and acidification, seem to have improved the conditions for these bloom-forming algal groups. Since environmental problems show few signs of improvement, knowledge of life cycles and triggering factors for recruitment of these organisms may offer an opportunity to manage bloom formation.

Future research would benefit from focusing on identifying the chemicals (kairomones) responsible for information transfer between consumer and prey. Furthermore, some algal species seem to respond considerably to exudates from zooplankters, whereas others are less sensitive, such as *Anabaena* in this study. It may thus be of interest to assess the possible evolutionary similarities among kairomone sensitive species, and to quantify the importance of the adapations in comparison to other consumer-avoidance adaptations. Recruitment of algae from sediment to water may also be of interest for research on benthic–pelagic coupling, which hitherto mainly has focused on energy flow and fluxes of substances between sediment and water. This study, however, points out that also life history traits of organisms may be of importance, suggesting that models of biogeochemical cycling may be more complete if they also incorporate life-cycle patterns of organisms (Marcus and Boero 1998).

In conclusion, in addition to the more direct pathway of consumption by fish, through zooplankton to algae, this study proposes the presence of an indirect pathway that involves recruitment rate adjustment in some algal groups. While herbivory affects all algal groups to some extent, this behavioral mechanism would allow some groups to escape temporally from high zooplankton grazing pressure. The existence of such a predator-avoidance behavior, together with large "cyst banks" in the sediments, is suggested here to strongly affect the dynamics and succession of algal communities.

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