CHAPTER 10

FOOD-WEB INTERACTIONS IN LAKES

What is the impact of chemical information conveyance?

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Abstract. The structure of aquatic ecosystems is determined by complex interactions among individual organisms at different trophic levels. Although our basic understanding of how top-down and bottom-up processes interact to determine food-web dynamics has advanced, we still lack insights into how complex interactions and feedbacks affect the dynamics and structure of food webs. It is now becoming increasingly clear that, in addition to energy transfer from one trophic level to the other, there is exchange of information between these levels, facilitated by the release of infochemicals by the organisms. There is evidence from recent studies that the exchange of chemical information in freshwater ecosystems is likely to play a decisive role in shaping structure and functioning of these systems. Chemical communication among freshwater organisms mediates many aspects of both predation and interspecific competition, which play key roles in determining the community structure and ecosystem functioning. For example, consumer-induced defences in phytoplankton and zooplankton include modifications in the characteristics relating to life history, behaviour, morphology and biochemistry. These inducible defences affect trophic interactions by altering predator feeding rates through changes in attack rate or handling time or both. Also host-specific fungal parasitism in phytoplankton is probably controlled by infochemicals. The motile fungi recognize their host by host-secreted compounds. In this chapter I will discuss how infochemicals may affect the dynamics and structure of planktonic food webs.

Keywords: induced defence; phenotypic plasticity; infochemicals; plankton; population dynamics; ecosystem effects

INTRODUCTION

Among terrestrial organisms we consider it self-evident that interactions are not only influenced by visual signals but also by chemical signals, for example in predator–prey interactions. In aquatic systems, however, interactions based on chemical information transfer are less obvious (Brönmark and Hansson 2000). Predation is an important mortality factor for planktonic species; therefore, many planktonic organisms have developed a wide variety of defences to avoid predation by higher trophic levels. Many phytoplankton species are notoriously flexible in their morphology, growth form and biochemical composition. For example, several of these variable traits in phytoplankton have been interpreted as defence mechanisms against grazing. Pelagic phytoplankton employs different defence strategies to avoid

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being ingested and, if ingested, to pass unharmed through the grazer’s gut. Zooplankton feed with differing success on various phytoplankton species, depending primarily on size, shape, cell-wall structure and the production of toxins. Some evidence for size-related effects comes from experiments that involve feeding zooplankton with particles of different sizes, keeping their shape constant. For example, Burns (1968) found a clear relationship between the grazer’s body size and the maximum size of spherical beads that can be ingested. Hardness of algae also influences ingestibility (DeMott 1995). Gelatinous chlorophytes may be readily ingested but are poorly digested by zooplankters like *Daphnia* (Porter 1975), resulting in depressed zooplankton growth rates (Stutzman 1995). Zooplankton rarely feed on filamentous cyanobacteria because they are large and can be toxic (Lampert 1987). Further, extracellular substances released from cyanobacteria inhibit the grazing activity of daphnids (Haney et al. 1994). In contrast, detritus generated from filamentous cyanobacteria is both better ingested and assimilated by *Daphnia* spp. (Gulati et al. 2001). Mucus excretion by diatoms also inhibits copepod grazing (Malej and Harris 1993). Finally, nutrient-deficient algae may also be grazed with decreased efficiency, owing to either reduced ingestion rates (Sterner and Smith 1993) or reduced assimilation efficiency (Van Donk and Hessen 1993; Van Donk et al. 1997), which increases the probability of persistence of such algae during periods of low growth rates.

Some of these changes in defensive traits in the field can be explained by clonal replacement as conditions change (Wood and Leatham 1992; Yoshida et al. 2003). However, there is also evidence for phenotypic plasticity. For example, the dinoflagellate *Ceratium* shows considerable phenotypic plasticity in its horn lengths (Hutchinson 1967). On the other hand, the cyanobacterium *Microcystis* may phenotypically vary in its toxic effects (Benndorf and Henning 1989). The green algal genus *Scenedesmus* is notoriously phenotypically flexible (Trainor and Egan 1991). Individual strains of various *Scenedesmus* species can grow as unicells or form colonies (coenobia) of four or eight cells. The cells can also vary in the number and size of the spines.

It is well known that many algal species isolated as clones from the field change their morphology or growth form after several generations in laboratory cultures, suggesting that some unknown factor triggers their ‘typical’ or consistent appearance in the field. For example, spiny algae like *Staurastrum* lose their bizarre form, colonies like *Microcystis* grow as single cells, and flakes of *Aphanizomenon* grow as single filaments. In the field, large flakes of *Aphanizomenon* are frequently found in the presence of large *Daphnia* (Lynch 1980). A similar phenomenon has been observed in the diatom *Synedra*, which occurs as colonies consisting of dozens to hundreds of cells when *Daphnia* is present, but as single cells in the grazer’s absence. It is, however, difficult to determine if the observed effect is caused by selective grazing on small flakes and single cells or an active response to the grazers’ presence.

Recently, several studies have shown that not only in terrestrial but also in aquatic systems many organisms are receptive to chemical signals exuded not only by conspecifics but also by potential predators and grazers, which help them gather information about their environment. This so-called chemical communication is mediated by information-conveying chemicals (infochemicals) and is a well-known ecological phenomenon that facilitates interactions between organisms (Dicke and Sabelis 1992). Infochemicals are defined as chemical compounds that convey information between individuals and thereby evoke a physiological or behavioural response in the receiver (Dicke and Sabelis 1988). Consumer-induced defences in phytoplankton and zooplankton include changes in morphology (e.g., formation of spines and colonies), biochemistry (e.g., production of toxins, repellents), behavioural responses (e.g., migration, refuge use) and in life-history characteristics. Below I will review consumer-induced defences in plankton and discuss benefits and costs of induced defences and their impact on population dynamics and ecosystem functioning. Furthermore, I will discuss the current knowledge of the chemical nature of aquatic infochemicals and their transportation in the water. I also shortly review allelopathic interactions, attraction to food by means of infochemicals, and multitrophic indirect defences.

CONSUMER-INDUCED DEFENCES IN PHYTOPLANKTON

Hessen and Van Donk (1993) discovered that a chemical released from grazing *Daphnia* induced the formation of colonies in the green alga *Scenedesmus subspicatus*. On exposure to water in which daphnids had been cultured, *Scenedesmus* formed numerous large, four- to eight-celled colonies, with more rigid and longer spines (Figure 1). The induced changes in the algae conferred grazing resistance against small zooplankters and can be interpreted as an adaptive anti-herbivore strategy. Reduced algal palatability adversely affected feeding rates in zooplankton and reduced their growth rates and fecundity (Van Donk et al. 1999). Lampert et al. (1994) confirmed the findings that colony formation was mediated by chemicals released by daphnids, by adding water in which *Daphnia* had been swimming to spineless *Scenedesmus acutus*. Van Donk et al. (1999) examined the effect of *Daphnia* infochemicals on the morphology of fifteen strains of Chlorophyceae, two strains of Bacillariophyceae and three strains of Cyanophyceae. *Daphnia*-induced colony formation, which was restricted to Chlorophyceae was, in addition to the genus *Scenedesmus,* also observed in *Coelastrum*. Verschoor et al. (2004a) showed that species of Scenedesmaceae that responded to *Daphnia*, generally also responded to infochemicals from the rotifer *Brachionus calyciflorus*, and that colony size could be related to infochemical concentration.

The colony formation in response to grazing-associated infochemicals does not seem to be unique to freshwater algae: it has been reported by Wolfe et al. (1997) for marine phytoplankton (*Phaeocystis*, a haptophyte) in response to infochemicals released by zooplankton.

In the desmid *Staurastrum* the presence of *Daphnia* induced the formation of mucus and clumping of the algal cells, making them less edible for zooplankton. However, this was caused by the stirring of the water due to filtering activity of daphnids and not to an infochemical (Wiltshire et al. 2003).

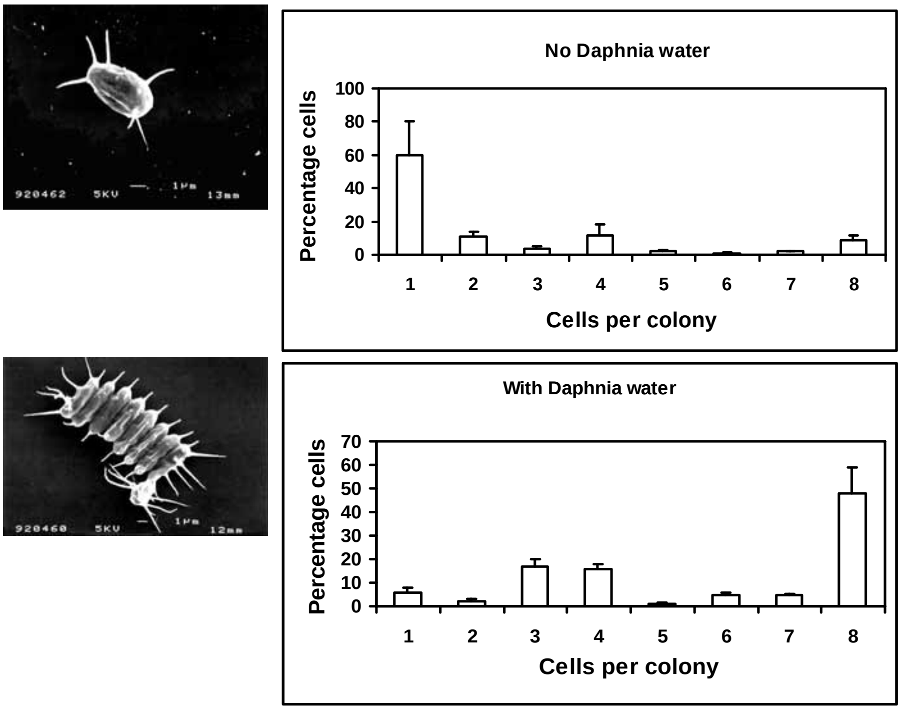

Figure 1. *Colony induction in a Scenedesmus culture in response to an infochemical released by Daphnia magna. Percentage of total number of cells forming colonies of varying cell numbers after 48 hours of growth. Single cells dominate in the cultures without Daphnia water (upper panel), while eight-cell colonies dominate in the infochemical treatments (lower panel) (From Van Donk et al. 1999)*

Jang et al. (2003) demonstrated that several strains of *Microcystis aeruginosa* increased toxin production in response to direct and indirect exposure to herbivorous zooplankton. This supports the hypothesis that this response is an induced defence strategy, mediated by the release of infochemicals from zooplankton.

Hansson (1996; 2000) reported that several freshwater algal species may possibly regulate their recruitment rate from sediment depending on the presence or absence of grazers in the water column. For example, flagellated algae like *Gonyostomum semen* can use infochemicals released by herbivores to adjust the timing of their recruitment from the ‘seed-bank’, thereby reducing the exposure to grazing.

CONSUMER-INDUCED DEFENCES IN ZOOPLANKTON

Predator-induced responses in zooplankton have elicited increasing research interest during the last two decades. Since Larsson and Dodson (1993) reviewed the state-of-the-art research on chemical communication in planktonic animals, several studies on such aspects and new research lines on anti-predator defences in zooplankton have developed (Tollrian and Harvell 1999; Brönmark and Hansson 2000; Lass and Spaak 2003).

Rotifers, viz., *Brachionus calyciflorus*, have been the first planktonic organisms for which responses to infochemicals derived from their predators were observed (Gilbert 1966). Inducible morphological changes have also been described for ciliates of the genus *Euplotes* upon their exposure to infochemicals from ciliate predators of the genus *Lembadion* (Kuhlmann and Heckmann 1985).

The cladoceran *Daphnia* has developed several behavioural defence mechanisms. The daphnids are not only a good food source for planktivorous fish but also for invertebrate predators, such as *Chaoborus* larvae and *Notonecta*. One of the frequently studied behavioural response mechanisms in daphnids is diel vertical migration (DVM). *Daphnia* migrates down during the day to relatively darker, deeper waters to avoid fish. During the night they ascend to the warmer surface water layers of the lake, where algal food is more abundant. Although light plays an important role, DVM seems to be triggered by a chemical signal (Dodson 1988).

An analogous mechanism to DVM is diel horizontal migration (DHM) of *Daphnia* into the vicinity of water plants. The macrophytes act as shelter for the daphnids to protect them from fish during the day (Burks et al. 2000). Interestingly, these macrophytes have been shown to produce chemicals that repel *Daphnia*, and only the infochemicals exuded by fish can override the repellent effect of the chemical compounds produced by macrophytes (Burks et al. 2000).

Furthermore, *Daphnia* can change morphologically following exposure to predator infochemicals. These changes occur to a certain degree as a response to seasonal temperature changes, but also in response to infochemicals. There are reports of the formation of neckteeth, helmets and crests in *Daphnia* exposed to, respectively, *Chaoborus* (Krueger and Dodson 1981), planktivorous fish (Tollrian 1994) and a notonectid predator (Grant and Bayly 1981). Apart from this, Slusarczyk (1999) reported evidence for two chemical cues that regulate synchronization of sexual reproduction (formation of males and production of ephippial eggs or resting eggs) to protect the genome during periods of high predation risk. Not only does *Daphnia* react to infochemicals released from predators, but also to a chemical signal released by injured conspecifics. Filtered water that had contained crushed daphnids before filtration induced individual daphnids to remain deeper in the water column. They also aggregated more frequently in the presence of a chemical released by fish (Pijanowska and Kowalczewski 1997). This may be the result of mechanical interference in food collection and allelochemical interactions.

Zooplankters can also defend themselves by becoming less visible to their predators. Copepods in arctic, oligotrophic lakes are often pigmented by carotenoids, which protect them against UV radiation. This pigmentation, however, makes them more vulnerable to visual fish predation. Hansson (2004) found that the pigmentation in the copepods decreased when they came in contact with water in which fish had been swimming. Similarly, Tollrian and Heibl (2004) reported reduced pigmentation for *Daphnia*. The pigmentation was the lowest if the UV radiation was low as well. A lower pigmentation increased the mortality due to UV radiation, but decreased the mortality due to fish predation. So, there is a trade-off between risks from predation and ultraviolet radiation.

In contrast to several studies on freshwater plankton, the role of predator infochemicals in marine zooplankton has been investigated by only a few workers (e.g. Strand and Hamner 1990; Bollens et al. 1994; Cieri and Stearns 1999; Hamren and Hansson 1999). There is some evidence that marine copepods respond to mechanical or visual stimuli, rather than to chemicals exuded by predatory fish (Bollens et al. 1994). Several marine plankton species use bioluminescence for communication. However, Cieri and Stearns (1999) and Hamren and Hansson (1999) have demonstrated that marine planktonic crustaceans (copepods, mysidaceans) reduce feeding activity in the presence of fish infochemicals. The resulting reduction in gut fullness is perhaps adaptive in reducing visibility to predators (Bollens and Stearns 1992); this has also been shown for other planktonic organisms (Giguère and Northcote 1987). Thus, predator infochemicals may also play an important role for anti-predator defences in marine plankton.

BENEFITS AND COSTS OF INDUCED DEFENCES

Induced defences provide protection against different predators and allow organisms to adapt phenotypically to multi-predator regimes (Tollrian and Dodson 1999). The defence can be attuned depending on the predator present. Despite the fact that some machinery is required to initiate defence, the costs of inducible defence can be low, because the defence is only initiated in the presence of the predator. Generally, defences are believed to bring about costs that are averted if the predators are absent; otherwise constitutive defences would have been favoured by natural selection (Tollrian and Harvell 1999). For *Daphnia*, researchers were confronted with great difficulties to demonstrate the expected physiological costs of neckteeth formation (Tollrian and Dodson 1999). The costs are reported by some authors to involve trade-offs of life-history reactions to *Chaoborus* infochemicals, i.e., no direct costs result from neckteeth formation for *Daphnia* (Repka and Pihlajamaa 1996). In contrast, morphological defences in ciliates have been found to lead to metabolic costs. In *Euplotes*, protein synthesis is necessary for predator-induced changes in morphology (Kusch and Kuhlmann 1994). These metabolic costs cause increased generation times (Kuhlmann 1992). Consequently, the reduced population growth rates as well as reduced anti-predator morphological changes bring about demographic costs (Kusch and Kuhlmann 1994). Similar demographic costs of anti-predator morphologies are reported for rotifers: at high food concentrations, the predator-induced morph of *Keratella testudo* has less than half of the intrinsic rate of population increase of the non-induced morph (Stemberger 1988). Furthermore, the extent of morphological defence has been observed to correlate with the prevailing predation risk in ciliates (Kusch 1995). The observed adjustment of morphological changes to the actual predation risk indicates that the costs involved are saved when predation risk is reduced or absent. In planktonic algae, colony formation appeared to have direct photosynthetic costs (Verschoor 2005). Furthermore, ecological costs consist of enhanced sinking of colonies out of the euphotic zone (Lürling and Van

Donk 2000). Such environmental costs, i.e. interactions of inducible defences with the environment, might also exist for neckteeth in *Daphnia* (Tollrian and Dodson 1999) and for vertical migration behaviour (Loose and Dawidowicz 1994) and for horizontal migration (Burks et al. 2001). Tollrian and Dodson (1999) state that costs may have been calculated in a simplified context. Phenotypic changes and inducible defences might impose various other costs and limits than simply metabolic costs (DeWitt et al. 1998). One limit may be that adaptations to one predator regime might be unfavourable in the presence of another predator. For example, morphological changes generally increase visibility that might be disadvantageous in the presence of predators that stalk their prey by vision (Tollrian 1995). Furthermore, selection should favour costs that are lower than the benefits and are as low as possible. Thus, costs might be absent or small and difficult to measure but still relevant for prey populations (Tollrian 1995; Tollrian and Dodson 1999).

CASCADING EFFECTS: POPULATION DYNAMICS AND ECOSYSTEM FUNCTIONING

All changes in prey morphology and behaviour in plankton in response to infochemicals from a potential predator will increase the probability of survival for an individual prey organism, but it may also have population- and even system-wide consequences. Diel vertical or horizontal migration of zooplankton in response to infochemicals from planktivorous fish will affect the resource availability for the fish as well as grazing pressure on phytoplankton. Although inducible defences have been investigated extensively at the level of individuals and populations, their importance for population dynamics and ecosystem functioning has hardly been investigated.

Vos et al. (2002) used a combination of individual-based modelling and experimental data from the field and laboratory to show that induced defences in *Daphnia* significantly reduced predation by juvenile perch on *Daphnia* populations during early summer. Induced defences thus prevent overexploitation of the *Daphnia* population by fish and allow the zooplankters to persist. Behavioural defences through diel vertical migration were shown to have a much stronger quantitative effect than defences through changes in life history (Vos et al. 2002). Vos et al. (2004a) predicted that nutrient enrichment could destabilize aquatic food chains when defences in prey are fixed or absent, while such destabilization, the so-called paradox of enrichment, could be absent when prey have inducible defences (Vos et al. 2004a).

Verschoor et al. (2004b) empirically tested the predictions by Vos et al. (2004a), using food chains consisting of inducible defended and undefended algae, herbivorous rotifers and carnivorous rotifers. In enriched food chains with undefended algae, they observed large-amplitude oscillations over several orders of magnitude, which incidentally resulted in extinction of the top predator. On the other hand, food chains with inducible defended algae stabilized immediately after the initial transient phase (Figure 2). Thus, induced defences prevented strong fluctuations and extinctions of higher trophic levels.

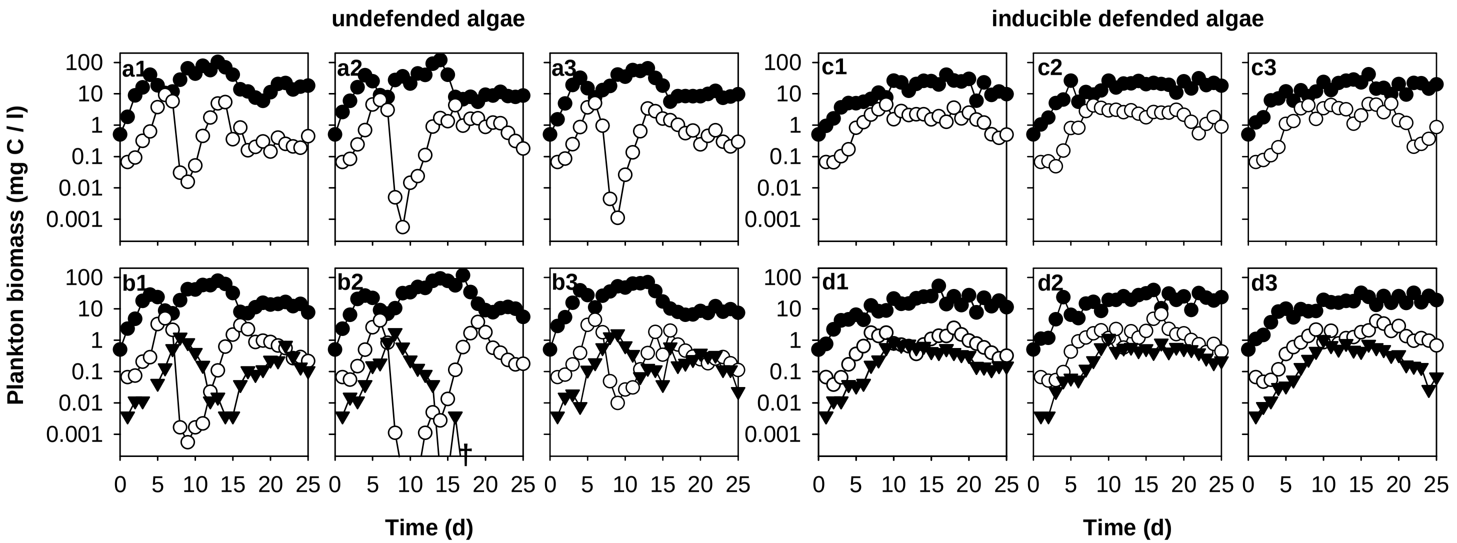

Figure 2. *Population dynamics of planktonic food chains in high-phosphorus treatments, with densities expressed as mg C* l^{-1}*. Solid circles represent phytoplankton biomass, open circles represent herbivorous zooplankton (Brachionus) and triangles represent carnivorous zooplankton (Asplanchna).* ***a****,* ***b****. food chains with undefended phytoplankton (Desmodesmus);* ***c****,* ***d****. food chains with inducible defences in phytoplankton (Scenedesmus); numbers indicate different replicates. Zooplankton extinctions are marked by* **†** *(From Verschoor et al. 2004b)*

Experiments with more species-rich food webs are needed to get a deeper insight into the defence responses at different trophic levels. The effects of chemical information transfer and induced defences at ecosystem level are still not understood, but induced defences have been predicted to cause all trophic levels to increase under enrichment, a pattern that is consistent with both field and laboratory observations (Vos et al. 2004b). Chemical interactions between planktonic organisms may hamper lake restoration by food-web manipulation but to test this, field studies are necessary.

THE CHEMICAL NATURE AND TRANSPORTATION OF INFOCHEMICALS

Although the presence of infochemicals has been confirmed in many systems, the chemical structures of many of these compounds are still quite obscure. Especially for freshwater environments the chemistry of these compounds is little known. Nonetheless, three kairomones, produced by *Lembadion* (predatory ciliate), *Amoeba* and the flatworm *Stenostomum*, which affect a freshwater ciliate, *Euplotes*, have been described (Kusch 1999; Kusch and Heckmann 1992). These compounds are complex proteins varying in molecular weight from 4.5 kDa to 31.5 kDa.

Most research on infochemicals excreted by predators of *Daphnia* is at present aimed at their characterization. Boriss et al. (1999) reported that trimethylamine (TMA) produced by fish was the compound responsible for the defence response of *Daphnia*. However, in a follow-up study Pohnert and Von Elert (2000) found that *Daphnia* responded to TMA only at unrealistically high concentrations. Furthermore, daphnids continued to exhibit DVM even when TMA was removed from the fish water (Pohnert and Von Elert 2000). Ringelberg and Van Gool (1998) suggested that it is not the fish themselves but bacteria associated with them that produce the infochemical, which triggers the daphnids to migrate. When the fish were treated with antibiotics in solution, so as to immobilize the fish-associated bacteria, the fish water induced significantly less DVM in the daphnids than in controls (fish water untreated with antibiotics). Nonetheless, because some significant biological activity still remained, apparently bacteria cannot be the sole causal factor for the DVM.

The response of *Daphnia* to the *Notonecta* infochemical resembled that of the fish factor (Dodson 1989; Riessen 1999). So far, the *Notonecta* cue has not been characterized. The response to the infochemical from *Chaoborus* fundamentally differed from the cues from fish and *Notonecta* (Dodson 1989; Loose et al. 1993; Riessen 1999). Thus, the chemical compounds involved may be different (Larsson and Dodson 1993; Loose et al. 1993; Riessen 1999). The difference is also clear from the different chemical characteristics (Tollrian and Von Elert 1994).

Until now, the infochemical released by *Daphnia* that causes *Scenedesmus* to form colonies has been poorly described. Wiltshire and Lampert (1999) reported that urea is the infochemical that induces *Scenedesmus* colony formation. However, Lürling and Von Elert (2001) found evidence that contradicts this. Earlier, in 1994, Lampert and co-workers had already obtained negative results with several concentrations of urea (Lampert et al. 1994). Therefore, the *Daphnia* factor is most likely not urea. This is also supported by the fact that urea would be formed by the general metabolism, while Von Elert and Franck (1999) presented evidence that the infochemical originates from a particular metabolic reaction. Kaler et al. (2000) propose oligonucleotides or nucleic acids and possibly peptides as possible structures for the consumer-released factor, solely based on UV spectra. This view is, however, not supported by the experimental work of Lampert et al. (1994) and Von Elert and Franck (1999). The chemical cue can be enriched on SPE cartridges (C_{18}) (Lampert et al. 1994; Von Elert and Franck 1999) and is heat- and pH-stable, water-soluble and non-volatile, and has a molecular weight < 0.5 kDa (Lampert et al. 1994). Furthermore, its retention by a strongly basic anion exchanger implies that it is an anionic compound and thus excludes urea (Von Elert and Franck 1999). Other experiments hint at the presence of hydrophilic groups, possibly a carboxyl group, and olefinic characteristics. The extract subjected to HPLC showed activity in only one fraction (Van Holthoon 2004). Because the extracts of mechanically crushed *Daphnia* or *Scenedesmus* did not show colonizing activity in the latter (Lampert et al. 1994; Von Elert and Franck 1999) an interaction between *Scenedesmus* and *Daphnia* may be needed to initiate production of the active compound (Lürling and Van Donk 1996). Lürling (1999) attributed colony formation to feeding activity of *Daphnia* rather than merely to the presence of daphnids, as starved animals did not induce colony formation in *Scenedesmus* (Lürling and Van Donk 1996). In analogy to the fish factor (Ringelberg and Van Gool 1998), bacteria in the gut of *Daphnia* may release such an infochemical (Fink 2001).

Once the chemicals responsible for transferring information between organisms are identified, important research tasks will be to assess how these chemicals are transported in the water and how important turbulence is for their dispersion. Until now, most studies have been performed in standing water or at laminar flow in laboratory settings, whereas in natural situations turbulent mixing dilutes chemical stimuli and creates patchiness in odour distributions resulting in a much more complex olfactory landscape (e.g. Zimmer-Faust et al. 1995; Zimmer et al. 1999), much as is the case with airborne infochemicals.

ALLELOPATHIC INTERACTIONS

Aquatic macrophytes have long been suspected of suppressing phytoplankton growth through the excretion of growth-inhibiting chemical substances (Van Donk and Van de Bund 2002). The production and excretion of chemicals by aquatic macrophytes could be an effective defence strategy against other photosynthetic organisms, epiphyton and phytoplankton, which compete with macrophytes for light and nutrients. This is, however, not an induced defence and, in contrast with the nature of the infochemicals inducing defence, more knowledge is available about the structure of allelopathic chemicals. These substances belong to rather different chemical classes such as sulphur compounds, polyacetylenes, polyphenols and oxygenated fatty acids (Gross 1999). Submerged macrophytes such as *Ceratophyllum, Stratiotes, Chara* and *Myriophyllum* may strongly inhibit algal growth, and sensitivity of different algal species to these chemicals differs (Körner and Nicklisch 2002; Mulderij et al. 2003). Consequently, these allelopathic substances may change the composition and dynamics of the phytoplankton community.

Allelopathic interactions have also been reported between phytoplankton species. A review about allelopathy in phytoplankton and the biochemical, ecological and evolutionary aspects, is given by Legrand et al. (2003). They state that chemical interactions, specifically allelopathy, are an important part of phytoplankton competition. For example, *Microcystis* is able to delay the start of the bloom of another phytoplankter *Peridinium* by release of a chemical compound, which also inhibits the growth of other cyanobacteria like *Nostoc* and *Anabaena* directly (Singh et al. 2001; Sukenik et al. 2002).

ATTRACTION TO FOOD BY MEANS OF INFOCHEMICALS

Chemical cues from potential food algae could be important for their consumers because they provide information on the food quality (Larsson and Dodson 1993). So, according to Van Gool and Ringelberg (1996), algae-associated odours could be detected by *Daphnia*. The daphnids were observed to swim towards the edible green alga *Scenedesmus*, but not towards toxic, less edible cyanobacteria. Haney et al. (1994) demonstrated that the food intake of the daphnids was reduced on exposing them to chemicals released by cyanobacteria. In fact, one would expect *Daphnia* to avoid areas where potentially harmful cyanobacteria are present. In contrast, in food-gradient experiments *Daphnia* strongly aggregated in zones with intermediate food levels but avoided zones with high food levels (Neary et al. 1994). The mechanism used by *Daphnia* to locate these regions is probably related to the concentration of algal cells rather than the presence of algal odours. So, several factors, including olfaction, affect *Daphnia*–algal interactions (Roozen and Lürling 2001).

A chemical attraction has also been found between a parasitic fungus and its algal host, a diatom, *Asterionela formosa* (Van Donk 1989; Ibelings et al. 2004). This fungal infection is very host-specific. The spores swim towards their algal host, attach themselves and penetrate the host cells. These spores form sporangia that mature and produce spores again. The zoospores can only locate a new host algal cell in the light, i.e., when the alga produces an exudate during photosynthesis. In the dark such exudates are not produced (Canter and Jaworski 1981).

MULTITROPHIC INDIRECT DEFENCE

Chemical attraction can also play a role in multitrophic indirect defences. For terrestrial ecosystems it has been found that in addition to a direct defence in plants, like a herbivore-induced toxin in the leaves, there is an indirect multitrophic defence. In response to grazing by caterpillars, for example, plants produce volatiles that attract the parasitic wasps that parasitize the caterpillars (Dicke 1999). Furthermore, some plants can induce their neighbouring plants to produce volatiles that attract predators, causing increase in predation on the herbivores (Dicke and Bruin 2001).

Indirect multitrophic defences have also been described for marine ecosystems. Dimethylsulfide is produced by the alga *Phaeocystis* when micro-zooplankton is grazing on them (Strom and Wolfe 2001). As a reaction copepods are attracted towards the microzooplankton and consume it, thereby reducing their grazing pressure on *Phaeocystis* and thus indirectly protecting the alga. Dimethylsulfide, which is volatile and will reach the surface of the water, will attract fish-eating birds to high-production areas with a high concentration of fish predating on the copepods (Steinke et al. 2002). This phenomenon will indirectly also result in protection of the alga.

The question that arises is: are such indirect, induced defence mechanisms present in freshwater ecosystems? Kagami et al. (2004) found that *Daphnia* can eat fungal zoospores and protect the alga *Asterionella* from fungal infection. These spores are more readily eaten when they are concentrated around their host and conceivably the algae can exude some infochemical attracting *Daphnia* to defend themselves. A similar explanation can be proposed for the interaction between cyanobacteria, their parasitic virus and the flagellates eating on this virus. Murray (1995) found that cyanobacteria excrete organic substances that attract these virus-eating flagellates. Further research is needed to test these hypotheses about multitrophic indirect defences in freshwaters.

CONCLUDING REMARKS

From the preceding sections it is clear that planktonic interactions are highly variable and complex. We are now more aware of the infochemicals that are involved in planktonic interactions and have begun to accumulate knowledge about the nature of these infochemicals. Nonetheless, we are still not able to identify and isolate them. Apparently, chemical communication mediates both predation and interspecific competition, and we know that induced defences moderate strong population fluctuations and the local extinctions of consumers that may result from these. However, we do not know yet what and how much impact chemical communication has on ecosystem functioning. One may hypothesize that chemical interactions between planktonic organisms hamper lake restoration by food-web manipulation, but field studies are necessary to test this.

Finally, I believe that future research in chemical ecology will help pave the way to a better understanding of species composition, top-down control of algae and the structure of aquatic food webs.

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