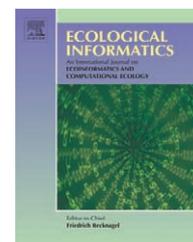


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# Infochemicals structure marine, terrestrial and freshwater food webs: Implications for ecological informatics

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## ABSTRACT

Here we consider how information transfer shapes interactions in aquatic and terrestrial food webs. All organisms, whether they are dead or alive, release certain chemicals into their environment. These can be used as infochemicals by any other individual in the food web that has the biological machinery to sense and process such information. Such machinery has evolved in bacteria, plants and animals and has thus become an inextricable part of the mechanisms that underlie feeding relations in food webs.

Organisms live in environments suffused with infochemicals and this information network can be tapped into by both predators and their prey. However, it also opens doors to confusion in the face of a bewildering abundance and complexity of information. Infochemical mixing, masking, crypsis and mimicry could cause such confusion, especially in species-rich communities.

We provide a point of entry into this field of enquiry by identifying seminal papers and major reviews and by discussing research lines that might enhance our mechanistic understanding of interactions in food webs. We highlight empirical work on the ways in which individuals use infochemicals and discuss model results on how this mediates patterns of population dynamics. We consider implications for ecosystem management and indicate how classical models and novel approaches from ecological informatics may contribute to linking the levels of individuals, populations and communities and their interactions with abiotic structuring forces in ecosystems.

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## 1. Introduction

Here we address the question how infochemicals affect the processes that structure aquatic and terrestrial food webs. A good starting point is the realization that all organisms on land and in water release certain chemicals into their environment. Some of these compounds are just waste products, while others have specific functions as signals.

Sex-, alarm- and aggregation pheromones clearly have such a signalling function in the animal world. Pheromones convey intraspecific signals. Infochemicals such as kairomones and synomones facilitate interspecific information transfer. For example, plant synomones are important in mutualisms between plants and insect pollinators. Dicke and Sabelis (1988) give an excellent introduction to infochemical terminology.

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Whatever the function is from the releaser's point of view, once these compounds are out there, they are available as potential sources of information to any other individual of any other species in the food web (Price et al., 1980; Turlings et al., 1990). Many carnivore species use prey-released substances to find their victims, both in aquatic and in terrestrial systems. For example, insect parasitoid species are known to 'eavesdrop' on the intraspecific chemical communication of their insect hosts. These parasitic wasps use aggregation- or sex pheromones of their victims for host location (Noldus and van Lenteren, 1985; Stowe et al., 1995; Fatouros et al., 2005; Wertheim et al., 2005). In other predators the exploitation of their prey's pheromone system is even more advanced. For example, some spiders are known to release chemicals identical to the sex pheromones emitted by female moths. These spiders feed exclusively on the male moths that are fatally attracted to them (Stowe et al., 1995 and references therein).

Chemical information transfer is not restricted to communication within or between adjacent trophic levels in food webs. Infochemical-mediated mutualisms exist between a variety of plant and carnivore species. Many plant species start to emit volatiles that are attractive to carnivores and parasitoids once they are infested with insect herbivores (Turlings et al., 1990; Vet and Dicke, 1992; Dicke and Vet, 1999; Turlings and Wäckers, 2004). This makes these predators more efficient in finding small prey in a large world, while plants may benefit through reduced herbivore damage (Vet et al., 1991; Tumlinson et al., 1992; Vet and Dicke, 1992; Van Loon et al., 2000). Interestingly, some plants can emit specific volatile blends for different herbivore species (De Moraes et al., 1998) and thus selectively attract parasitoids (Du et al., 1996; De Moraes et al., 1998).

However, such selective attraction of specialist natural enemies of herbivores does not always occur (Vet, 1999). Parasitoids may be attracted to plants and leaves infested with nonhost herbivores (Agelopoulos and Keller, 1994; Geervliet et al., 1998) or even to plant species that never contain hosts (Perfecto and Vet, 2003). Such attraction to seemingly irrelevant cues can be caused by the fact that volatile blends of different plant species have many 'green leaf volatiles' in common. Such infochemical similarity is ecologically relevant, because out in the field parasitoids and predators will inevitably encounter a variety of plant species, each of which can be infested with several herbivore species. In the past food web ecologists focused their studies entirely on direct interactions between predators and prey. Models mainly considered flows of biomass and energy. At present it is clear that these interactions can be mediated and modulated by infochemicals from many other species in the food web (Vos et al., 2001). One of the aims of ecoinformatics is to integrate such approaches. This could lead to an improved understanding of information processing in ecosystems at and between different levels of ecological organization. We review the role of infochemicals in this context.

### 1.1. Infochemical cues: reliability and ambiguity

A considerable body of knowledge has accumulated on how organisms use infochemicals to solve the problems of

finding food and avoiding predators. It is clear that chemical cues can be highly reliable sources of information. The scent of a predator may distinctly indicate predation risk (see Kats and Dill, 1998) while the scent of prey may clearly indicate the opportunity of a meal. However, chemical information can also be ambiguous, for a variety of reasons. Such ambiguity or noise may be as important in shaping feeding relations in food webs as the actual transfer of information. Below we show several ways in which chemical information can be indistinct.

For example, different species can send signals that are highly similar, and these may be perceived as identical to the receiver of this information. This results in infochemical crypsis. Both odour sources would then need to be 'inspected' by a receiver to ascertain the identity of each source.

*Infochemical mimicry* is a special type of crypsis in which the resemblance of odours confers a certain protection. In *Batesian infochemical mimicry* one species' odour resembles the odour of a second species that is well defended or inedible (see e.g. Augner and Bernays, 1998). The undefended species could obtain a certain degree of protection from smelling like a well defended species. In *Müllerian infochemical mimicry* the odours resemble each other, but each species is well defended. In this case the signal would be more 'honest' or reliable with respect to the defense level behind it. If several prey species would use a similar odour to signal inedibility, this resemblance could act as a form of protection because it would allow predators to learn more quickly and efficiently to avoid such prey.

Different species may vary a great deal in the quantity of volatiles they emit. A high quantity of some infochemicals could activate or even 'overwhelm' the sensory system of a receiver species to such an extent that infochemically less conspicuous species could 'hide' in its presence. This would be a case of *infochemical masking*.

In many cases a distinct signal consists of several volatile compounds in a precise ratio. If different co-occurring species share some of these compounds in the volatile blends they emit, such precise ratios may be lost in the volatile mixture. Under such *infochemical mixing* signals could lose their distinct character. For example, a mixture of the sex pheromones of two different species may lose its attractive properties (Potting et al., 1999).

Some compounds seem to play a variety of roles in ecosystems. For example, in marine food webs the volatile compound dimethyl sulphide (DMS) and its precursor dimethyl sulphoniopropionate (DMSP) play important roles in a number of interactions including anti-feeding effects and the attraction of predacious seabirds such as petrels. DMS is released by a variety of marine organisms, including pelagic algae and bacteria, coral reefs, benthic diatoms and *Spartina* macrophytes in salt marshes. Grazing by herbivorous zooplankton and the presence of algal and bacterial species that contain DMSP-lyase all contribute to the release of DMS into sea water, and eventually into the atmosphere, where it has profound effects on global climate processes. DMS reflects the presence of a complex web of interactions. It often does not distinctly signal the presence of a particular species. However, it is a reliable source of information on 'marine biological

activity', which can be a sufficient cue to the presence of 'food' for a variety of marine species, such as procellariiform seabirds (Nevitt et al., 1995; Steinke et al., 2002, also see the marine section further below).

The ecological effects of infochemical ambiguity could vary with the biology of the receiver species. A generalist predator or omnivore would hardly be bothered by such ambiguity because it could simply include the different sender species in its diet. In contrast, a specialist consumer would be significantly bothered by nonprey species that emit volatile blends resembling prey-released mixtures of infochemicals. Nonprey species could cause specialist consumers to waste valuable time (Vos et al., 2001). It is possible that generalist and specialist consumers sense infochemicals in nearly identical ways, while they may have evolved different ways to process the available information (Smid et al., 2002). The available evidence points at well developed learning abilities in generalists (e.g. Geervliet et al., 1998) versus high-speed neural signalling and information processing in specialists (Bernays, 1998; Bernays and Funk, 1999). Infochemical mimicry implies associational defences between different prey species that will thus experience a dilution of attack by specialist predators (Launchbaugh and Provenza, 1993; Vos et al., 2001).

Prey are not the only source of chemical information. Predator-released infochemicals are used by a great variety of both aquatic and terrestrial prey species to tune their defences to the risk of predation (Kats and Dill, 1998; Tollrian and Harvell, 1999). Such induced defences, which are a type of phenotypic plasticity, may involve the formation of spines, thorns, helmets or other defensive morphologies, as well as defensive behaviours, such as refuge use, diel migrations, reduced activity levels, and induced life history changes, such as reproduction at an early age and at a reduced size.

Organisms often have one single response to infochemical cues from a variety of similar sender species. For example, behavioural defences and life history changes can be induced in *Daphnia* waterfleas by 'fish-water' from a variety of freshwater fish species. Similarly, algae can respond with the formation of morphological defences to water conditioned by different species of herbivorous zooplankton, such as daphnids and rotifers (Verschoor et al., in press).

Infochemical use and the associated phenotypic plasticity in individuals throughout aquatic and terrestrial food webs have tremendous implications for our understanding of direct and indirect interactions in complex communities (Werner and Peacor, 2003; Bolker et al., 2003).

In this review we clarify this role of infochemicals and phenotypic plasticity in multitrophic communities. To do so, we discuss (1) how individuals are linked to higher levels of ecological organization through feeding links in food webs, (2) how these feeding links are modulated by infochemicals in exemplary marine, terrestrial and freshwater systems, (3) the promises and risks of applying infochemicals in ecosystem management and (4) how classical modelling and novel ecological informatics approaches could contribute to an integration of existing information from theoretical, laboratory and field studies on the biotic and abiotic mechanisms that structure terrestrial and aquatic food webs.

## 1.2. Linking levels of organization: from individuals to food webs

Individuals have intricately and flexibly integrated physiologies, behaviours and morphologies. These allow them to function in environments shaped by abiotic conditions, the food web and the information network around them.

Laboratory studies have resulted in an extensive body of knowledge at the individual level, especially in terrestrial plant–insect communities. The larger part of animal biodiversity on the planet consists of insect communities living on terrestrial plants. Laboratory bio-tests have shown how insects are attracted to infochemicals related to prey, potential mates or mutualists and how they are repelled by strong competitors and predators. Similar studies have been performed using aquatic model systems (see reviews by Zimmer and Butman, 2000; Van Donk, in press). Infochemical research in terrestrial ecology has had a strong focus on herbivore-induced volatile emissions by plants and the responses thereon of the third trophic level. Such indirect defences are thus well-studied in terrestrial systems. In contrast, infochemical research in aquatic systems developed mainly through work on predator avoidance and other direct induced defences against consumers. These differences are reflected in the examples discussed further below.

Although it is harder to observe animals in lakes or at the sea bottom and measure infochemicals in situ (but see Zimmer et al., 1999), it is relatively easy to take water samples from the field and to test these for infochemical activity in laboratory bio-tests. Thus it is possible to relate the defensive responses of prey species at lower trophic levels to the actual presence and density of consumers at higher trophic levels in the food web.

It is a largely unresolved question how much biological realism and complexity needs to be incorporated in food web models to allow accurate forecasting of food web patterns and processes. The current generation of descriptive and quantitative food web models does a great job at generating accurate patterns, as long as conditions do not change. However, especially when a novel factor or environmental catastrophe perturbs the system, the current lack of mechanistic underpinning of food web models still precludes effective forecasting. Nonetheless, these models are indispensable as heuristic tools. They generate essential questions and hypotheses that need to be addressed to arrive at a more predictive role for food web models. These could be used in dealing with species invasions, major pollution incidents and species losses from already overexploited ecosystems.

The simplest ordinary differential equation models made by ecologists to understand patterns at the food web level treat individuals as part of a community of well-mixed gas molecules, i.e. behavioural characteristics and memory of organisms are ignored. Predators are treated as if bumping into prey at a certain rate and to convert these into predator biomass with a certain conversion efficiency. Thus all individual level variation and plasticity are reduced to population level averages. Interestingly, when variation and heterogeneity are introduced in such models, they may or may not show qualitatively different behaviour, depending on the particular model and type of variation incorporated. It is an

important question which individual level phenomena generate important emergent patterns and processes at higher levels of ecological organization.

It is clear that individual level mechanisms and behaviours have important effects on birth, immigration, emigration and death, which are the key factors determining local densities and dynamics of populations. These populations and the predator–prey relations among them define the food web nodes and feeding links in food webs we aim to understand. In food web models such feeding links are represented by functional responses, which describe how the intake rates of predators change with prey density. The shape of such functional response curves has major effects at higher levels of organization, for example on population stability (Case, 2000). Functional responses change when animals are confused, learn, use refuges or territories and when they change their diet during ontogeny or when the relative abundance of different prey species changes. All of these processes are affected, marked or mediated by infochemicals. The same holds true for processes of immigration and emigration. Even in marine systems, where strong currents cause dispersal, the actual settlement of individuals is often mediated by infochemical cues (Marinelli and Woodin, 2002). Some individual level processes such as prey switching must obviously have effects on the functioning of food webs. Switching between prey types implies the turning on and off of feeding links in the food web.

In summary, the signal-to-noise ratio of chemical information is important in determining how individual level mechanisms and behaviours generate effects at the levels of populations and communities.

## 2. Three examples from different habitats

### 2.1. Infochemicals and interactions in terrestrial insect–plant communities

In a seminal paper Price et al. (1980) pointed at the importance of multitrophic context and information transfer for our understanding of the interactions among plants, insect herbivores and their natural enemies such as insect carnivores and parasitoid wasps. Plants are capable of emitting infochemicals in much larger quantities than the insect herbivores infesting them. Natural selection may have acted on plants to emit highly detectable volatile information in response to herbivore attack to recruit the natural enemies of their herbivores. In contrast, herbivores are most likely under strong selection pressure to be as inconspicuous as possible to their natural enemies (Vet et al., 1991; Vet and Dicke, 1992; Dicke and Vet, 1999).

Plant species do vary considerably in the reliability and specificity of the volatile information they release (Dicke and Vet, 1999). Some plants release novel volatile compounds after herbivory, while other species only show quantitative changes in the ratios of compounds comprising the volatile blend (Dicke and Vet, 1999; Vet, 1999). Plants also release volatiles when they are not infested with herbivores, for example at high temperatures (Sharkey and Singaas, 1995). Abiotic factors such as water stress and reduced light have major effects on

the quantity of volatiles emitted, with the former increasing and the latter decreasing volatile release (Paré and Tumlinson, 1996). Some volatile compounds are shared between the infochemical blends from plant species as different as lima bean, apple, cucumber, corn and cotton (Paré and Tumlinson, 1996 and references therein).

Recently, research in this field has focused on the information value of volatiles released by plants infested with multiple herbivore species. Previous research had shown that plants may selectively attract parasitoid species, when infested with a single herbivore species (De Moraes et al., 1998). However, such a simple situation is not the norm in the field, where the majority of plant species will be attacked by a complex of herbivore species (Lawton and Schröder, 1978; Futuyama and Gould, 1979; Futuyama, 1983; Vos et al., 2001). This implies that natural enemies will often have to choose between plants infested with a complex of host and nonhost herbivores versus plants infested with nonhosts only (Vos et al., 2001). The parasitoid *Cotesia glomerata* showed to have difficulties discriminating between these types of infestation in dual-choice flight experiments (Vos et al., 2001). This parasitoid needed to land on and inspect infested leaves in order to discriminate between those with and without host caterpillars. Sampling in *Brassica oleracea* fields showed that all plants were herbivore-infested, with 73% of the plants containing between two and seven herbivore species (Vos et al., 2001). Taken together, these results suggest that natural enemies may waste considerable amounts of time on nonprey when herbivore diversity is high.

A dynamic model was used to evaluate the potential consequences of such wasted time for the dynamics of communities of increasing species richness. The model analysis showed that diversity promoted parasitoid species persistence, because it damped violent population fluctuations and thus reduced the risk of local parasitoid extinctions (Vos et al., 2001). However, when parasitoids wasted too much time on plants and leaves with nonhost species this could lead to the decline of such parasitoid populations (Vos et al., 2001). The take-home message is that seemingly irrelevant (non-prey) species may be very important in shaping food web interactions and community dynamics (Vos, 2001). In this example every single species contributed to the probabilities of persistence and extinction of every other species in the community. Such effects have been overlooked in major ecological biodiversity debates on the ‘redundancy’ of species in complex food webs (Vos et al., 2001).

Several studies have shown that different parasitoid species are confused to different degrees by the presence of nonhost herbivores and by plant species that never contain hosts. For example, the parasitoid *Cotesia rubecula* is innately highly efficient in the presence of ‘irrelevant’ potato plants, while *C. glomerata* needs to learn to ignore these (Perfecto and Vet, 2003). However, *C. rubecula* is attracted to nonhost caterpillars on *Brassica* plants (Van Poecke et al., 2003), just like the parasitoid species *C. glomerata*. Interestingly, the parasitoid species *Cotesia plutellae* does discriminate between host- and nonhost infested *Brassica* plants (Shiojiri et al., 2000). This implies that this parasitoid is able to perceive and process minor infochemical differences in the volatile blends of these plants, which are not used by the other parasitoid species.

*Brassica* plants seem to emit quantitatively different volatile blends for different types of herbivory, such as leaf chewing versus piercing, but to provide less distinct information on herbivore species identity (Van Poecke et al., 2003).

Interactions mediated by infochemicals related to nonprey have also been studied in a parallel model system, using herbivorous spider mites and predatory mites on *Brassica* or Lima bean plants. These studies have focused on evolutionary aspects (Shimoda and Dicke, 2000), foraging success (Dicke et al., 2003), information processing (De Boer and Dicke, 2005) and learning (De Boer et al., 2005). It is important to understand how predators deal with nonprey, because these constitute the majority of species in food webs (from a predator's point of view).

### 2.1.1. Infochemicals and agro-ecosystem management: promises and caveats

Pheromones already play a role in orchard pest management. Especially sex pheromone traps are used to selectively remove pest species (Suckling, 2000), without the harmful side effects we see when using pesticides. Ideas exist to attract natural enemies to crops using carnivore or parasitoid sex pheromones or by spraying plants with plant hormones such as jasmonate that cause plants to emit volatiles attractive to natural enemies. This would lure parasitoids and carnivores from the surrounding area into fields with plants that are not yet infested with herbivores. Such a scenario would be attractive from the plants' point of view, but could be problematic for the natural enemies involved. Since all the plants in such a sprayed field are 'crying for help', natural enemies could waste a lot of time searching on plants without herbivores. Most insect parasitoid and carnivore species are relatively short-lived and a large part of the attracted natural enemy population could die off before having done much good in terms of suppressing herbivores. Indiscriminate spraying of crops with elicitors such as jasmonate could thus turn these fields into population sinks for natural enemies, leaving both the crop and its surroundings devoid of their beneficial effects (Vos, unpublished model analysis based on Vos et al., 2001). One way out of this problem would be to select for plants that 'cry loudly' when attacked by herbivores, and to use these in agricultural settings. Such an approach has also been advocated by Rasmann et al. (2005), who discovered variation among maize plants in their ability to attract a beneficial nematode that attacks corn rootworms. The nematodes are attracted to the insect-induced belowground plant signal (*E*)- $\beta$ -caryophyllene. If plants in crops release such attractants in adequate amounts, spraying with elicitors such as jasmonates would not be necessary. Another possibility that could be used as a complementary measure to spraying jasmonates would be to help increase the lifespan of beneficial carnivores and parasitoids. This could prevent their local extinction (Vos, unpublished model analysis based on Vos et al., 2001). As the far majority of carnivores also require nectar or pollen sources (Wäckers and van Rijn, 2005), this could be achieved by ensuring that these food supplements are made available within the agro-ecosystem. Nectar and pollen can be provided in various ways, including the use of commercially available food sprays, enhancing (extra-) floral nectar production by the crop itself, or the use of flowering vegetation within or around

the field. Flowering field edges have proven to be effective in providing nectar and pollen as an alternative food source for parasitoids and predators. Such edges could be part of landscape management to achieve linkages and integration between natural habitat and agricultural areas and to promote functional biodiversity.

Here modelling would be an indispensable tool to integrate existing knowledge and to identify knowledge gaps at different spatial scales and levels of ecological organization. Interdisciplinary projects that use modelling to integrate laboratory- and field-based knowledge initially typically face large knowledge gaps, especially when attempts are made to link processes at different levels of organization. Preliminary modelling typically reveals that existing data are of limited value in answering new questions and that novel types of data need to be collected. As such research projects mature, and appropriate data accumulate, models develop from heuristic tools (that identify knowledge gaps and generate hypotheses) into predictive tools for ecosystem management.

An interesting individual based modeling framework was developed by Potting et al. (2005). This framework allows a lot of detail and freedom in modelling behavioural decisions by insects in agro-ecosystems, for example under different scenarios for vegetation diversification or for different sizes of plant patches in the field (Bukovinsky et al., 2005). The framework is flexible in allowing an evaluation of different biological control scenarios and push-pull strategies to induce desired migratory responses in herbivore pest species.

### 2.2. Infochemicals and interactions in the pelagic of freshwater lakes

Algae, herbivorous zooplankton and fish are major ecological players in the pelagic of freshwater lakes. In these lakes dominant zooplankton species such as *Daphnia* waterfleas constitute an important link between algae and higher trophic levels. Both *Daphnia* and zooplanktivorous fish such as perch have high feeding rates and a clear potential to exert strong top-down control on lower trophic levels. The effects of predator-released infochemicals have been well studied in such systems. Here we review the main results to exemplify how information transfer affects the link between individual and population level phenomena. This linkage needs elucidation to further fundamental ecological insight and has implications for its application in the management of lakes.

Zooplanktivorous perch are visually hunting fish. This implies that daphnids are most vulnerable to these predators under good light conditions, i.e. during daytime, in the upper water layers of lakes. Many species and clones of *Daphnia* respond to a high concentration of fish-released kairomones (see for infochemical terminology Dicke and Sabelis, 1988) with diel vertical migrations. Fish-released infochemicals modulate the daphnids' phototactic behaviour such that they spend the day in deep dark cold water layers where algal food levels are low and the night in the warm upper water layers where algal food is abundant (Ringelberg, 1999; Vos et al., 2002). This predator avoidance strategy is most

effective in deep lakes. In shallow lakes fish-induced life history changes, such as a reduced size at first reproduction (SFR) may act as the daphnids' last line of defence (Hülsmann, 2001). A smaller SFR may allow daphnids to reproduce before they are eaten by fish, as a smaller daphnid is less visible to fish searching for prey. Different clones of a single *Daphnia* species may show distinct responses to fish kairomones. For example, Boersma et al. (1998) measured *Daphnia magna* life history changes and phototactic behaviour in response to fish-water, using 16 clones. Most of the clones showed a response in one to four traits. Five clones showed a smaller SFR. While four other clones showed a reduced age at first reproduction. Eight clones showed a primary phototactic response to fish kairomones. Of these, three clones showed this response in combination with a reduced SFR, while three clones exhibited a change in phototactic behaviour as the only response (Boersma et al., 1998).

To study the relative effects of diel vertical migrations and a reduced SFR on *Daphnia* population dynamics under heavy fish predation Vos et al. (2002) used an individual-based demographic model within the OSIRIS modelling framework (see Mooij and Boersma, 1996). This model combines field data with laboratory results on the life history effects of temperature, food and fish-released infochemicals. The model keeps track of the size, fecundity and instar duration of individual daphnids under field conditions and calculates potential population growth rates from these. By comparing this potential population growth rate to the observed population growth rate in the lake, predation mortality rate in the field is estimated. The effects of diel vertical migration are incorporated by modelling overall instar duration as the weighted average of time spent in the upper and lower water layers, which differ in temperature and predation pressure. Using this model Vos et al. compared historical lake data for daphnids that had responded to an increasing fish predation pressure with both diel vertical migration (DVM) and a reduced SFR, with four alternative scenarios. In these scenarios daphnids (i) always stayed in the upper water layers, without a change in SFR, (ii) only used DVM, (iii) only used a reduced SFR, or (iv) always stayed down in the deeper water layers, without a change in SFR. The model analysis showed that the *Daphnia* population decreased exponentially during the peak of predation pressure by fish, in this case during the last week of June. DVM, the behavioural response to fish kairomones, clearly slowed down the *Daphnia* population decline, while the effect of a reduced SFR was marginal. Interestingly, in the scenario where daphnids stayed deep down in the lake, a population decline was prevented altogether. This scenario had only been used as a 'control' that had been lacking in all previous theoretical studies. These had focused on the adaptive value of DVM versus 'staying up'. The model result suggested that a 'staying down' strategy could confer significant fitness benefits in periods of peak predation pressure. This raised the question why such a strategy would not be more prevalent in nature. Interestingly, a subsequent literature search on *Daphnia* depth selection behaviour revealed that a staying down response at high concentrations of fish infochemicals has been observed in a variety of *Daphnia* species and clones, both in the laboratory and in stratified lakes. It was interesting to experience that a model could

correctly predict a pattern in nature that we had been previously unaware of.

This research had been part of an EU-funded project called SNIFFS, which aimed to elucidate the structuring role of infochemicals in freshwater food webs. One aspect of the project was to evaluate the potential use of infochemicals in lake ecosystem management. At present the chemical identity of both the 'fish-factor' and the 'Daphnia-factor' are still unknown. However, models such as the one mentioned above could be used to evaluate infochemical biomaniipulation scenarios. It would be worth while to study scenarios in which fish cues are added to a lake early on in the year. *Daphnia* defences would then be fully developed by the time young-of-the-year fish reach the size at which they hunt for daphnids. This could possibly prevent a large biomass of such planktivorous fish from developing. A larger *Daphnia* population could then graze down algal populations to a low level. The resulting clear water phases could be helpful in projects that aim to restore lakes to a clear water state. It would be advisable to test such scenarios theoretically using more complex food web models, and experimentally at a smaller scale, before perturbing lakes in the field with large quantities of infochemicals. These could have strong unanticipated indirect effects on the functioning of the food web.

Preliminary theoretical and experimental laboratory studies on freshwater food chains have been performed using algae, herbivorous rotifers and carnivorous rotifers. Rotifers are small and have short life cycles. These are ideal characteristics for studies of small laboratory food webs. The algal strains used in these studies differ in their defensive responses to herbivorous zooplankton. Some stay unicellular, others form colonies of different sizes, depending on the concentration of herbivore-released infochemicals (Hessen and Van Donk, 1993). Theoretical studies show different population level effects of flexible versus no responses to information on the presence of consumers. These different response scenarios lead to different patterns of trophic structure, i.e. to a different distribution of biomass over trophic levels (Vos et al., 2004b), to differences in resilience following a perturbation of the system (Vos et al., 2006) and result in different conditions for population stability and persistence (Vos et al., 2004a). Population dynamics experiments using bitrophic and tritrophic planktonic food chains showed large population fluctuations and occasional extinctions when algae did not respond to herbivore infochemicals, and a monotonic approach towards a stable equilibrium when algae did use herbivory-related infochemicals to induce colonies (Verschoor et al., 2004).

In summary, infochemicals play a major ecological role in induced defences and predator avoidance behaviour in freshwater food chains. Model studies show that these ecological mechanisms generate pronounced effects at the community level.

### 2.3. Infochemicals and interactions in marine communities

Infochemicals mediate predation, mating, aggregation, habitat selection and induced defences in marine communities

(Zimmer and Butman, 2000 and references therein). For example, Zimmer et al. (1999) measured infochemical production, release and transport in marine habitats and identified the role of amino acids as signal molecules that mediated the searching behaviour and foraging success of *Ilyanassa* mud snails. These authors measured rates of advection and turbulent mixing, and estimated shear velocities and roughness Reynolds numbers in the benthic boundary layer. An online computerised microprobe system measured the spatial distribution of signal molecules. The particular field site populated by mud snails was shown to more easily transmit stronger chemical signals over greater distances than other estuarine and ocean habitats. Injured prey, such as fiddler crabs and hard clams, released significantly attractive amounts of dissolved free amino acids into the sea water. Mud snails did not respond to intact clams and crabs, but were attracted to artificial mixtures of amino acids. The physical transport of infochemicals was found to be more important for mud snail attraction than the molecular properties of specific amino acids (Zimmer et al., 1999). Similarly, blue crabs require infochemicals (also amino acids) to be transported at speeds above 1 cm/s to ensure successful prey location (Finelli et al., 2000, see also Keller et al., 2003; Moore et al., 1994).

These examples show how marine feeding relations can be mediated by both infochemicals and abiotic forces. Live injured prey commonly occur in soft bottom benthic communities as many predator species engage in sublethal predation, thus only consuming small parts of their prey's bodies. It is interesting that amino acids can be marine signalling molecules. These (info-)chemicals are nutrients at the same time. Thus they play a role in both the food web and in the marine information network. Amino acids are likely to constitute a reliable source of information on the presence of injured prey, and perhaps on food quality as well.

Relatively little is known about the chemical ecology of signalling molecules in marine systems. However, marine prey are as likely to weigh their food and oxygen needs against predation risk as organisms in any other habitat. Marine copepods are well known to exhibit fish-induced diel vertical migrations. It is likely that perceived predation risk also affects behavioural defences such as refuge use in coral reefs and burial depths of benthic species in soft bottom systems. Risk-sensitive burial in benthic communities has implications for particle mixing and bio-irrigation with major consequences for biogeochemical processes and the distribution of microbes and meiofauna in sediments (Herman et al., 1999).

An interesting compound, dimethyl sulphide (DMS) seems to be important (i) in the context of anti-feeding through its relation with acrylate production (Wolfe, 2000), (ii) as an attractant signalling molecule to bird species at higher trophic levels (Nevitt et al., 1995, Nevitt, 2000), (iii) for its effects on cloud formation and climate processes and thus its role in the global sulphur cycle (Lovelock et al., 1972; Charlson et al., 1987; Giordano et al., 2005).

DMS occurs in a wide variety of both aquatic and terrestrial plant species. Land-based chemical ecologists may know it for its contribution to the aroma of Syrah and Grenache Noir

wines, in which DMS may significantly enhance fruity, truffle and black olive notes (Segurel et al., 2004). In marine systems, DMS contributes to the smell of the sea. It is released when its precursor dimethyl sulphoniopropionate (DMSP, an osmolyte) is degraded by bacterial and algal DMSP-lyase. DMSP enters the sea water when algae and bacteria are damaged by viruses or herbivorous zooplankton such as copepods and protists (Steinke et al., 2002 and references therein). Dramatic pulses of DMS production may occur when blooms of the haptophytes *Emiliania huxleyi* or *Phaeocystis pouchetti* start to decline (Nevitt, 2000 and references therein). Several authors have suggested that DMS could facilitate indirect algal defences through multitrophic interactions, similar to those occurring in terrestrial systems, where herbivore-infested plants emit volatiles that attract the carnivores of these herbivores (see Wolfe, 2000; Steinke et al., 2002; Van Donk, in press). Steinke et al. (2002) suggested that volatile infochemicals such as DMS that are released during herbivory by microzooplankton on phytoplankton, can be exploited by mesozooplankton copepods, thus enabling them to more efficiently graze on microzooplankton. This would indirectly decrease the grazing pressure on phytoplankton. Attraction of foraging seabirds to areas with a high DMS concentration could have further top-down effects on the local marine food chain (Van Donk, in press).

However, this picture of a putative marine indirect defense is simplified and still seems a bit controversial. Attraction of copepods to DMS is suggested, but not shown in Steinke et al. (2002). DMS is also produced when krill is feeding, and some of the attracted seabirds, such as cape petrels, feed almost exclusively on this prey (Soave et al., 1996). However, the entire complex of seabird species attracted to such feeding sites has a considerably wider diet breadth, which includes zooplankton, squid and fish. It is not straightforward whether the resulting complex, multitrophic food web interactions actually protect the algae from grazing. Moreover, pulses of DMS do not only occur in foci of planktonic activity in the open oceans. They are also released by benthic diatoms in microbial mats (Jonkers et al., 1998), saltmarsh macrophytes (Dacey et al., 1987), coral reefs (Broadbent and Jones, 2004) and benthic flatworms in mudflats (Van Bergeijk and Stal, 2001). The relative roles of bacteria and phytoplankton in the production of DMS remain unclear.

The volatile nature of DMS in sea water causes it to enter the atmosphere, where it after oxidation acts as a source of condensation nuclei in the process of cloud formation. Clouds reflect both incoming solar radiation and outgoing heat, but the net result is a cooling effect. DMS is thus important in evaluations of potential positive and negative feedbacks in scenarios for global warming and climate change. Most of the biogenic DMS in the atmosphere is ocean-derived (see Gondwe et al., 2003).

A number of Earth-System modelling approaches have included DMS and its role in the atmosphere. For example, Bopp et al. (2003) coupled an atmosphere-ocean general circulation model to a marine biogeochemical model to evaluate the consequences of increased greenhouse gases (CO<sub>2</sub>), and temperature, on global DMS flux to the atmosphere. Their model study predicted a small increase in DMS flux, and thus a negative feedback on global warming. However, the estimated large spatial heterogeneities in air-sea DMS fluxes

could significantly affect regional temperature and rainfall patterns (Bopp et al., 2003).

### 3. Discussion

Predators use prey-released and prey-associated infochemicals to find their victims, while prey employ predator-released infochemicals to avoid their consumers. Thus signalling molecules mediate ecological games of hide-and-seek in marine, terrestrial and freshwater food webs. The examples from these different habitats showed that (i) information transfer can jump trophic levels, as in the case of herbivore-induced plant volatiles attracting carnivores to their herbivorous prey, (ii) single compounds such as dimethyl sulphide can be involved in highly complex and intricate webs of multitrophic interactions, with ecological and physical effects at spatial scales ranging from damaged algal cells to the global atmosphere, (iii) modelling is essential in integrating knowledge from the field and laboratory and is crucial to making accurate predictions for ecology and ecosystem management, (iv) much can be done using ordinary differential equations, but individual based and spatially explicit models are essential in evaluations of the consequences of individual level behaviours and phenomena at higher levels of ecological organization, (v) complex links and interactions exist between food webs and their infochemical environments, (vi) abiotic factors such as temperature, light intensity, water stress and current velocities interact with infochemicals in shaping responses in individual organisms. Such abiotic factors also have effects on the production, diffusion and physical behaviour of infochemicals.

In order to further develop theory on the role of infochemicals in shaping food webs, one would need to study how the concentration of various infochemicals affects the ecological mechanisms that are known to affect population- and community-level processes. For example, observations could have shown that the ecological mechanism of density-dependence through refuge use or territoriality is important in a certain system, for example a coral reef. Then studies of how infochemical concentrations shape such refuge use or territoriality could help to accurately and mechanistically incorporate this knowledge in community-level models.

Infochemicals could mediate local species abundances through effects on immigration and emigration rates. Functional responses, which are crucial to population level processes, will be affected by the relative abilities of predator and prey species to use chemical information on each other's presence. Generalists and specialists may differ significantly in their learning ability and in the neurological speed with which they process environmental information.

Chemical ecology will continue to identify the active infochemicals in volatile blends and technological advances will allow online field measurements of infochemical concentrations in the near future. This opens doors to combined studies of the spatio-temporal dynamics of both populations and infochemicals. Such studies will be essential for a deeper understanding of community level patterns and processes.

Food web research has traditionally focused on food web level phenomena such as compartmentalization, connectivi-

ty, numbers of species and interaction strengths. These have been well described. The next step is to identify and understand the mechanisms that cause these phenomena.

Linking ecological scales and information flows from the levels of cells to ecosystems requires advanced techniques for computation and data assimilation. Novel approaches in the field of ecological informatics will greatly contribute to such synthesis. Multi-level insight in the functioning of ecosystems will enhance our ability to make well-informed decisions in ecosystem management.

Here we would like to advocate a strong ecological component in the field of ecological informatics. Integrating computational and empirical approaches is a scientific as well as a social challenge. At present, empirical ecological work and computation techniques seem to be arts with rather separate audiences. We hope that the field of ecological informatics will bring together people, insights and perspectives from ecology and the computational sciences. We feel that much progress can be made by bridging their views and interests.

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