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REVIEW

The chemical ecology of copepods

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An increasing number of studies show the importance of chemical interactions in the aquatic environment. Our understanding of the role of chemical cues and signals in larger crustaceans has advanced in the last decades. However, for copepods, the most abundant metazoan zooplankton and essential for the functioning of the marine food web, much is still unknown. We synthesize current knowledge about chemical ecology of copepods including foraging, survival and reproduction. We also compile information on the sensory apparatus and new analytical approaches that may facilitate the identification of signal molecules. The review illustrates the importance of chemical interactions in many aspects of copepod ecology and identifies gaps in our knowledge, such as the lack of identified infochemicals and electrophysiological studies to confirm the function of sensory structures. We suggest approaches that are likely to further our understanding of the role of chemical interactions in the pelagic ecosystem.

KEYWORDS: copepods; chemical ecology; pheromones; chemosensation; mate finding; kairomones; host finding; metabolomics

INTRODUCTION

Copepods are present in most aquatic habitats, ranging from the waterbodies of Bromelia leaves over ground water reservoirs and benthic habitats to the vast three-dimensional space of lakes and oceans. They constitute the most important link between pelagic primary producers and higher trophic levels in marine food webs (Turner, 2004) and contribute to the cycling of elements in the oceans. Copepods belong to diverse feeding guilds and include grazers, detritivores, omnivores, carnivores, as well as parasitic forms. Most species have limited visual capabilities and are often restricted to chemosensory and hydro-mechanical information to perceive their surroundings (Folt and Goldman, 1981; Heuch *et al.*, 2007). Male copepods for example successfully locate females (Bagoien and Kjørboe, 2005; Yen and Lasley, 2010) and food in the absence of visible light (Stearns, 1986), although there are exceptions where copepods localize prey visually (Gophen and Harris, 1981).

The importance of chemical signals is well established in most organisms—including bacteria, algae, yeast, vascular plants, invertebrates and mammals (Wyatt, 2009). Chemical ecology refers to the study of chemically mediated interactions between organisms. The chemistry is arguably best understood for terrestrial insects, and knowledge is much less developed for aquatic organisms. Larger aquatic crustaceans are an exception. Decapods have served as a model system in aquatic chemical ecology and neurophysiology for almost half a century, and the role of chemoreception in foraging and reproduction is well established. A variety of small primary metabolites like free amino acids and derivatized nucleobases act as feeding attractants in decapods (reviewed in Breithaupt, 2011). Other crustaceans are known to use peptides in intraspecific signalling. Peptide signals are, for example, involved in gregarious settling in cirripedes and larval release in decapods (reviewed by Rittschof and Cohen, 2004). The structure of the first crustacean sex pheromone, uridine diphosphate was only recently determined (Hardege *et al.*, 2011). Detailed knowledge about the chemical composition of cues and signals in smaller crustaceans like copepods is however still scarce.

In addition to mediating resource acquisition and mate finding, chemical signals have indirect structuring effects on ecosystems. Predator-derived cues can for example intimidate prey in ways that influence food web dynamics. Copepods do react to predator cues and at the same time emit compounds that trigger defensive traits in their prey. Such non-consumptive effects are typically strong in aquatic food webs and may even supersede the effect of direct consumptive effects (Preisser *et al.*, 2005). We review the known examples of this below, even

though the relative importance of indirect effects in copepod ecology has yet to be explored. The ubiquitous importance of copepods in aquatic ecosystems and the evidence supporting their dependence on non-visual information suggests that we need to understand the chemical ecology of copepods, both intra- and inter-specific interactions, to comprehend the pelagic food web. In addition, copepods are now harvested and cultured for both human consumption and as feed in finfish aquaculture. This is a development that is likely to continue in the contemporary overexploited oceans. Parasitic copepods are further the most important health issue in salmon farms, where they cause decreased growth and higher mortality in both farmed fish and wild stocks. Understanding the chemical ecology of copepods may open up new possibilities in large-scale culturing of copepods as well as in pest management of parasitic copepods that depend on chemical cues to identify and localize hosts and mates.

In the following we review the research on copepod chemical ecology over the past 110 years. The review shows the importance of chemical cues for the main events in the life of a copepod. These include resource acquisition, mate finding, host finding and assessment of predation risk (Fig. 1). We have organized the review under these subheadings and compile knowledge of the chemosensory apparatus of copepods, and include an introduction to the physical and chemical constraints of chemical communication in the aquatic microenvironment. Most examples are from pelagic calanoid or cyclopoid copepods, reflecting the larger volume of research available from these groups, but we also include examples from benthic harpacticoids and parasitic life forms when present. We identify gaps of knowledge and suggest future directions to further our understanding of copepod chemical ecology.

Throughout the review we use the term “cues” for compounds that have (seemingly) not evolved specifically to convey information but allow an “individual to guide its future actions” (Smith and Harper, 2003; Thomas, 2010), whereas the term “signals” is reserved for evolved signal systems, e.g. when specific emitting or receiving organs are present. Signals within a species are also referred to as “pheromones” (Karlson and Lüscher, 1959).

COPEPOD SENSING

Most copepods have light receptors (naupliar eyes) that are not directly involved in mate finding and foraging, as these tasks are efficiently handled in the absence of light (Stearns, 1986; Dagg *et al.*, 1989). There are few exceptions where copepods evolved paired corneal lenses, e.g.

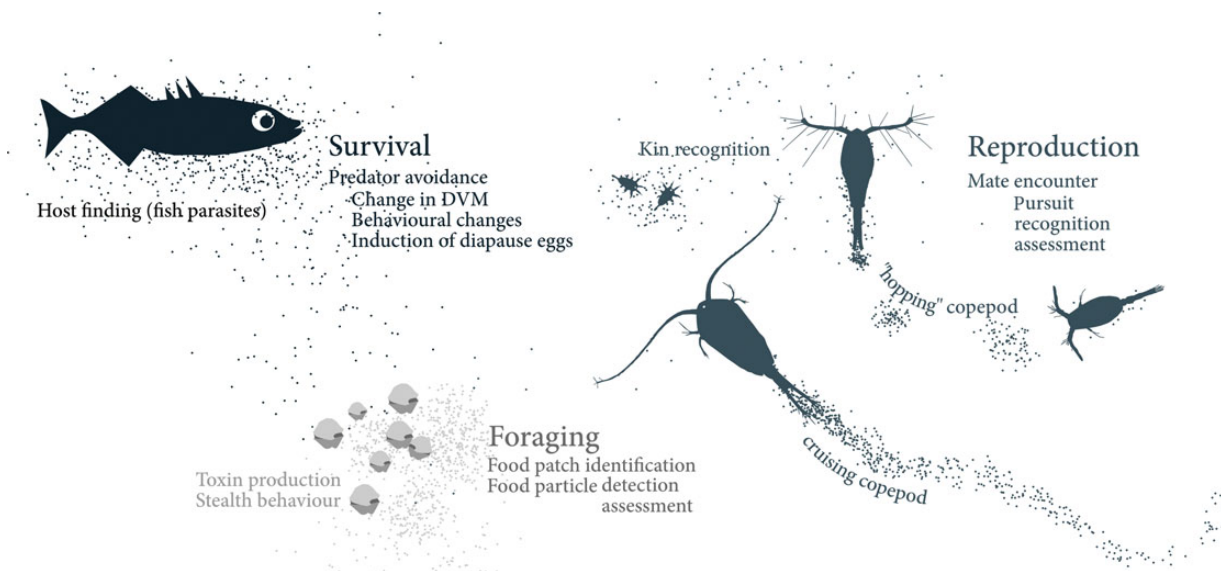


Fig. 1. Illustration of the involvement of chemical cues during the three main activities in the life of a copepod: foraging, survival and reproduction. Copepods find mates by navigating pheromone gradients, they localize food and resource patches from chemical cues. At the same time prey organisms, e.g. phytoplankton cells may sense exudates from the copepods and respond with grazer-induced responses to evade predation. Similarly, there is some evidence of copepods sensing the presence of predators and taking measures to avoid them based on chemosensory information.

Corycaeus anglicus that feed several times more efficiently in the presence of light, which suggests that *Corycaeus* spp. are visually oriented predators (Gophen and Harris, 1981) and other species that may use bioluminescence in mate recognition (Chae and Nishida, 2004). Light sensing is important for orientation and serves as a proximate cue for DVMs (Tranter *et al.*, 1981; Stearns and Forward, 1984). Rapid changes in light may also trigger predator avoidance behaviour (Buskey and Hartline, 2003). Copepods further detect hydro-mechanical and chemical stimuli using specialized organs located on the antennae, feeding appendages and body surface (e.g. Strickler and Bal, 1973; Huys and Boxshall, 1991). The shape and distribution of copepod sensilla is variable (Huys and Boxshall, 1991; Bradford-Grieve, 2002), but some general groups can be identified: (i) mechanosensory setae (i.e. Strickler and Bal, 1973; Yen *et al.*, 1992), (ii) chemosensory sensilla (i.e. Barrientos, 1980; Fields *et al.*, 2007) and (iii) bimodal sensilla with both mechano- and chemosensory properties (i.e. Weatherby *et al.*, 1994; Paffenhöfer and Loyd, 1999). In addition, chemosensory function has been suggested for other structures (d) such as the frontal organ, integumental organs and the cephalic dorsal hump (Elofsson, 1971; Fleminger, 1973; Nishida, 1989).

There are several different approaches that are best used in combination to discern the function and structure of chemical cues and their sensors. The use of chemical information in decision-making can be determined by behavioural experiments. These however provide little

insight about the sensors involved. A chemosensory function of certain sensory structures is mainly assigned by a comparison of the external morphological (using scanning electron and light microscopy) and the ultrastructure of sensory structures [using transmission electron microscopy (TEM)] with sensilla of known function in terrestrial arthropods and larger crustaceans. A more rigorous proof of the function of the sensory structures by physiological studies is often lacking, especially regarding chemosensory sensilla.

Mechanosensory setae

Mechanosensory setae come in different shapes (e.g. Huys and Boxshall, 1991; Bundy and Paffenhöfer, 1993). Typically, the outer morphology is in the shape of spines and they are “rigid, sclerotized structures” (Boxshall and Huys, 1998). Larger mechanosensory setae can be feathered and have a main shaft with many attached setules (fine bristles), e.g. the terminal setae in *Calanus finmarchicus*. However, setules can also be present on shorter setae. The setae are connected to the antennule via modified cuticular structures, which are typically called a “socket”. Mechanosensory setae are innervated by non-branching dendrites originating from one but normally two bipolar sensory cells. When the distal dendrites enter the lumen of the seta, they are typically surrounded by enveloping cells (Weatherby and Lenz, 2000). From the setae the distal dendrites pass through the tubular scolopale within the scolopale cell. This structure is embedded by sheath

cells and anchored by an anchor cell. The proximal dendrites then lead to the sensory cell body to which the axon is also connected (Strickler and Bal, 1973; Weatherby *et al.*, 1994; Weatherby and Lenz, 2000). In some species, e.g. *Undinula vulgaris*, the axons are myelinated (Lenz *et al.*, 2000; Buskey *et al.*, 2012), which decrease the reaction time of the copepod after sensing a potential threat (Lenz, 2012). The mechanosensory function has been confirmed by studies where the stimulation of the setae on the antennules by mechanical cues triggered neural responses (Yen *et al.*, 1992; Lenz and Yen, 1993; Fields *et al.*, 2002).

Chemosensory sensilla

Unimodal chemosensory sensilla are termed aesthetascs. In copepods, chemosensory function is attributed due to their morphological similarity with aesthetascs of larger crustaceans (i.e. Grünert and Ache, 1988) where there is confirmed electrophysiological evidence of their chemosensory function (Derby *et al.*, 1984). They are thin walled and have pores either at the tip (Barrientos, 1980) or throughout the cuticle (Hallberg *et al.*, 1997), which facilitates contact with chemical stimuli. Chemosensory sensilla can possess several (typically ~10–30) sensory cells that are each the origin of two dendritic outer structures (transformed cilia, Hallberg *et al.*, 1997), which can fill out the lumen of the sensilla (Gresty *et al.*, 1993; Lenz *et al.*, 1996). In addition to the antennal chemosensory sensilla, chemosensors are also present on the feeding appendages. Brush- and worm-like setae have been identified on the feeding appendages of the calanoid family Scolecitrichidae (Nishida and Ohtsuka, 1997). Brush-like setae have open endings that contain a large number of cilia, while “worm-like” setae are characterized by a tapered tip. Brush- and worm-like setae have to date only been reported from some calanoid copepods (Ferrari and Markhaseva, 1996; Nishida and Ohtsuka, 1997). It has to be noted that neurophysiological studies on chemosensation in copepods are rare. However, for the salmon louse *Lepeophtheirus salmonis* an electrophysiological response was triggered when the antennules were in contact with fish extract (Fields *et al.*, 2007).

Bimodal sensilla

Several studies show the presence of bimodal sensilla with both mechano- and chemosensory characteristics. TEM studies with *Temora stylifera* (Paffenhöfer and Loyd, 1999) and *Pleuromamma xiphias* (Weatherby *et al.*, 1994) revealed ultrastructural features indicative of both sensory types. Similar setae are also present in insects and larger crustaceans (e.g. Altner *et al.*, 1983; Garm

et al., 2003). They are innervated by two types of sensory cells. The presence of scolopale (electron-dense microtubular filaments) in the inner enveloping cell, a large rootlet system and dense microtubule bundles indicate mechanosensory function of one type, while the putative chemosensory cells normally lack these features and resembles the ones found in chemosensory aesthetascs (Crouau, 1997; Hallberg and Skog, 2011). The bimodal sensilla also have an apical pore, which is believed to enable the direct contact with chemical cues (Doall *et al.*, 1998; Paffenhöfer and Loyd, 2000). In copepods, putative bimodal sensilla are found on cephalic appendages [maxillipede and the antenna (A2), Weissburg *et al.*, 1998; Paffenhöfer and Loyd, 1999], which suggests that they are involved in food evaluation. Bimodal sensilla are also found along the entire length of the antennule (Lenz *et al.*, 1996; Weatherby *et al.*, 1994).

Other potential chemosensory organs

A chemosensory function is often assumed when the ultrastructure reveals dendrites that extend into a finely branched ciliary region in close contact with the outside medium (Slifer, 1970), but often morphological similarities with known chemosensory sensilla are used to speculate about their function.

The integument of copepods is covered by different types of pit-sensilla, peg-sensilla, hair sensilla and spine-sensilla (Fleminger, 1973; Koomen, 1992; Koomen and von Vaupel-Klein, 1998), several of which are morphologically similar to chemosensory sensilla on the antennules (Fleminger, 1973; Gill, 1986; Ohtsuka and Mitsuzumi, 1990); however, their function has never confirmed by physiological studies.

Elofsson (Elofsson, 1971) described a putative chemosensory cephalic organ in four copepod species. It seems to be homologous to the organ of Bellonci and analogous to the X-organ, which is described as neurosecretory and chemosensory in other crustaceans (Elofsson and Lake, 1971). In copepods, the cephalic organ consists of three main functional units. The first one consists of two dendrites ending in two small setae on the frontal cephalosome (Elofsson, 1971; Gill, 1986), previously termed “frontal organ” (Park, 1966). The second unit is characterized by a few large dendrites, which are branched into several ciliary bundles, hence the resemblance with the organ of Bellonci (Elofsson, 1971). The third unit consists of a larger number of dendrites where the ciliary structure extends to the epidermis in the anterior end of the copepod (Elofsson, 1971). The dendrites in these units originate from sensory cells in the protocerebrum of the animal. The second unit is suspected to receive internal chemical stimuli, while the third unit is probably

detecting external chemical cues. In the parasitic copepod *Pachypygus gibber* the cephalic organ seems to play a role in host and sex detection by “atypical” males, which in contrast to the stationary males have a free-swimming phase (Hipeau-Jacquotte, 1986). The dendrites of the structure have direct contact to the surrounding water through cuticular pores and canals. Its presence in other species of copepods is, however, unclear.

Besides the cephalic organ described by Elofsson (Elofsson, 1971), Nishida (Nishida, 1989) described a “cephalic dorsal hump” on the cephalosome of *Paracalanus parvus*, which is only found in males. The author suggests that it is involved in chemosensory identification of potential partners due to the sexual dimorphism and morphological similarities with chemosensory structures. A comparable organ is, however, present in both sexes in two species of *Attheyella* spp. found in the tanks of bromeliads (Por and Hadel, 1986). Martin and Laverack (Martin and Laverack, 1992) provide an overview of the occurrence of a possible function of dorsal organs in various crustacean groups. Coherent evidence and especially physiological studies on these structures are, however, still lacking.

Spatial distribution of sensors and their function

Especially the antennules (A1) of copepods are covered by a large number of sensilla both of the mechanosensory and chemosensory type, typically in a trithek arrangement with two mechanosensory setae followed by a single chemosensory aesthetasc per segment (Yen, 1988; Huys and Boxshall, 1991; Bundy and Paffenhöfer, 1993; Ohtsuka and Huys, 2001). Towards the distal ends of the antennules chemosensory sensilla typically become less abundant (Huys and Boxshall, 1991; Lenz and Yen, 1993; Lenz *et al.*, 1996). However, this arrangement varies among segments and species (e.g. Barrientos, 1980; Huys and Boxshall, 1991). Similar to insects (e.g. Hansson, 1995; Hallberg *et al.*, 1997), copepod chemosensors also show sexual dimorphism. Males of several pelagic copepods have a quadrithek arrangement, with two unimodal chemosensory and two mechanosensory sensilla (Giesbrecht, 1892; Huys and Boxshall, 1991). The doubling of aesthetascs in males suggests an evolutionary adaptation to find mates in the pelagic, where males are generally the searching gender. This sexual dimorphism is so far only observed in copepod superfamilies that include pelagic species (Huys and Boxshall, 1991; Boxshall and Huys, 1998; Ohtsuka and Huys, 2001; Bradford-Grieve, 2002). Autoradiography of males revealed that exudates from *Calanus pacificus* females accumulate at the chemosensory aesthetascs on the antennules of the males (Griffiths and Frost, 1976), which

further supports the role of the antennal aesthetascs in mate finding.

Besides the antennules, all types of sensilla are also present especially on the antenna (A2) and the maxilliped (Friedman and Strickler, 1975; Friedman, 1980; Gill, 1986). Primarily bimodal sensilla with a dual chemo- and mechanosensory function and brush-like sensilla can be found on the maxillipeds (Nishida and Ohtsuka, 1997; Paffenhöfer and Loyd, 1999), which suggests a gustatory or taste equivalent function since copepods handle food items using these appendages, and sometimes reject particles after encounter, based on their size and often also based on their chemical signature (Donaghay and Small, 1979; Paffenhöfer and Van Sant, 1985; Vanderploeg and Paffenhöfer, 1985).

Pores and glandular structures

While copepod sensors have been extensively studied, the source of pheromones and other bioactive exudates in copepods is less known. Glandular structures are present in all body regions of copepods (compiled by Bell *et al.*, 2000). While the function and products of some glands like the labral glands (food processing, Arnaud *et al.*, 1988a,b), luminous glands and pores (production of luminescent secretion, Bowlby and Case, 1991), maxillary glands and nephrocytes (release of metabolic endproducts, Le Borgne, 1986) have been determined, the function and products for many of the other glandular structures are so far unknown. The prosome of copepods shows numerous integumental pores (Von Vaupel Klein, 1982; Mauchline, 1988a,b; Seifried and Dürbaum, 2000). Integumental glands have been found within proximity to such pores for example in the calanoid *Hemidiaptomus ingens* (Brunet *et al.*, 1991) as well as *Temora longicornis* (Bannister, 1993). The U-pore of the harparcticoid *Ectinosoma carnivore* is the source of mucus filaments (Seifried and Dürbaum, 2000). Pores have also been found in close proximity to the gonopore, the urosome and on the caudal rami (Cuoc and Defaye, 2011; Nishida and Nonomura, 2011) but their function is unknown. Shell glands are probably involved in the formation of the eggshells, but they also seem to release small amounts of compounds before and after egg-laying events (Barthélémy *et al.*, 2001). Østergard and Boxshall (Østergard and Boxshall, 2004) describe a glandular nuptial organ in females of the parasitic copepod family Chondracanthidae. They found that the much smaller males attach themselves to this organ, which might indicate a sex pheromone function. The authors however conclude that although this structure is seemingly excretory, it is probably not used for pheromone production but rather provide food for parasitic males. These previous examples

illustrate that the specific origin of copepod pheromones and other exudates is mostly unresolved.

THE PHYSICAL BOUNDARIES OF COPEPOD CHEMOSENSATION

Due to the nature of diffusion in aquatic environments distant chemical communication in plankton has a lower size limit. Using a simple model, Dusenbery and Snell (Dusenbery and Snell, 1995) showed that for chemical communication to have a positive effect on encounters with prey or mates an individual needs to have a minimum spherical radius of around 100 μm (reviewed in Lonsdale *et al.*, 1998). Otherwise, a pheromone trail will erode faster than it is laid out due to molecular diffusion. Small organisms could, however, still benefit from releasing attractants that increase the reaction distance, e.g. the use of sperm attractants from eggs in fertilization biology where the solute cloud around the egg offers a larger target than the egg. The dimensionless Péclet number (Pe) gives an indication to whether solute transport is dominated by molecular diffusion or convection.

$$Pe = L \times \frac{U}{D} \quad (1)$$

Where L is the length scale, U the velocity, and D the diffusion coefficient. Small copepods and early life stages (<100 μm) will have $Pe < 10$ and solute transport result from both convection and diffusion assuming that $D = 10^{-5} \text{ cm}^2 \text{ s}^{-1}$. They will experience water as more viscous compared with larger (>5 mm) copepods for which $Pe > 25\,000$ and solute transport dominated by convection. Most copepods live at intermediate Pe numbers and may even traverse from low to high during development from egg to adult copepods. Rapid movement may momentarily change the physical regime and help copepods to overcome the difficulties associated with feeding at low Reynolds numbers (Kiørboe *et al.*, 2009). Most prey of copepods have $Pe \ll 1$ and will consequently be surrounded by a local solute cloud that does not extend into chemical trails (Kiørboe, 2008a). Larger prey and aggregates are an exception. Encounter rate with prey scales to the squared detection distance (Box I), i.e. the distance at which a prey can be perceived. Adaptions that increase detection distance will consequently increase encounter rates exponentially (Kiørboe, 2008b), which suggest strong evolutionary drivers to increase reaction distance to resources and to decrease reaction distance to predators. The solute cloud around planktonic cells (Fig. 2) can theoretically also be detected from a distance. Work by Strickler (Strickler, 1982) and Moore *et al.* (Moore *et al.*, 1999) shows that the solute

Box I Encounter rates in the plankton

$$\beta = \pi R^2 v C$$

The encounter rate (β) for pelagic copepods scales to the squared reaction distance (R , the distance at which a prey can be perceived), the velocity of predator and prey $v = (v_{\text{prey}}^2 + v_{\text{predator}}^2)^{0.5}$ (Evans, 1989) as well as the concentration of prey C (Gerritsen and Strickler, 1977). The motility pattern, especially the rate of change of direction will modify this relationship (see Visser and Kiørboe, 2006 for details).

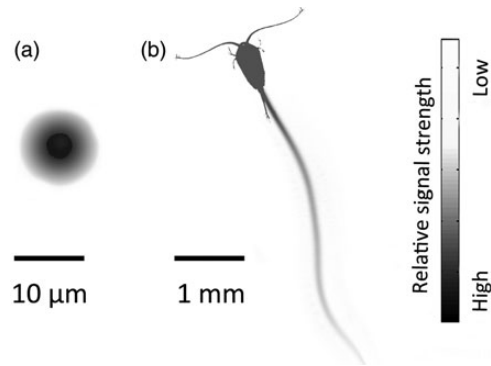


Fig. 2. (a) Illustration of the solute cloud around a cell and (b) an artistic interpretation of the pheromone trail in the wake of a pheromone-producing copepod. At the scale of a phytoplankton cell, solute transport is mainly due to diffusion, whereas copepods are often large enough to produce scented trails.

cloud elongates in copepod feeding currents to reach the sensory apparatus earlier. This is also supported by numerical models (Andrews, 1983; Jiang *et al.*, 2002). In addition Koehl and Strickler (Koehl and Strickler, 1981) showed that the feeding current can be actively directed by the copepods. The feeding current can therefore be used to scan the vicinity for food items. Recent investigations question the role of distant chemoreception in smaller calanoid copepods, where the Péclet number of the prey is very small. High-speed movies of *Paracalanus* and *Pseudocalanus* sp. show that a mechanical cue of a particle in very close proximity to the sensilla is needed to trigger a capture response (Tiselius *et al.*, 2013). The authors suggest that distant chemoreception of food particles is restricted to unusually “large and leaky” cells.

Moderate small-scale turbulence increases encounter rates with food items by increasing the relative speed between food items and copepod, chemical communication is, however, more likely to be disrupted by turbulent water movement (Visser and Jackson, 2004; Seuront and Stanley, 2014).

Many copepods are large enough to leave chemical trails in their wake, the critical size is hard to determine as it depends on the exudation rate and sensitivity threshold of the trailing males (Equation 2), but males of many species > 1 mm have been observed to track female trails from a distance. The theoretical release rate of

pheromones (Q) needed to produce a pheromone trail of a certain length can be estimated from the copepod sensitivity thresholds (C), observed trail lengths (L) and the diffusion coefficient (D).

$$Q = 4\pi DCL \quad (2)$$

Assuming a diffusion coefficient (D) of $10^{-5} \text{ cm}^2 \text{ s}^{-1}$, a trail length of 10 cm and sensitivity threshold in the range of 10^{-8} – 10^{-11} M (Yen *et al.*, 1998; Kiørboe, 2008a; Yen and Lasley, 2010) lead to an estimated pheromone release rate on the order of $Q \approx 10^{-14}$ – $10^{-17} \text{ mol s}^{-1}$ (Snell and Carmona, 1994; Kiørboe, 2008b). Such a release rate means that copepods have to exude only a fraction of their own weight per day (<0.01%) to continuously produce a pheromone trail if we assume that the molecular weight of the compounds resembles that of amino acids (Bagoien and Kiørboe, 2005). For a more complete record on the hydrodynamics of chemical cues in aquatic organisms see, e.g. Webster and Weissburg (Webster and Weissburg, 2009) and references therein.

FORAGING

Evidence for involvement of chemical stimuli in foraging

Poulet and Marsot (Poulet and Marsot, 1978) were the first to find evidence that demonstrated the role of chemical stimuli in copepod foraging. They found that microcapsules filled with algal homogenates were ingested at higher rates than capsules without homogenates. Several studies have subsequently shown the involvement of chemical compounds in food finding and assessment (Table I). Threshold concentrations for feeding attractants to trigger patchy distributions of copepods are often 10^{-6} M or above (e.g. Poulet and Gill, 1988; Steinke *et al.*, 2006), which is high compared with the nanomolar (10^{-9} M) threshold concentration of larger crustaceans (e.g. Daniel and Derby, 1991). The low sensitivity suggests that these chemical cues may be more involved in gustatory evaluation of food items than in distant perception of food in nature. Behavioural studies, however, show that copepods are able to detect and track larger particles, for example abandoned appendicularian houses or sinking aggregates (marine snow), by following the chemical plume trailing behind these particles (Lombard *et al.*, 2013).

Chemically mediated foraging mechanisms

The encounter rate with prey is directly proportional to the concentration of prey (Box I), and copepods benefit from aggregating in-depth strata or patches with elevated

prey densities (Tiselius, 1992). Multiple sensory modalities probably drive this patchiness, including direct perception of the encounter rate with prey, chemosensory and hydro-mechanical information. Chemical cues alone have been suggested to be sufficient to trigger patchy distributions of copepods (Poulet and Ouellet, 1982; Woodson *et al.*, 2007a,b), although the support for this is inconsistent.

Cowles and Strickler (Cowles and Strickler, 1983) noted that the behaviour of *Centropages typicus* changed in the presence of food and suggested that the copepods sense food concentration, either from chemical or physical cues. The role of chemical stimuli was later verified when *Acartia tonsa* was shown to feed more in the presence of cell free exudates from the prey (Cowles *et al.*, 1988). Benthic copepods also utilize chemical information to localize resources. The harpacticoid *Ectinosoma carnivora* for example switches from straight to helical trajectories in the presence of food (Seifried and Dürbaum, 2000). Other harpacticoids selectively navigate towards fish or algal scents in Y-maze experiments (Table I, Hicks, 1977; Fechter *et al.*, 2004).

Copepods are able to selectively feed in mixtures of different food species. *Acartia tonsa* for example have higher clearance rates on fast growing *Thalassiosira weissflogii* than on slow growing (Cowles *et al.*, 1988). Copepods are also able to discriminate against toxic prey (Hundley *et al.*, 1986; Demott and Moxter, 1991; Teegarden, 1999; Selander *et al.*, 2006). The ability of copepods to distinguish between morphologically similar cells suggests that the discrimination is mediated by chemosensory information (Paffenhöfer and Van Sant, 1985).

The chemical information flow is reciprocal as prey cells respond to exudates from copepods and take measures to evade predation. Chain and colony-forming phytoplankton split up into single cells or smaller units that are harder to find or handle for the inducing copepod (Jakobsen and Tang, 2002; Long *et al.*, 2007; Selander *et al.*, 2011, 2012; Bergkvist *et al.*, 2012). Other species form longer chains (Jiang *et al.*, 2010), change their swimming behaviour (Selander *et al.*, 2011) or time their excystment using zooplankton cues (Rengefors *et al.*, 1998). Several members of the dinoflagellate genus *Alexandrium* increase their toxicity in response to copepod cues (Selander *et al.*, 2006, 2012; Wohlrab *et al.*, 2010; Yang *et al.*, 2011). The signals are species specific. *Centropages typicus* for instance triggers a several fold increase in toxicity in *Alexandrium minutum*, whereas *Pseudocalanus* sp. does not (Bergkvist *et al.*, 2008). There is obviously a complex chemical interplay mediating the trophic interactions between copepods and their prey, and the signalling molecules involved have yet to be resolved.

Table I: List of chemical stimuli shown to trigger behavioural changes in copepods that are considered to be involved in food finding and assessment

Species	Stimuli	Concentration (M)	Exposure	Response	Reference
Order Calanoida (pelagic species)					
<i>Acartia clausi</i>	Algal homogenate	400 mg mL ⁻¹	Micro capsules	Ingestion	Poulet and Marsot (1978)
<i>A. hudsonica</i>	Leucine	0.5 × 10 ⁻²	Dissolved	Aggregation (but inconsistent)	Poulet and Ouellet (1982)
<i>A. hudsonica</i>	Alanine	0.5 × 10 ⁻²	Dissolved	Aggregation (but inconsistent)	Poulet and Ouellet (1982)
<i>A. hudsonica</i>	Valine	0.5 × 10 ⁻²	Dissolved	Aggregation (but inconsistent)	Poulet and Ouellet (1982)
<i>A. hudsonica</i>	Glutamine	0.5 × 10 ⁻²	Dissolved	Aggregation (but inconsistent)	Poulet and Ouellet (1982)
<i>A. hudsonica</i>	Glycine	0.5 × 10 ⁻²	Dissolved	Aggregation (but inconsistent)	Poulet and Ouellet (1982)
<i>A. hudsonica</i>	Leucine	10 ⁻¹	Micro capsules	Feeding	Poulet and Marsot (1980)
<i>A. tonsa</i>	Culture medium from <i>Thalassiosira weissflogii</i>	Corresponding to 1500 cells mL ⁻¹	Filtered conditioned medium	Increased feeding	Cowles <i>et al.</i> (1988)
<i>A. tonsa</i>	Cell free media from <i>Tetraselmis</i> culture	n.a.	Injected layer	Increased residence time in layer	Woodson <i>et al.</i> (2007a)
<i>Calanus pacificus</i>	Cell free media from <i>Tetraselmis</i> culture	n.a.	Injected layer	Increased residence time in layer	Woodson <i>et al.</i> (2007a)
<i>C. finmarchicus</i>	Cell free media from <i>Tetraselmis</i> culture	n.a.	Injected layer	Increased swimming speed, turning rate and residence time in layer	Woodson <i>et al.</i> (2007a)
<i>Eurytemora affinis</i>	Cell free media from <i>Tetraselmis</i> culture	n.a.	Injected layer	Increased turning rate and residence time in layer	Woodson <i>et al.</i> (2007a)
<i>E. herdmani</i>	Glutamic acid	10 ⁻⁴	Layered water	Aggregation	Poulet and Ouellet (1982)
<i>E. herdmani</i>	Aspartic acid	10 ⁻⁵	Layered water	Aggregation	Poulet and Ouellet (1982)
<i>E. herdmani</i>	Algal homogenate	400 mg mL ⁻¹	Micro capsules	Ingestion	Poulet and Marsot (1978)
<i>Metridia pacifica</i>	Cell free media from <i>Tetraselmis</i> culture	n.a.	Injected layer	Increased swimming speed, turning rate and residence time in layer	Woodson <i>et al.</i> (2007a)
<i>Pseudocalanus minutus</i>	Microalga exudates (<i>Skeletonema costatum</i>)	n.a.	Conditioned seawater	Changed swimming behaviour (increased speed, more frequent swimming bursts and higher net to gross displacement ratio)	Buskey (1984)
<i>P. minutus</i>	Morpholine	12 × 10 ⁻⁶	Dissolved	Increased swimming speed, but only if copepods had been conditioned to associate morpholine with food	Buskey (1984)
<i>Temora longicornis</i>	ASP, GLU, ASN, SER, GLN, HIS	10 ⁻⁶	Dissolved	Increased beat frequency of Maxilla 1	Gill and Poulet (1988)
<i>Temora longicornis</i>	GLY, TYR, PHE, LEU, ORN, LYS	10 ⁻⁶	Dissolved	Increased beat frequency of Maxilla 1	Gill and Poulet (1988), Poulet and Gill (1988)
<i>Temora longicornis</i>	ASP, GLU	10 ⁻⁶	Dissolved	Increased beat frequency of Maxilla 1	Gill and Poulet (1988)
<i>Temora longicornis</i>	ARG, ALA, TAUR, AABA, VAL, ILE	10 ⁻⁶	Dissolved	Increased beat frequency of Maxilla 1	Gill and Poulet (1988)
<i>Temora longicornis</i>	TRP PHE	10 ⁻⁶	Dissolved		Gill and Poulet (1988)
<i>Temora longicornis</i>	DMS	10 ⁻⁶	Dissolved	Tail flipping and redirection of flow	Steinke <i>et al.</i> (2006)
<i>Temora longicornis</i>	Cell-free media from <i>Tetraselmis</i> and <i>Rhodomonas</i> culture	n.a.	Injected layer	Increased residence time in layer	Woodson <i>et al.</i> (2007b)
Order Siphonostomatoida (parasitic species)					
<i>Lepeophtheirus salmonis</i>	Isophorone, 6-methyl-5-hepten-2-one	72 × 10 ⁻⁶	Dissolved	Increased activity and significant preference in choice experiment	Bailey <i>et al.</i> (2006)
Order Harpacticoida (mainly benthic species)					
<i>Echinosoma melaniceps</i> (Harpacticoid)	Freshly killed ostracods	n.a.	Addition of ostracod to petridish	Change from ballistic motion to helical search behaviour	Seifried and Dürbaum (2000)
<i>Echinosoma carnivore</i> (Harpacticoid)	Freshly killed ostracods	n.a.	Addition of ostracod to petridish	Change from ballistic motion to helical search behaviour	Seifried and Dürbaum (2000)
<i>Leptastacus coulli</i> (Harpacticoid)	Water conditioned with pieces of the fish <i>Mugil cephalus</i> (≈5 g per 100 mL for ≈12 h)	n.a.	Flow in tubular Y-maze	Significant choice in preference of fish conditioned water in Y maze experiments	Fechter <i>et al.</i> (2004)
<i>Praeleptomesochra similis</i>	Water conditioned with flesh from Striped mullet (<i>Mugil cephalus</i>)	≈0.05 g mL ⁻¹ for 12 h	Flow in tubular Y-maze	Significant choice in preference of fish conditioned water in Y maze experiments	Fechter <i>et al.</i> (2004)

Free amino acids are abbreviated in the stimuli column.

The molecular composition of feeding stimuli

A limited number of compounds acting as feeding attractants have been identified, the majority of which are free amino acids (Table II). Copepods may, for example, aggregate in vertical layers with elevated concentration of several different amino acids (Poulet and Ouellet, 1982; Table I). Copepods respond to other compounds associated with prey organisms too. Dimethyl sulphide (DMS) for example elicits tail flipping behaviour and redirection of the feeding current in copepods at micro-molar concentrations (Steinke *et al.*, 2006). DMS is considered a feeding attractant for a wide variety of marine organisms, ranging from microzooplankton to seabirds (Pohnert *et al.*, 2007). Since copepods have a relatively low sensitivity to most known stimuli, it is likely that additional compounds are involved in distant chemoreception. Potential candidates are primary metabolites present in high concentrations as well as compounds released or taken up by the organism, e.g. respired carbon dioxide (CO₂) or oxygen from autotrophs.

Feeding deterrents

Phytotoxins isolated from harmful algal bloom forming phytoplankters have been suggested to constitute chemical defences against grazers (Cembella, 2003). This is mainly based on correlative evidence, where copepods have been observed to show increased mortality as well as reduced egg production after ingesting toxic alga (i.e. Huntley *et al.*, 1986; Koski *et al.*, 1999), or to avoid toxic prey in feeding experiments (i.e. Teegarden, 1999). Adverse effects may consequently be confounded by other traits correlated with the presence of phytotoxins (Selander *et al.*, 2006). Regardless, it is clear that copepods do avoid some food items, and that they are likely to use chemosensory information to do so (e.g. Teegarden, 1999, Selander *et al.*, 2006). The grazer deterrent role of phytotoxins is supported by the up-regulation of some toxins in response to grazer cues (reviewed by Van Vonk *et al.*, 2011).

Host finding in parasitic copepods

The chemical signature of the host fish elicits characteristic search behaviour in infectious stages of the sea lice *L. salmonis*. The rate of movement with loops and spirals increases and the encounter rate with nearby fish rises correspondingly. In addition, the hydro-mechanical signature of the host triggers a specific behaviour that facilitates landing on the host (reviewed by Mordue Luntz and Birkett, 2009). Among the active compounds are isophorone and 6-methyl-5-hepten-2-one that has been

isolated from salmon conditioned water (Bailey *et al.*, 2006).

COPEPOD RESPONSES TO PREDATOR CUES (KAIROMONES)

Behavioural adjustments in the presence of predators are well known in many animal groups (reviewed in Kats and Dill, 1998). Chemical predator cues have the potential to serve as an early warning in environments with variable predator densities. Buskey *et al.* (Buskey *et al.*, 2012) concluded that chemoreception is not important for the detection of predators in marine copepods due to the lack of evidence, but there are some studies showing predator-induced responses in copepods (summarized in Table II). Copepod responses to predator cues involve behavioural, morphological or life history changes. Some initiate DVM to avoid visual predators (Neill, 1990; Bollens *et al.*, 1994), others reduce swimming speed and visible pigmentation (van Duren and Videler, 1996; Hylander *et al.*, 2012). The tidal pool dwelling harpacticoid *Tigriopus californicus* for example reduces swimming activity and stays close to the surface if the sea anemone *Anthopleura elegantissima* is present (Dethier, 1980). Fish predation induces diapause egg formation in the freshwater copepod *Diaptomus sanguineus* (Hairston and Walton, 1986) and salamander cues suppress hatching of resting eggs in freshwater calanoids (Blaustein, 1997). It is notable that many examples are from limnic systems, perhaps predator cues are less relevant in the open ocean, where cues might not be as correlated with future predation risks as in smaller confined water bodies. Predator cues further induce faster development as in the freshwater copepod *Notodiptomus conifer* (Gutierrez *et al.*, 2010). Finally, predator cues have been shown to affect reproductive output in *Eurytemora herdmanni* where mysid cues lead to a reduction of mating success and offspring production (Lasley-Rasher and Yen, 2012).

These findings suggest that the role of predator cues may have been overlooked in copepods and that copepods similar to other organisms utilize chemosensory information to optimize the trade-off between resource acquisition and predation risk. The concentration of predator cues is, however, often high and it would be interesting to see more ecologically relevant experiments in the future.

REPRODUCTION

Mate finding, recognition and assessment are mediated by chemosensory information (Snell and Morris, 1993; Lonsdale *et al.*, 1998; Snell, 2010; Yen and Lasley, 2010).

Table II: List of chemically mediated responses to predator cues

Species	Predator	Response	Exposure	Habitat	Identified compounds	Reference
Order Calanoida (pelagic species)						
<i>Acartia hudsonica</i>	Fish Three-spined stickleback <i>Gasterosteus aculeatus</i>)	No response to chemical stimuli	Conditioned seawater	Marine	No	Bollens <i>et al.</i> (1994)
<i>A. hudsonica</i>	Fish Atlantic silver side (<i>Menidia menidia</i>)	Reduced gut fullness in daytime	Conditioned water	Estuarine	No	Cieri and Stearns (1999)
<i>A. tonsa</i>	Fish Atlantic silver side (<i>Menidia menidia</i>)	Reduced gut fullness in daytime	Conditioned water	Estuarine	No	Cieri and Stearns (1999)
<i>Arctodiaptomus similis</i>	Caged salamander <i>Salamandra infraimmaculata</i>	Suppressed hatching of resting eggs	Caged and free salamander larvae	Limnic	No	Blaustein (1997)
<i>Argyrodiaptomus falcifer</i>	Fish (<i>Cnesterodon decemmaculatus</i>)	Altered vertical migration (VM) pattern and increased escape response	Conditioned water	Limnic	No	Gutierrez <i>et al.</i> (2011)
<i>Calanoid copepods</i>	Fish, mainly Roach (<i>Rutilus rutilus</i>) and Perch (<i>Perca fluviatilis</i>)	Reduced carotenoid pigmentation	Field samples and experimental evidence	Limnic	No	Hansson (2004)
<i>Calanopia americana</i>	Ctenophores <i>Mnemiopsis leidyi</i>	VM removed	Crude body mucus	Marine	No ^a	Cohen and Forward (2005)
<i>Calanopia americana</i>	Killifish <i>Fundulus heteroclitus</i>	VM removed or shifted	Crude body mucus	Marine	No ^a	Cohen and Forward (2005)
<i>Diaptomus kenai</i>	Midge larvae <i>Chaoborus trivittatus</i>	VM	Conditioned water	Limnic	No	Neill (1990)
<i>D. sanguineus</i>	Fish	Induce diapause eggs		Limnic	No	Hairston and Walton (1986)
<i>Diaptomus sp</i>	Nine spined sticklebacks (<i>Pungitus pungitus</i>)	Reduction in carotenoid pigmentation	Field samples and experimental additions of fish conditioned water	Limnic	No	Hansson (2000)
<i>Eudiaptomus gracilis</i>	Fish (<i>Rutilus rutilus</i>)	Reduced carotenoid pigmentation	Caged fish, conditioned water	Limnic	No	Hylander <i>et al.</i> (2009, 2012)
<i>E. herdmani</i>	Mysids <i>Neomysis americana</i>	Reduced copulation frequency, successful spermatophore transfer and nauplii production	Conditioned water	Estuarine	No	Lasley-Rasher and Yen (2012)
<i>Leptodiaptomus aschlandi</i>	Cladoceran <i>Bythotrephes</i>	Deeper vertical distribution	Conditioned water	Limnic	No	Bourdeau <i>et al.</i> (2011)
<i>Notodiaptomus conifer</i>	Fish (<i>Cnesterodon decemmaculatus</i>)	Shorter time to maturation (faster development)	Conditioned water	Limnic	No	Gutierrez <i>et al.</i> (2010)
<i>N. conifer</i>	Fish (<i>Cnesterodon decemmaculatus</i>)	Altered VM pattern and increased escape response	Conditioned water	Limnic	No	Gutierrez <i>et al.</i> (2011)
<i>Temora longicornis</i>	Fish grey mullet <i>Chelon labrosus</i>	Reduction of swimming speed	Conditioned water	Marine	No	van Duren and Videler (1996)
Order Cyclopoida (mainly pelagic species)						
<i>Cyclopoid copepods</i>	Roach (<i>Rutilus rutilus</i>) and Perch (<i>Perca fluviatilis</i>)	No response to chemical stimuli	Field samples and experimental evidence	Limnic	No	Hansson(2004)
<i>Diacyclops thomasi</i>	Predatory cladoceran <i>Bythotrephes</i>	Deeper vertical distribution	Conditioned water	Limnic	No	Bourdeau <i>et al.</i> (2011)
<i>Thermocyclops decipiens</i>	Midge larvae <i>Chaoborus</i>	Reversed DVM	Conditioned water	Limnic	No	Minto <i>et al.</i> (2010)
<i>Tropocyclops prasinus</i>	<i>brasiliensis</i>					
Order Harpacticoida (tidepool habitat)						
<i>Tigriopus californicus</i>	Sea anemone <i>A. elegantissima</i>	Avoidance behaviour, accumulation at surface	Stationary sea anemone in aquaria	Marine	No	Dethier (1980)

^aAlthough not tied to the biological activity, the presence of uronic acids and sulphated glycosaminoglycan were shown in active extracts, and authors consider them to be candidate kairomones.

Parker (Parker, 1902) was the first to recognize the importance of chemical cues for copepod reproduction. He realized that males of *Labidocera aestiva* were attracted to waterborne signals from the females but not to those of males. Seventy years later Katona (Katona, 1973) described the male tracking behaviour of *Eurytemora affinis* following female pheromone trails. Since then, male pheromone following behaviour has been described for at least 20 copepod species (Doall et al., 1998; Yen and Lasley, 2010; see Table III).

Detection, pursuit and encounter

Mating is often encounter limited in pelagic copepods (Kjørboe, 2007). The organisms’ size, motility and the seasonally variable number of potential mates complicate mate finding in planktonic organisms. In pheromone-producing species males typically respond to pheromone signals emitted by the females. Awareness of the presence of mates can be triggered at concentrations much lower than those that elicit mate-pursuing behaviour (Nihongi et al., 2004; Heuschele and Kjørboe, 2012; Seuront, 2013). Male search behaviour is characteristic and can be

distinguished from normal feeding behaviour by increased directional swimming velocities (Heuschele and Kjørboe, 2012; Seuront, 2013). When males of *Oithona davisae* for example perceive the presence of female chemical cues in the water they increase their swimming activity, but do not reach the velocities associated with direct trail following behaviour (Heuschele and Kjørboe, 2012).

The spatial distribution of pheromone trails depends on the movement pattern and ecology of the copepod. Assuming that pheromones are released continuously, hovering and cruising pelagic copepods will form a continuous trail, whereas ambush feeding copepods that show a “hop and sink” behaviour will leave behind a series of almost unconnected plumes or “clouds” (Weissburg et al., 1998; Kjørboe, 2008b, Figs 1 and 2). Benthic copepods will release pheromones close to the substrate and therefore the trails will be distributed in a mainly two-dimensional plane compared with the three-dimensional habitat of pelagic copepods. For parasitic copepods, pheromone distribution will also depend on the behaviour of the host. In experiments with sea lice, *L. salmonis*, where males could choose directions in a

Table III: Copepod species with documented use of pheromones in reproduction

	Calanoida													Harpactoida		Cyclopoida		Siphonostomatoida	
Recognition level based on diffusible pheromones	1	2	3, 22	4, 22	14, 15, 16	5	6	7, 8	13	2	9	9*	10	11, 12, 22, 23	11	17	18	19, 20	21
Quality (Age, relatedness)																			
State (virgin/mated)																			
Population																			
Sex																			
Family																			



Black lines with dots indicate heterospecific attraction between two species. 1, Tsuda and Miller (1998); 2, Griffiths and Frost (1976); 3, Colin (1995), 4, Bagøien and Kjørboe (2005); 5, Katona (1973) (*E. affinis* searched for *E. herdmani* and *P. pelagicus*); 6, Yen et al. (2011); 7, Blades and Youngbluth (1980); 8, Parker (1902); 9, Jacoby and Youngbluth (1983) (suspected range chemical cues); 10, Dur et al. (2011); 11, Goetze and Kjørboe (2008) (*T. longicornis* following *T. stylifera*); 12, Doall et al. (1998); 13, Nihongi et al. (2004); 14, Chow-Fraser and Maly (1988) (mating behaviour of *Diaptomus minutus* and *Diaptomus oregonensis*, choosiness for gravid females, but no trail following behaviour); 15, Watras (1983); 16, Van Leeuwen and Maly (1991); 17, Lazzaretto et al. (1990); 18, Lazzaretto et al. (1993) (male and female release signals); 19, Uchima and Murano (1988); 20, Heuschele and Kjørboe (2012); 21, Ingvarsdottir et al. (2002); 22, Goetze (2008); 23, Yen and Lasley (2010).

**Pseudodiaptomus pelagicus* Herrick, 1884 renamed from *Pseudodiaptomus coronatus* Williams, 1906.

Y-maze, virgin females attracted males significantly more than other life stages (Ingvarsdottir *et al.*, 2002).

Once a male encounters a pheromone trail it starts to pursue the emitting female. This is characterized by an increase in swimming speed and a distinctive circling swimming pattern to localize the female path. Behavioural responses to olfactory signals from potential partners are not only restricted to males. Female *T. longicornis* showed an increase in small jumps ("hops") when placed in male-conditioned water compared with female-conditioned water (van Duren and Videler, 1996). Likewise females of the harpacticoid copepod *Tisbe holothuriae* responded to the scent of males by accumulating next to a cellulose dialysis tube containing males (Lazzaretto *et al.*, 1993).

Mate recognition and quality assessment

Mate recognition and mate quality assessment can happen at several stages during the mating process: before, during and after the copulation. Once a copepod encounters the pheromone trail of another individual it has to decide whether to pursue this individual or continue searching for a better partner. Given the time and mortality costs of pursuing behaviour in copepods (van Duren and Videler, 1996), males would benefit from being able to distinguish between hetero- and conspecific individuals, between the sexes, reproductive states and other quality indicators.

Males of the harpacticoids *Tigriopus brevicornis* and *T. californicus* do not respond to the smell of females of the related species *Tigriopus fulvus* (Lazzaretto *et al.*, 1990). However, males of several calanoid copepods follow heterospecific females and also attempt to mate with them in the laboratory (Goetze, 2008; Table III). This indicates a low level of specificity in the pheromone signal.

In several copepod species males prefer to mate with virgin females (e.g. Uchima, 1985; Ingvarsdottir *et al.*, 2002); a strategy that increases their reproductive success and simultaneously minimizes costs involved in spermatophore production and search behaviour (Chow-Fraser and Maly, 1988; Weissburg *et al.*, 1998; Kiørboe, 2008a). In *Diaptomus leptopus*, the presence of gravid females changes the swimming behaviour of males to more convoluted swimming trajectories compared with the presence of male or non-gravid females (Van Leeuwen and Maly, 1991). Similar behaviour was observed in *O. davisae*, where the presence of virgin females elicited increased swimming activity and led to more directional swimming paths of males (Heuschele and Kiørboe, 2012). This suggests that the chemical signature depends on the females' reproductive state and age (Lazzaretto *et al.*, 1993; Ingvarsdottir *et al.*, 2002). The release of pheromones could also be

influenced by actions of the males. In the calanoid *Tortanus (Atortus) rubidus* the attached spermatophore leaves a "genital plug" (Barthélémy *et al.*, 1998, 2003), and in the parasitic *Lepeophtheirus pectoralis* males seal the genital plug of the females after transferring their sperm (Karlson and Lüscher, 1959; Anstensrud, 1990). This mechanism could reduce the release of pheromones as suggested by Corni *et al.* (2000, 2001), and consequently would reduce encounters of that female with other males.

Chemical cues might also play a role in sexual selection in copepods. A recent study indicates that copepods of both sexes prefer to mate with younger individuals in *O. davisae* (Ceballos and Kiørboe, 2011). In *T. fulvus*, males are even able to discriminate between females from different populations based on chemical cues and show greater interest in the female scent from their own population compared with a geographically separate population (Lazzaretto *et al.*, 1994).

It is not clear what determines the level of specificity. It is possible that the pheromone consists of a cocktail of compounds with different levels of overlap between species, it could also be that pheromones are structurally similar enough to trigger cross-reactivity, or that post-processing of the sensory input limits the level of specificity. The levels of specificity are illustrated in Table III. This system is likely based on a multimodal approach with a cue hierarchy (Yen and Lasley, 2010). While some species evaluate the information contained in the diffusible pheromone signature from afar, others rely on information from lock-and-key mechanisms upon physical contact (Lee, 1972; Snell and Morris, 1993; Snell, 2010; Yen and Lasley, 2010) and also use surface-bound glycoproteins (Snell and Carmona, 1994) to recognize and evaluate potential partners.

Kin recognition

Chemical cues also play a role in kin recognition. Females of the harpacticoid *T. fulvus* only cannibalize unrelated offspring (Lazzaretto *et al.*, 1990; Lazzaretto and Salvato, 1992). The authors concluded that the nauplii must carry a specific chemical signature, which is either coded genetically or transferred during the development of the zygotes (Lazzaretto *et al.*, 1990). A similar test in the harpacticoid *Harpacticus* sp. however revealed that individuals consumed kin and non-kin at the same rate, and kin recognition cannot be assumed to be a universal trait in plankton (Dahms and Qian, 2006). The selective pressure for kin recognition might be small in the open sea where it is unlikely that an organism would meet its offspring. However, the situation is different in small tidal pools, the natural habitat of *T. fulvus* where the chances to repeatedly encounter your kin are higher.

CHEMICAL CHARACTERIZATION OF PHEROMONES AND OTHER INFOCHEMICALS

The characterization of copepod pheromones in the aquatic environment is a challenge due to small amounts and complex background of other compounds. To date, no sexual pheromones have been structurally determined. Pheromone activity can be due to specific compound(s) alone, or in combination with primary metabolites. CO₂ is probably the most abundantly exuded compound due to respiration. The main nitrogen excretion products are ammonia (60–100%), urea (maximum 10%) and amino acids (~20%) (Regnault, 1987). In *Eucalanus pileatus* amino acids are released as bursts at irregular time points (Gardner and Paffenhöfer, 1982), which could therefore be used to communicate with other individuals. Abundant compounds from the primary metabolism and excretion products will however not provide a high degree of specificity unless the relative abundance of the different compounds is used as a fingerprint of specific organisms.

Rittschof and Cohen (Rittschof and Cohen, 2004) reviewed peptides identified as crustacean infochemicals. The authors conclude that the chemical properties of peptides (solubility, short half-lives) and the potential for a high degree of specificity due to the many possible

amino acid sequences of even a small peptide makes them ideal information carriers. Given the phylogenetic relationship between copepods and decapods, the authors further suggest that peptides are also likely candidates for copepod pheromones. The first described crustacean sexual pheromone, uridine diphosphate (Hardege *et al.*, 2011) is however not a peptide.

Some studies provide initial information on the chemical properties of copepod sex pheromones. The female pheromones in *T. fulvus* were determined to have a molecular weight between 100 and 1000 Da (Lazzaretto *et al.*, 1994). In sea lice, *L. salmonis*, pheromones are semi-volatile and lipophilic (Ingvarsdottir *et al.*, 2002). Crayfish *Pachygrapsus crassipes* (Kittredge *et al.*, 1971) pheromone activity remained after heat treatment, in contrast to the contact pheromones in the copepod *E. affinis* (Katona, 1973). Chemical signalling may be disrupted by contaminants. In the presence of diesel oil male *T. longicornis* had difficulties finding and following female pheromone trails (Seuront, 2011).

A novel approach to pheromone identification is to incubate males and females separately and compare as much as possible of their exometabolome to find specific female signatures. Figure 3, e.g. shows a mirrored comparison of exudates from female and male *O. davisae*. Dots indicate compounds that are produced in much larger

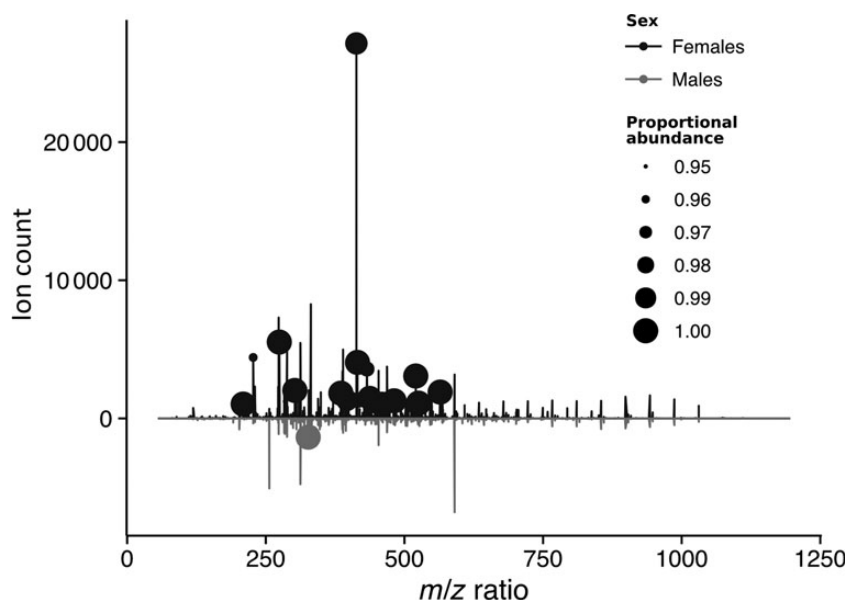


Fig. 3. Illustration of the differences in the exudate composition of male and female *O. davisae*. Dots indicate compounds that are relatively more abundant (>1000 peak height) and to 90% or more produced by the respective sex compared to the other. Exudates were extracted from same-sex incubations using solid-phase extraction columns and analysed using liquid chromatography–mass spectrometry. We then subtracted the peak height for each compound found in the control sample from both male and female compounds, and controlled for the number of individuals in the sample.

amounts by one of the sexes relative to the other. Such metabolomic approaches provide a tool to identify pheromone candidates. The candidate compounds can then be directly tested for pheromone activity in bioassay experiments, which may provide a short cut compared with traditional bioassay-guided fractionation. The approach was for example recently used to characterize the first sexual pheromone in a benthic diatom (Gillard *et al.*, 2012). The use of metabolic profiling is favoured when the small quantities of pheromone candidate molecules that can be obtained from copepods also limit bioassay-guided fractionation designs. In insects separation techniques are often combined with electrophysiological studies, a method that has, with one exception (Fields *et al.*, 2007) only been used with mechanosensory sensilla in copepods (Yen *et al.*, 1992; Lenz and Yen, 1993; Fields *et al.*, 2002).

SUMMARY AND FUTURE DIRECTIONS

A vast body of literature shows that chemical cues and signals are involved in every aspect of copepod life (Fig. 1). They mediate foraging, reproduction and predator avoidance. Some chemically mediated traits like predator induced avoidance behaviours and kin recognition are more likely to evolve in freshwater lakes and tidal pools. In these, infochemical concentrations are probably more directly linked to present and future predation risks and the chance of eating your own offspring is higher than in the open sea.

This review reveals many aspects of the chemical ecology of copepods that are still poorly understood. Very little is for example known about the chemical structure of pheromones and other infochemicals and research on chemical ecology in copepods clearly needs to advance into signal characterization. The recent developments in analytical chemistry and especially in metabolomics have the potential to catalyse the identification of aquatic infochemicals in coming years, by complementing traditional approaches like bioassay-guided fractionation. Structural elucidation of infochemicals will open up new research areas, where the role of cues and signals in, e.g. reproductive isolation, speciation, population dynamics and food web dynamics can be understood. Moreover, it will make it possible to identify receptor proteins, neurophysiological signal transduction and processing pathways. It will also allow for novel applied applications like infochemical-based control of parasitic copepods or regulation of sex ratio in intensive copepod cultures. Behavioural experiments

with regard to reproduction are relatively numerous, but studies on chemical cues in foraging and predator-induced responses are still underrepresented. The ecological relevance and effect of chemically mediated interactions in nature needs to be addressed in the future.

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