The chemical ecology of copepods

Heuschele, Jan; Selander, Erik

Published in:
Journal of Plankton Research

Link to article, DOI:
10.1093/plankt/fbu025

Publication date:
2014

Document Version
Publisher's PDF, also known as Version of record

Citation (APA):
Heuschele, J., & Selander, E. (2014). The chemical ecology of copepods. Journal of Plankton Research, 36(4), 895-913. DOI: 10.1093/plankt/fbu025

Journal of
Plankton Research

plankt.oxfordjournals.org

J. Plankton Res. (2014) 36(4): 895–913. *First published online April 9, 2014 doi:10.1093/plankt/fbu025*

REVIEW

The chemical ecology of copepods

JAN HEUSCHELE[1]* AND ERIK SELANDER[1,2]

[1]CENTRE FOR OCEAN LIFE, NATIONAL INSTITUTE OF AQUATIC RESOURCES, TECHNICAL UNIVERSITY OF DENMARK, KAVALERGÅRDEN 6, CHARLOTTENLUND 2920, DENMARK AND [2]DEPARTMENT OF BIOLOGICAL AND ENVIRONMENTAL SCIENCES, UNIVERSITY OF GOTHENBURG, BOX 463, GÖTEBORG SE40530, SWEDEN

*CORRESPONDING AUTHOR: janheuschele@gmail.com

Received May 17, 2013; accepted March 10, 2014

Corresponding Editor: Roger Harris

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

available online at www.plankt.oxfordjournals.org

INTRODUCTION

Copepods are present in most aquatic habitats, ranging from the waterbodies of Bromelia leafs 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 (Bagøien and Kiørboe, 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.

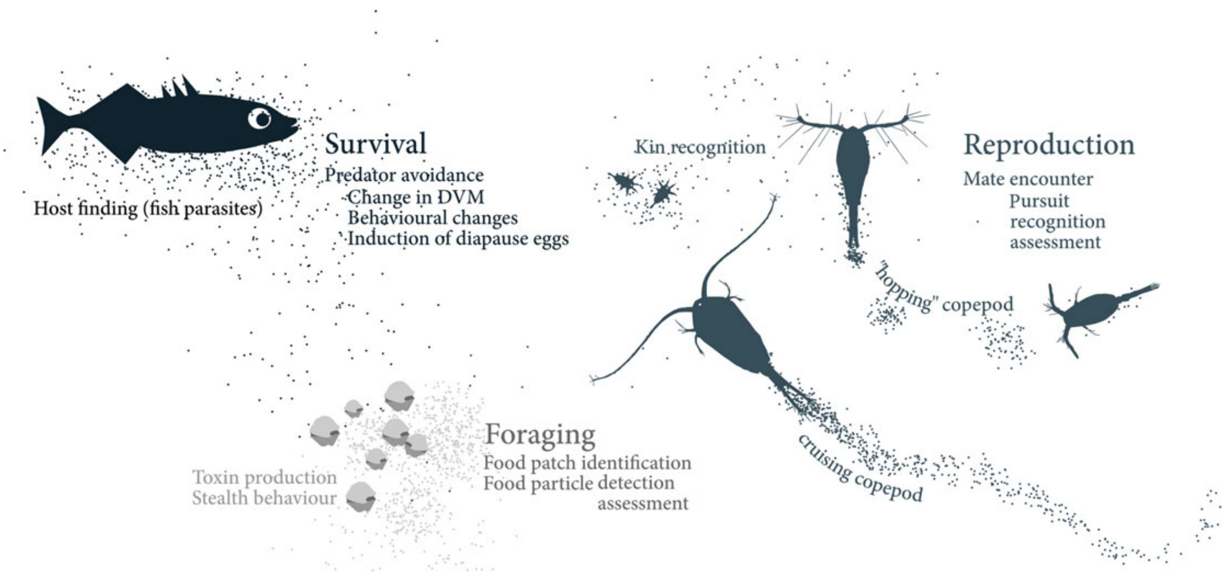


Fig. 1. Illustration of the involvement of chemical cues during the three main activities in the life of a copepod: foraging, survival and reproduction. Copepods find mates by navigating pheromone gradients, they localize food and resource patches from chemical cues. At the same time prey organisms, 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 *Coryceaus* 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 harpacticoid *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 (Østergaard 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.

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

Where L is the length scale, U the velocity, and D the diffusion coefficient. Small copepods and early life stages (<100 µm) will have $\mathrm{Pe} < 10$ and solute transport result from both convection and diffusion assuming that $D = 10^{-5}\ \mathrm{cm}^2\ \mathrm{s}^{-1}$. They will experience water as more viscous compared with larger (>5 mm) copepods for which $\mathrm{Pe} > 25\,000$ 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 $\mathrm{Pe} \ll 1$ 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 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 Peclet 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.

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 $v = (v^2_{\mathrm{prey}} + v^2_{\mathrm{predator}})^{0.5}$ (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).

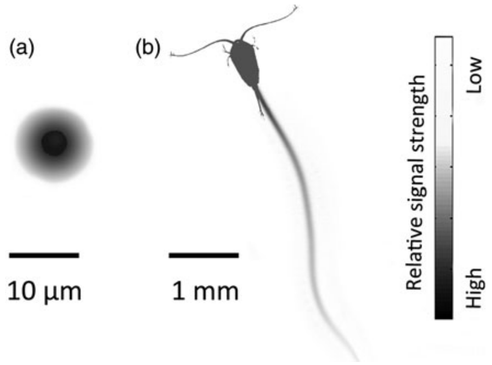


Fig. 2. (**a**) Illustration of the solute cloud around a cell and (**b**) an artistic interpretation of the pheromone trail in the wake of a pheromone-producing copepod. At the scale of a phytoplankton cell, solute transport is mainly due to diffusion, whereas copepods are often large enough to produce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

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).

$$Q = 4\pi DCL \tag{2}$$

Assuming a diffusion coefficient (D) of 10^{-5} cm^2 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} 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 (Bagøien 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 *Thallasiosira weissflogii* than on slow growing (Cowles *et al.*, 1988). Copepods are also able to discriminate against toxic prey (Huntley *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)					
Acartia clausi	Algal homogenate	400 mg mL^{-1}	Micro capsules	Ingestion	Poulet and Marsot (1978)
A. hudsonica	Leucine	0.5×10^{-2}	Dissolved	Aggregation (but inconsistent)	Poulet and Ouellet (1982)
A. hudsonica	Alanine	0.5×10^{-2}	Dissolved	Aggregation (but inconsistent)	Poulet and Ouellet (1982)
A. hudsonica	Valine	0.5×10^{-2}	Dissolved	Aggregation (but inconsistent)	Poulet and Ouellet (1982)
A. hudsonica	Glutamine	0.5×10^{-2}	Dissolved	Aggregation (but inconsistent)	Poulet and Ouellet (1982)
A. hudsonica	Glycine	0.5×10^{-2}	Dissolved	Aggregation (but inconsistent)	Poulet and Ouellet (1982)
A. hudsonica	Leucine	10^{-1}	Micro capsules	Feeding	Poulet and Marsot (1980)
A. tonsa	Culture medium from *Thallasiosira wissflogii*	Corresponding to 1500 cells mL^{-1}	Filtered conditioned medium	Increased feeding	Cowles *et al.* (1988)
A. tonsa	Cell free media from *Tetraselmis* culture	n.a.	Injected layer	Increased residence time in layer	Woodson *et al.* (2007a)
Calanus pacificus	Cell free media from *Tetraselmis* culture	n.a.	Injected layer	Increased residence time in layer	Woodson *et al.* (2007a)
C. finmarchicus	Cell free media from *Tetraselmis* culture	n.a.	Injected layer	Increased swimming speed, turning rate and residence time in layer	Woodson *et al.* (2007a)
Eurytemora affinis	Cell free media from *Tetraselmis* culture	n.a.	Injected layer	Increased turning rate and residence time in layer	Woodson *et al.* (2007a)
E. herdmani	Glutamic acid	10^{-4}	Layered water	Aggregation	Poulet and Ouellet (1982)
E. herdmani	Aspartic acid	10^{-5}	Layered water	Aggregation	Poulet and Ouellet (1982)
E. herdmani	Algal homogenate	400 mg mL^{-1}	Micro capsules	Ingestion	Poulet and Marsot (1978)
Metridia pacifica	Cell free media from *Tetraselmis* culture		Injected layer	Increased swimming speed, turning rate and residence time in layer	Woodson *et al.* (2007a)
Pseudocalanus minutus	Microalga exudates (*Skeletonema costatum*)	n.a.	Conditioned seawater	Changed swimming behaviour (increased speed, more frequent swimming bursts and higher net to gross displacement ratio)	Buskey (1984)
P. minutus	Morpholine	12×10^{-6}	Dissolved	Increased swimming speed, but only if copepods had been conditioned to associate morpholine with food	Buskey (1984)
Temora longicornis	ASP, GLU, ASN, SER, GLN, HIS	10^{-6}	Dissolved	Increased beat frequency of Maxilla 1	Gill and Poulet (1988)
Temora longicornis	GLY, TYR, PHE, LEU, ORN, LYS	10^{-6}	Dissolved	Increased beat frequency of Maxilla 1	Gill and Poulet (1988), Poulet and Gill (1988)
Temora longicornis	ASP, GLU	10^{-6}	Dissolved	Increased beat frequency of Maxilla 1	Gill and Poulet (1988)
Temora longicornis	ARG, ALA, TAUR, AABA, VAL, ILE	10^{-6}	Dissolved	Increased beat frequency of Maxilla 1	Gill and Poulet (1988)
Temora longicornis	TRP PHE	10^{-6}	Dissolved		Gill and Poulet (1988)
Temora longicornis	DMS	10^{-6}	Dissolved	Tail flipping and redirection of flow	Steinke *et al.* (2006)
Temora longicornis	Cell-free media from *Tetraselmis* and *Rhodomonas* culture		Injected layer	Increased residence time in layer	Woodson *et al.* (2007b)
Order Siphonostomatoida (parasitic species)					
Lepeophtheirus salmonis	Isophorone, 6-methyl-5-hepten-2-one	72×10^{-6}	Dissolved	Increased activity and significant preference in choice experiment	Bailey *et al.* (2006)
Order Harpacticoida (mainly benthic species)					
Echtinosoma melaniceps (Harpaticoid)	Freshly killed ostracods	n.a.	Addition of ostracod to petridish	Change from ballistic motion to helical search behaviour	Seifried and Dürbaum (2000)
Echtinosoma carnivore (Harpacticoid)	Freshly killed ostracods	n.a.	Addition of ostracod to petridish	Change from ballistic motion to helical search behaviour	Seifried and Dürbaum (2000)
Leptastacus coulli (Harpacticoid)	Water conditioned with pieces of the fish *Mugil cephalus* (≈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 *et al.* (2004)
Praeleptomesochra similis	Water conditioned with flesh from Striped mullet (*Mugil cephalus*)	≈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 *et al.* (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 (CO_2) 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 *Notodiaptomus conifer* (Gutierrez *et al*., 2010). Finally, predator cues have been shown to affect reproductive output in *Eurytemora herdmani* 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)						
Acartia hudsonica	Fish Three-spined stickleback *Gasterosteus aculeatus)*	No response to chemical stimuli	Conditioned seawater	Marine	No	Bollens *et al.* (1994)
A. hudsonica	Fish Atlantic silver side (*Menidia menidia*)	Reduced gut fullness in daytime	Conditioned water	Estuarine	No	Cieri and Stearns (1999)
A. tonsa	Fish Atlantic silver side (*Menidia menidia*)	Reduced gut fullness in daytime	Conditioned water	Estuarine	No	Cieri and Stearns (1999)
Arctodiaptomus similis	Caged salamander *Salamandra infraimmaculata*	Suppressed hatching of resting eggs	Caged and free salamander larvae	Limnic	No	Blaustein (1997)
Argyrodiaptomus falcifer	Fish (*Cnesterodon decemmaculatus*)	Altered vertical migration (VM) pattern and increased escape response	Conditioned water	Limnic	No	Gutierrez *et al.* (2011)
Calanoid copepods	Fish, mainly Roach (*Rutilus rutilus*) and Perch (*Perca fluviatilis*)	Reduced carotenoid pigmentation	Field samples and experimental evidence	Limnic	No	Hansson (2004)
Calanopia americana	Ctenophores *Mnemiopsis leidyi*	VM removed	Crude body mucus	Marine	No[a]	Cohen and Forward (2005)
Calanopia americana	Killifish *Fundulus heteroclitus*	VM removed or shifted	Crude body mucus	Marine	No[a]	Cohen and Forward (2005)
Diaptomus kenai	Midge larvae *Chaoborus trivittatus*	VM	Conditioned water	Limnic	No	Neill (1990)
D. sanguineus	Fish	Induce diapause eggs		Limnic	No	Hairston and Walton (1986)
Diaptomus sp	Nine spined sticlebacks (*Pungitus pungitus*)	Reduction in carotenoid pigmentation	Field samples and experimental additions of fish conditioned water	Limnic	No	Hansson (2000)
Eudiaptomus gracilis	Fish (*Rutilus rutilus*)	Reduced carotenoid pigmentation	Caged fish, conditioned water	Limnic	No	Hylander *et al.* (2009, 2012)
E. herdmani	Mysids *Neomysis americana*	Reduced copulation frequency, successful spermatophore transfer and nauplii production	Conditioned water	Estuarine	No	Lasley-Rasher and Yen (2012)
Leptodiaptomus aschlandi	Cladoceran *Bythotrephes*	Deeper vertical distribution	Conditioned water	Limnic	No	Bourdeau *et al.* (2011)
Notodiaptomus conifer	Fish (*Cnesterodon decemmaculatus*)	Shorter time to maturation (faster development)	Conditioned water	Limnic	No	Gutierrez *et al.* (2010)
N. conifer	Fish (*Cnesterodon decemmaculatus*)	Altered VM pattern and increased escape response	Conditioned water	Limnic	No	Gutierrez *et al.* (2011)
Temora longicornis	Fish grey mullet *Chelon labrosus*	Reduction of swimming speed	Conditioned water	Marine	No	van Duren and Videler (1996)
Order Cyclopoida (mainly pelagic species)						
Cyclopoid copepods	Roach (*Rutilus rutilus*) and Perch (*Perca fluviatilis*)	No response to chemical stimuli	Field samples and experimental evidence	Limnic	No	Hansson(2004)
Diacyclops thomasi	Predatory cladoceran *Bythotrephes*	Deeper vertical distribution	Conditioned water	Limnic	No	Bourdeau *et al.* (2011)
Thermocyclops decipiens *Tropocyclops prasinus*	Midge larvae *Chaoborus brasiliensis*	Reversed DVM	Conditioned water	Limnic	No	Minto *et al.* (2010)
Order Harpacticoida (tidepool habitat)						
Tigriopus californicus	Sea anemone *A. elegantissima*	Avoidance behaviour, accumulation at surface	Stationary sea anemone in aquaria	Marine	No	Dethier (1980)

[a] Although 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.

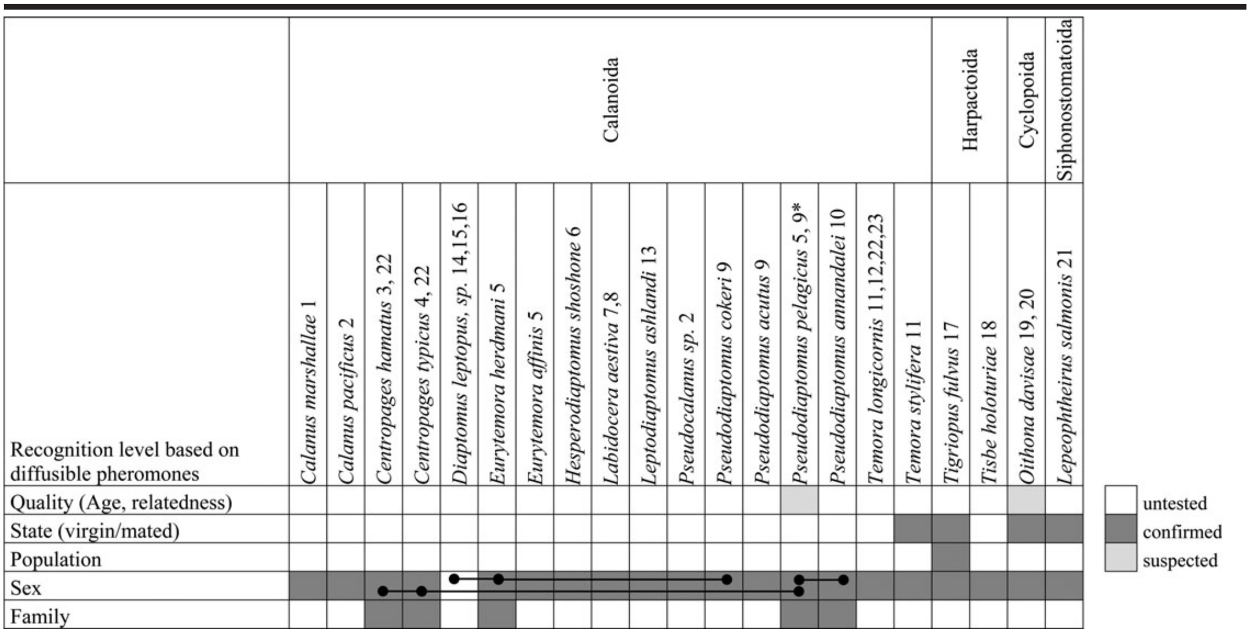
Parker (Parker, 1902) was the first to recognize the importance of chemical cues for copepod reproduction. He realized that males of *Labidocera aestiva* were attracted to waterborne signals from the females but not to those of males. Seventy years later Katona (Katona, 1973) described the male tracking 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 (Kiørboe, 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 Kiørboe, 2012; Seuront, 2013). Male search behaviour is characteristic and can be distinguished from normal feeding behaviour by increased directional swimming velocities (Heuschele and Kiørboe, 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 Kiørboe, 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; Kiørboe, 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	*Calanus marshallae* 1	*Calanus pacificus* 2	*Centropages hamatus* 3, 22	*Centropages typicus* 4, 22	*Diaptomus leptopus, sp.* 14,15,16	*Eurytemora herdmani* 5	*Eurytemora affinis* 5	*Hesperodiaptomus shoshone* 6	*Labidocera aestiva* 7,8	*Leptodiaptomus ashlandi* 13	*Pseudocalanus sp.* 2	*Pseudodiaptomus cokeri* 9	*Pseudodiaptomus acutus* 9	*Pseudodiaptomus pelagicus* 5, 9*	*Pseudodiaptomus annandalei* 10	*Temora longicornis* 11,12,22,23	*Temora stylifera* 11	*Tigriopus fulvus* 17	*Tisbe holoturiae* 18	*Oithona davisae* 19, 20	*Lepeophtheirus salmonis* 21
Quality (Age, relatedness)														░						░	
State (virgin/mated)																	▨	▨		▨	▨
Population																		▨			
Sex	▨	▨	▨ ●	▨ ●	●	▨ ●	▨	▨	▨	▨	▨	▨ ●	▨	▨ ● ●	▨ ●	▨	▨	▨	▨	▨	▨
Family			▨	▨		▨								▨	▨						

	untested
▨	confirmed
░	suspected

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 Kiørboe (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 Kiørboe (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 Kiørboe (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 harpactoid 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 harpactioid *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. CO_2 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

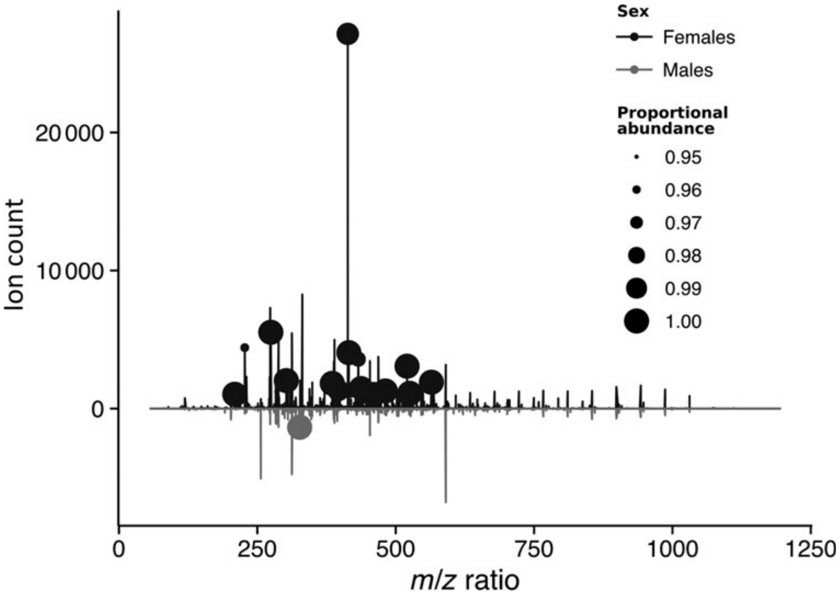


Fig. 3. Illustration of the differences in the exudate composition of male and female *O. davisae*. Dots indicate compounds that are relatively more abundant (>1000 peak height) and to 90% or more produced by the respective sex compared to the other. Exudates were extracted from same-sex incubations 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.

ACKNOWLEDGEMENTS

We thank T. Kiørboe, R. Gonçalves and two anonymous referees for helpful comments on the manuscript, M. Plambech and G. Nylund for help with copepod exudate extraction and analysis.

FUNDING

This work was supported by the Danish National Strategic Research Council—IMPAQ (grant no. 10-093522).

REFERENCES

Altner, I., Hatt, H. and Altner, H. (1983) Structural properties of bimodal chemo- and mechanosensitive setae on the pereiopod chelae of the crayfish, *Austropotamobius torrentium*. *Cell Tissue Res.*, **228**, 357–374.

Andrews, J. C. (1983) Deformation of the active space in the low Reynolds number feeding current of calanoid copepods. *Can. J. Fish. Aquat. Sci.*, **40**, 1293–1302.

Anstensrud, M. (1990) Mating strategies of two parasitic copepods [(*Lernaeocera branchialis* (L.)(Pennellidae) and *Lepeophtheirus pectoralis* (Müller)(Caligidae)] on flounder: polygamy, sex-specific age at maturity and sex ratio. *J. Exp. Mar. Biol. Ecol.*, **136**, 141–158.

Arnaud, J., Brunet, M. and Mazza, J. (1988a) Labral glands in *Centropages typicus* (Copepoda, Calanoida). I. Sites of synthesis. J. Morphol., **197**, 21–32.

Arnaud, J., Brunet, M. and Mazza, J. (1988b) The labral glands in *Centropages typicus* (Copepoda, Calanoida). II. Sites of secretory release. *J. Morphol.*, **197**, 209–219.

Bagøien, E. and Kiørboe, T. (2005) Blind dating—mate finding in planktonic copepods. I. Tracking the pheromone trail of *Centropages typicus*. *Mar. Ecol. Prog. Ser.*, **300**, 105–115.

Bailey, R. J., Birkett, M. A., Ingvarsdóttir, A. *et al.* (2006) The role of semiochemicals in host location and non-host avoidance by salmon louse (*Lepeophtheirus salmonis*) copepodids. *Can. J. Fish. Aquat. Sci.*, **63**, 448–456.

Bannister, N. J. (1993) Distribution and structure of sub-cuticular glands in the copepod *Temora longicornis*. *J. Mar. Biol. Ass. UK*, **73**, 97–107.

Barrientos, Y. (1980) Ultrastructure of sensory units of the first antennae of calanoid copepods. M.Sc. Thesis. University of Ottawa, ON.

Barthélémy, R.-M., Cuoc, C., Caubit, X. *et al.* (2001) The shell glands in some calanoid copepods (Crustacea). *Can. J. Zool.*, **79**, 1490–1502.

Barthélémy, R.-M., Cuoc, C., Defaye, D. *et al.* (1998) Female genital structures in several families of Centropagoidea (Copepoda: Calanoida). *Philos. T. Roy. Soc. B*, **353**, 721–736.

Barthélémy, R. M., Ohtsuka, S. and Soh, H. Y. (2003) Mating plug in the planktonic copepod *Tortanus* (Atortus) *rubidus*. *Plankton Biol. Ecol.*, **50**, 25–26.

Bell, S., Bron, J. E. and Sommerville, C. (2000) The distribution of exocrine glands in *Lepeophtheirus salmonis* and *Caligus elongatus* (Copepoda: Caligidae). *Contrib Zool*, **69**, 9–20. http://dpc.uba.uva.nl/ctz/vol69/nr01/art01.

Bergkvist, J., Selander, E. and Pavia, H. (2008) Induction of toxin production in dinoflagellates: the grazer makes a difference. *Oecologia*, **156**, 147–154.

Bergkvist, J., Thor, P., Jakobsen, H. *et al.* (2012) Grazer-induced chain length plasticity reduces grazing risk in a marine diatom. *Limnol. Oceanogr.*, **57**, 318–324.

Blades, F. and Youngbluth, M. J. (1980) Morphological, physiological and behavioural aspects of mating in calanoid copepods. In Kerfoot, W. C. (ed.), *Evolution and Ecology of Zooplankton Communities*. University Press of New England, Hanover, New Hampshire, pp. 39–51.

Blaustein, L. (1997) Non-consumptive effects of larval Salamandra on crustacean prey: can eggs detect predators? *Oecologia*, **110**, 212–217.

Bollens, S. M., Frost, B. W. and Cordell, J. R. (1994) Chemical, mechanical and visual cues in the vertical migration behaviour of the marine planktonic copepod *Acartia hudsonica*. *J. Plankton Res.*, **16**, 555–564.

Bourdeau, P. E., Pangle, K. L. and Peacor, S. D. (2011) The invasive predator Bythotrephes induces changes in the vertical distribution of native copepods in Lake Michigan. *Biol. Invasions*, **13**, 2533–2545.

Bowlby, M. R. and Case, J. E. (1991) Ultrastructure and neuronal control of luminous cells in the copepod *Gaussia princeps*. *Biol. Bull. Mar. Biol. Lab. Woods Hole*, **180**, 440–446.

Boxshall, G. A. and Huys, R. (1998) The ontogeny and phylogeny of copepod antennules. *Philos. T. Roy. Soc. B*, **353**, 765–786.

Bradford-Grieve, J. M. (2002) Colonization of the pelagic realm by calanoid copepods. *Hydrobiologia*, **485**, 223–244.

Breithaupt, T. (2011) *Chemical Communication in Crustaceans*. Springer, New York.

Brunet, M., Cuoc, C., Arnaud, J. *et al.* (1991) Tegumental glands in a copepod *Hemidiaptomus ingens*: structural, ultrastructural and cytochemical aspects. *Tissue and Cell*, **23**, 733–743.

Bundy, M. and Paffenhöfer, G. (1993) Innervation of copepod antennules investigated using laser scanning confocal microscopy. *Mar. Ecol. Prog. Ser.*, **102**, 1–14.

Buskey, E. J. (1984) Swimming pattern as an indicator of the roles of copepod sensory systems in the recognition of food. *Mar. Biol.*, **79**, 165–175.

Buskey, E. and Hartline, D. (2003) High-speed video analysis of the escape responses of the copepod *Acartia tonsa* to shadows. *Biol. Bull. US*, **204**, 28–37.

Buskey, E. J., Lenz, P. H. and Hartline, D. K. (2012) Sensory perception, neurobiology, and behavioural adaptations for predator avoidance in planktonic copepods. *Adapt. Behav.*, **20**, 57–66.

Ceballos, S. and Kiørboe, T. (2011) Senescence and sexual selection in a pelagic copepod. *PLoS One*, **6**, e18870. doi:10.1371/journal.pone.0018870.

Cembella, A. D. (2003) Chemical ecology of eukaryotic microalgae in marine ecosystems. *Phycologia*, **42**, 420–447.

Chae, J. and Nishida, S. (2004) Swimming behaviour and photoresponses of the iridescent copepods, *Sapphirina gastrica* and *Sapphirina opalina* (Copepoda: Poecilostomatoida). *J. Mar. Biol. Ass.*, **84**, 727–731.

Chow-Fraser, P. and Maly, E. (1988) Aspects of mating, reproduction, and co-occurrence in 3 freshwater Calanoid Copepods. *Freshwater Biol.*, **19**, 95–108.

Cieri, M. D. and Stearns, D. E. (1999) Reduction of grazing activity of two estuarine copepods in response to the exudate of a visual predator. *Mar. Ecol. Prog. Ser.*, **177**, 157–163.

Cohen, J. H. and Forward, R. B. Jr. (2005) Photobehaviour as an inducible defense in the marine copepod *Calanopia americana*. *Limnol. Oceanogr.*, **50**, 1269–1277.

Colin, S. (1995) A kinematic analysis of trail-following in *Temora longicornis* and four other copepods: how the male finds his mate. MS thesis. State University of New York at Stony Brook.

Corni, M., Vigoni, V. and Scanabissi, F. (2000) Ultrastructural aspects of the reproductive morphology and spermatophore placement of *Centropages kroyeri* Giesbrecht, 1892 (Copepoda, Calanoida). *Crustaceana*, **73**, 433–445.

Corni, M., Vigoni, V. and Scanabissi, F. (2001) Some ultrastructural features of the reproductive morphology and spermatophore placement of *Temora stylifera* Dana, 1849 (Copepoda, Calanoida). *Crustaceana*, **74**, 79–90.

Cowles, T. J., Olson, R. J. and Chisholm, S. W. (1988) Food selection by copepods-discrimination based on the basis of food quality. *Mar. Biol.*, **100**, 41–49.

Cowles, T. J. and Strickler, J. R. (1983) Characterization of feeding activity patterns in the planktonic copepod *Centropages typicus* Kroyer under various food conditions. *Limnol. Oceanogr.*, **28**, 106–115.

Crouau, Y. (1997) Comparison of crustacean and insect mechanoreceptive setae. *Int. J. Insect. Morphol. Embryol.*, **26**, 181–190.

Cuoc, C. and Defaye, D. (2011) Female genitalia in Cyclopidae (Copepoda, Cyclopoida): how to reinterpret the internal structures? In Defaye, D., Suarez-Morales, E. and von Vaupel-Klein, J. C. (eds), *Studies on Freshwater Copepoda: A Volume in Honour of Bernard Dussart*. Koninklijke Brill, NV Leiden, The Netherlands, Crustaceana Monographs, 16, pp. 119–148.

Dagg, M. J., Frost, B. W. and Walser, W. E. (1989) Copepod diel migration, feeding, and the vertical flux of pheopigments. *Limnol. Oceanogr.*, **34**, 1062–1071.

Dahms, H. U. and Qian, P. Y. (2006) Kin recognition during intraspecific predation of Harpacticus sp. (Copepoda, Harpacticoida). *Zoolog Stud.*, **45**, 395–403.

Daniel, P. C. and Derby, C. D. (1991) Mixture suppression in behaviour: the antennular flick response in the spiny lobster towards binary odorant mixtures. *Physiol. Behav.*, **49**, 591–601.

Demott, W. R. and Moxter, F. (1991) Foraging on cyanobacteria by copepods—responses to chemical defenses and resource abundance. *Ecology*, **72**, 1820–1834.

Derby, C. D., Carr, W. E. S. and Ache, B. W. (1984) Purinergic olfactory cells of crustaceans: response characteristics and similarities to internal purinergic cells of vertebrates. *J. Comp. Physiol. A*, **155**, 341–349.

Dethier, N. M. (1980) Tidepools as refugees: predation and the limits of the harpacticoid copepod *Tigriopus californicus* (Baker). *J. Exp. Mar. Biol. Ecol.*, **42**, 99–111.

Doall, M., Colin, S., Strickler, J. *et al.* (1998) Locating a mate in 3D: the case of *Temora longicornis*. *Philos. T. Roy. Soc. B*, **353**, 681–689.

Donaghay, P. L. and Small, L. F. (1979) Food selection capabilities of the estuarine copepod *Acartia clausi*. *Mar. Biol.*, **52**, 137–146.

Dur, G., Souissi, S., Schmitt, F. G. *et al*. (2011) Mating and mate choice in *Pseudodiaptomus annandalei* (Copepoda: Calanoida). *J. Exp. Mar. Biol. Ecol.*, **402**, 1–11.

Dusenbery, D. B. and Snell, T. W. (1995) A critical body size for use of pheromones in mate location. *J. Chem. Ecol.*, **21**, 427–438.

Elofsson, R. (1971) The ultrastructure of a chemoreceptor organ in the head of copepod crustaceans. *Acta Zoologica*, **52**, 299–315.

Elofsson, R. and Lake, P. S. (1971) On the cavity receptor organ (X-organ or organ of Bellonci) of *Artemia salina* (Crustacea: Anostraca). *Cell Tissue Res.*, **121**, 319–326.

Evans, G. T. (1989) The encounter speed of moving predator and prey. *J. Plankton Res.*, **11**, 415–417.

Fechter, A., Thistle, D., Arlt, G. *et al*. (2004) Do Harpacticoids (Copepoda) use water-borne cues to aid in locating food parcels? *Mar. Ecol.*, **25**, 217–223.

Ferrari, F. D. and Markhaseva, E. L. (1996) *Parkius karenwishnerae*, a new genus and species of calanoid copepod (Parkiidae, new family) from benthopelagic waters of the eastern tropical Pacific Ocean. *Proc. Biol. Soc. Wash.*, **109**, 264–285.

Fields, D. M., Shaeffer, D. S. and Weissburg, M. J. (2002) Mechanical and neural responses from the mechanosensory hairs on the antennule of *Gaussia princeps*. *Mar. Ecol. Prog. Ser.*, **227**, 173–186.

Fields, D. M., Weissburg, M. J. and Browman, H. I. (2007) Chemoreception in the salmon louse *Lepeophtheirus salmonis*: an electrophysiology approach. *Dis. Aquat. Organ.*, **78**, 161–168.

Fleminger, A. (1973) Pattern, number, variability, and taxonomic significance of integumental organs (sensilla and glandular pores) in the genus Eucalanus (Copepoda, Calanoida). *Fish. Bull.*, **71**, 965–1010.

Folt, C. and Goldman, C. R. (1981) Allelopathy between zooplankton: a mechanism for interference competition. *Science*, **213**, 1133–1135.

Friedman, M. M. (1980) Comparative morphology and functional significance of copepod receptors and oral structures. In Kerfoot, W. C. (ed.), *Evolution and Ecology of Zooplankton Communities*. Univ. Press of New England, Hanover, pp. 185–197.

Friedman, M. M. and Strickler, J. R. (1975) Chemoreceptors and feeding in calanoid copepods (Arthropda-Crustacea). *Proc. Natl Acad. Sci. USA*, **72**, 4185–4188.

Gardner, W. S. and Paffenhöfer, G. A. (1982) Nitrogen regeneration by the subtropical marine copepod *Eucalanus pileatus*. *J. Plankton Res.*, **4**, 725–734.

Garm, A., Hallberg, E. and Høeg, J. T. (2003) Role of maxilla 2 and its setae during feeding in the shrimp *Palaemon adspersus* (Crustacea: Decapoda). *Biol. Bull.*, **204**, 126–137.

Gerritsen, J. and Strickler, J. R. (1977) Encounter probabilities and community structure in zooplankton—mathematical-model. *J. Fish. Res. Board of Canada*, **34**, 73–82.

Giesbrecht, W. (1892) Systematik und Faunistik der pelagischen Copepoden des Golfes von Neapel und der angrenzenden Meeres-Abschnitte. *Fauna Flora Golf. Neapel*, **19**, 1–831.

Gill, C. (1986) Suspected mechano-and chemosensory structures of *Temora longicornis* (Copepoda: Calanoida). *Mar. Biol.*, **93**, 449–457.

Gill, C. and Poulet, S. (1988) Responses of copepods to dissolved free amino acids. *Mar. Ecol. Prog. Ser.*, **43**, 269–276.

Gillard, J., Frenkel, J., Devos, V. *et al*. (2012) Metabolomics enables the structure elucidation of a diatom sex pheromone. *Angew. Chem. Int. Ed.*, **52**, 854–957.

Goetze, E. (2008) Heterospecific mating and partial prezygotic reproductive isolation in the planktonic marine copepods "*Centropages typicus*" and "*Centropages hamatus*". *Limnol. Oceanogr.*, **53**, 433–445.

Goetze, E. and Kiørboe, T. (2008) Heterospecific mating and species recognition in the planktonic marine copepods *Temora stylifera* and *T.* longicornis. Mar. Ecol. Prog. Ser., **370**, 185–198.

Gophen, M. and Harris, R. P. (1981) Visual predation by a marine cyclopoid copepod, *Corycaeus anglicus*. *J. Mar. Biol. Assoc. UK*, **61**, 391–399.

Gresty, K. A., Boxshall, G. A. and Nagasawa, K. (1993) Antennulary sensors of the infective copepodid larva of the salmon louse, *Lepeophtheirus salmonis* (Copepoda: Caligidae). In: Boxshall, G. A. and Defaye, D. (eds), *Pathogens of Wild and Farmed Fish: Sea Lice*. CRC Press, pp. 83–98.

Griffiths, A. M. and Frost, B. W. (1976) Chemical communication in the marine planktonic copepods *Calanus pacificus* and *Pseudocalanus sp. Crustaceana*, **30**, 1–8.

Grünert, U. and Ache, B. (1988) Ultrastructure of the aesthetasc (olfactory) sensilla of the spiny lobster, Panulirus argus. *Cell Tissue Res.*, **251**, 95–103.

Gutierrez, M. F., Gagneten, A. M. and Paggi, J. C. (2011) Behavioural responses of two cladocerans and two copepods exposed to fish kairomones. *Mar. Freshw. Behav. Phy.*, **44**, 289–303.

Gutierrez, M. F., Paggi, J. C. and Gagneten, A. M. (2010) Fish kairomones alter life cycle and growth of a calanoid copepod. *J. Plankton Res.*, **32**, 47–55.

Hairston, N. G. and Walton, W. E. (1986) Rapid evolution of a life history trait. *Pro., Natl. Acad. Sci. USA*, **83**, 4831–4833.

Hallberg, E., Johansson, K. U. I. and Wallén, R. (1997) Olfactory sensilla in crustaceans: morphology, sexual dimorphism, and distribution patterns. *Int. J. Insect Morphol. Embryol.*, **26**, 173–180.

Hallberg, E. and Skog, M. (2011) Chemosensory sensilla in crustaceans. In Breithaupt, T. and Thiel, M. (eds), *Chemical Communication in Crustaceans*. Springer, Heidelberg, pp. 103–121.

Hansson, B. S. (1995) Olfaction in Lepidoptera. *Cell. Mol. Life Sci.*, **51**, 1003–1027.

Hansson, L. (2004) Plasticity in pigmentation induced by conflicting threats from predation and UV radiation. *Ecology*, **85**, 1005–1016.

Hansson, L. A. (2000) Induced pigmentation in zooplankton: a trade-off between threats from predation and ultraviolet radiation. *Proc. R. Soc. B*, **267**, 2327–2331.

Hardege, J. D., Bartels-Hardege, H. D., Fletcher, N. *et al*. (2011) Identification of a female sex pheromone in *Carcinus maenas*. *Mar. Ecol. Prog. Ser.*, **436**, 177–189.

Heuch, P., Doall, M. and Yen, J. (2007) Water flow around a fish mimic attracts a parasitic and deters a planktonic copepod. *J. Plankton Res.*, **29**, i3–i16.

Heuschele, J. and Kiørboe, T. (2012) The smell of virgins: mating status of females affects male swimming behaviour in *Oithona davisae*. *J. Plankton Res.*, **34**, 929–935.

Hicks, G. R. F. (1977) Observations on substrate preference of marine phytal harpacticoids (Copepoda). *Hydrobiologia*, **56**, 7–9.

Hipeau-Jacquotte, R. (1986) A new cephalic type of presumed sense organ with naked dendritic ends in the atypical male of the parasitic copepod *Pachypygus gibber* (Crustacea). *Cell Tissue Res.*, **245**, 29–35.

Huntley, M., Sykes, P., Rohan, S. *et al*. (1986) Chemically mediated rejection of dinoflagellate prey by the copepods *Calanus pacificus* and *Paracalanus parvus*: mechanism, occurrence and significance. *Mar. Ecol. Prog. Ser.*, **28**, 105–120.

Huys, R. and Boxshall, G. A. (1991) *Copepod Evolution*. Ray Society, London, Vol. 159.

Hylander, S., Larsson, N. and Hansson, L.-A. (2009) Zooplankton vertical migration and plasticity of pigmentation arising from simultaneous UV and predation threats. *Limnol. Oceanogr.*, **54**, 483–491.

Hylander, S., Souza, M. S., Balseiro, E. *et al*. (2012) Fish-mediated trait compensation in zooplankton. *Funct. Ecol.*, **26**, 608–615.

Ingvarsdottir, A., Birkett, M., Duce, I. *et al*. (2002) Role of semiochemicals in mate location by parasitic sea louse, *Lepeophtheirus salmonis*. *J. Chem. Ecol.*, **28**, 2107–2117.

Jacoby, C. and Youngbluth, M. (1983) Mating behavior in three species of Pseudodiaptomus (Copepoda: Calanoida). *Mar. Biol.*, **86**, 77–86.

Jakobsen, H. H. and Tang, K. W. (2002) Effects of protozoan grazing on colony formation in *Phaeocystis globosa* (Prymnesiophyceae) and the potential costs and benefits. *Aquatic Microbial. Ecol.*, **27**, 261–273.

Jiang, X., Lonsdale, D. J. and Gobler, C. J. (2010) Grazers and vitamins shape chain formation in a bloom-forming dinoflagellate, *Cochlodinium polykrikoides*. *Oecologia*, **164**, 455–464.

Jiang, H., Osborn, T. R. and Meneveau, C. (2002) Chemoreception and the deformation of the active space in freely swimming copepods: a numerical study. *J. Plankton Res.*, **24**, 495–510.

Karlson, P. and Lüscher, M. (1959) "Pheromones": a new term for a class of biologically active substances. *Nature*, **183**, 55–56.

Katona, S. (1973) Evidence for sex pheromones in planktonic copepods. *Limnol. Oceanogr.*, **18**, 574–583.

Kats, L. B. and Dill, L. M. (1998) The scent of death: chemosensory assessment of predation risk by prey animals. *Ecoscience*, **5**, 361–394.

Kiørboe, T. (2007) Mate finding, mating, and population dynamics in a planktonic copepod *Oithona davisae*: there are too few males. *Limnol. Oceanogr.*, **52**, 1511–1522.

Kiørboe, T. (2008a) *A Mechanistic Approach to Plankton Ecology.* Princeton University Press, Princeton, NJ.

Kiørboe, T. (2008b) Optimal swimming strategies in mate-searching pelagic copepods. *Oecologia*, **155**, 179–192.

Kiørboe, T., Andersen, A., Langlois, V. J. *et al*. (2009) Mechanisms and feasibility of prey capture in ambush-feeding zooplankton. *Proc. Natl Acad. Sci. USA*, **106**, 12394–12399.

Kittredge, J. S., Terry, M. and Takahashi, T. (1971) Sex pheromone activity of the molting hormone, Crustecdysone, on male crabs (*Pachygrapsus crassipes*, *Caner antennarius*, and *C. anthonyi*). *Fish. Bull.*, **69**, 337–343.

Koehl, M. and Strickler, J. R. (1981) Copepod feeding currents: food capture at low Reynolds number. *Limnol. Oceanogr.*, **26**, 1062–1073.

Koomen, P. (1992) The integumental perforation pattern of the *Euchirella messinensis* female (Copepoda, Calanoida): corrections, additions, intraspecific variation, and a checklist of pore sites. *Crustaceana*, **63**, 113–159.

Koomen, P. and von Vaupel Klein, J. C. (1998) The integumental perforation pattern of the *Undeuchaeta incisa* female (Copepoda, Calanoida). *J. Mar. Systems*, **15**, 401–412.

Koski, M., Engström, J. and Viitasalo, M. (1999) Reproduction and survival of the calanoid copepod *Eurytemora affinis* fed with toxic and nontoxic cyanobacteria. *Mar. Ecol. Prog. Ser.*, **186**, 187–197. http://www.int-res.com/abstracts/meps/v186/p187-197/ (accessed 18 February 2014).

Lasley-Rasher, R. S. and Yen, J. (2012) Predation risk suppresses mating success and offspring production in the coastal marine copepod, *Eurytemora herdmani*. *Limnol. Oceanogr.*, **57**, 433–440. doi:10.4319/lo.2012.57.2.0433.

Lazzaretto, I., Franco, F. and Battaglia, B. (1994) Reproductive behaviour in the Harpacticoid copepod *Tigriopus fulvus*. *Hydrobiologia*, **293**, 229–234.

Lazzaretto, I., Franco, F., Serman, A. *et al*. (1993) Aspects of mating behaviour in two harpacticoid copepods: *Tigriopus fulvus* and *Tisbe holothuriae*. *Rendiconti Lincei*, **4**, 337–344.

Lazzaretto, I. and Salvato, B. (1992) Cannibalistic behaviour in the harpacticoid copepod *Tigriopus fulvus*. *Mar. Biol.*, **113**, 579–582.

Lazzaretto, I., Salvato, B. and Libertini, A. (1990) Evidence of chemical signaling in *Tigriopus fulvus* (Copepoda, Harpacticoida). *Crustaceana*, **59**, 171–179.

Le Borgne, R. P. (1986). The release of soluble end products of metabolism. In Corner, E. D. S. and O'Hara, S. C. M. (eds), *The Biological Chemistry of Marine Copepods*. Clarendon Press, Oxford. pp. 109–164.

Lee, C. M. (1972) Structure and function of the spermatophore and its coupling device in the Centropagidae (Copepoda: Calanoida). *Bull. Mar. Ecol.*, **8**, 1–20.

Lenz, P. H. (2012) The biogeography and ecology of myelin in marine copepods. *J. Plankton Res.*, **34**, 575–589.

Lenz, P. H., Hartline, D. K. and Davis, A. D. (2000) The need for speed. I. Fast reactions and myelinated axons in copepods. *J. Comp. Phys. A*, **186**, 337–345.

Lenz, P. H., Weatherby, T. M., Weber, W. *et al*. (1996) Sensory specialization along the first antenna of a calanoid copepod, *Pleuromamma xiphias* (Crustacea). *Mar. Freshwater Behav. Physiol.*, **27**, 213–221.

Lenz, P. H. and Yen, J. (1993) Distal setal mechanoreceptors of the first antennae of marine copepods. *B. Mar. Sci.*, **53**, 170–179.

Lombard, F., Koski, M. and Kiørboe, T. (2013) Copepods use chemical trails to find sinking marine snow aggregates. *Limnol. Oceanogr.*, **58**, 185–192.

Long, J. D., Smalley, G. W., Barsby, T. *et al*. (2007) Chemical cues induce consumer-specific defenses in a bloom-forming marine phytoplankton. *Proc. Natl Acad. Sci. USA*, **104**, 10512–10517.

Lonsdale, D. J., Frey, M. and Snell, T. W. (1998) The role of chemical signals is copepod reproduction. *J. Marine Syst.*, **15**, 1–12.

Martin, J. W. and Laverack, M. S. (1992) On the distribution of the crustacean dorsal organ. *Acta Zoologica*, **73**, 357–368.

Mauchline, J. (1988a) Taxonomic value of pore pattern in the integument of calanoid copepods (Crustacea). *J. Zool.*, **214**, 697–749.

Mauchline, J. (1998b) The biology of calanoid copepods. *Adv. Mar. Biol.*, **33**, 1–710.

Minto, W. J., Arcifa, M. S. and Perticarrari, A. (2010) Experiments on the influence of *Chaoborus brasiliensis* Theobald, 1901 (Diptera: Chaoboridae) on the diel vertical migration of microcrustaceans from Lake Monte Alegre, Brazil. *Brazilian J. Biol.*, **70**, 25–35.

Moore, P. A., Fields, D. M. and Yen, J. (1999) Physical constraints of chemoreception in foraging copepods. *Limnol. Oceanogr.*, **44**, 166–177.

Mordue Luntz, A. J. and Birkett, M. A. (2009) A review of host finding behaviour in the parasitic sea louse, *Lepeophtheirus salmonis* (Caligidae: Copepoda). *J. Fish Diseases*, **32**, 3–13. doi:10.1111/j.1365-2761.2008.01004.x.

Neill, W. E. (1990) Induced vertical migration in copepods as a defence against invertebrate predation. *Nature*, **345**, 524–526.

Nihongi, A., Lovern, S. B. and Strickler, J. R. (2004) Mate-searching behaviours in the freshwater calanoid copepod *Leptodiaptomus ashlandi*. *J. Marine Syst.*, **49**, 65–74.

Nishida, S. (1989) Distribution, structure and importance of the cephalic dorsal hump, a new sensory organ in calanoid copepods. *Mar. Biol.*, **101**, 173–185.

Nishida, S. and Nonomura, T. (2011) Structure of novel exocrine glands in *Calanus* species with notes on their possible function. *J. Mar. Biol. Assoc. UK*, **91**, 801–805.

Nishida, S. and Ohtsuka, S. (1997) Ultrastructure of the mouthpart sensory setae in mesopelagic copepods of the family Scolecitrichidae. *Plankton Biol. Ecol.*, **44**, 81–90.

Ohtsuka, S. and Huys, R. (2001) Sexual dimorphism in calanoid copepods: morphology and function. *Hydrobiologia*, **453**, 441–466.

Ohtsuka, S. and Mitsuzumi, C. (1990) A new asymmetrical near-bottom calanoid copepod, *Paramisophria platysoma*, with observations of its integumental organs, behaviour and in-situ feeding habit. *Bull. Plankton Soc. Japan*, **36**, 87–101.

Østergaard, P. and Boxshall, G. A. (2004) Giant females and dwarf males: a comparative study of nuptial organs in female Chondracanthidae (Crustacea: Copepoda). *Zool. Anz.*, **243**, 65–74.

Paffenhöfer, G. A. and Loyd, P. A. (1999) Ultrastructure of setae of the maxilliped of the marine planktonic copepod *Temora stylifera*. *Mar. Ecol. Prog. Ser.*, **178**, 101–107.

Paffenhöfer, G. A. and Loyd, P. A. (2000) Ultrastructure of cephalic appendage setae of marine planktonic copepods. *Mar. Ecol. Prog. Ser.*, **203**, 171–180.

Paffenhöfer, G. A. and Van Sant, K. B. (1985) The feeding response of a marine planktonic copepod to quantity and quality of particles. *Mar. Ecol. Prog. Ser.*, **27**, 55–65.

Park, T. S. (1966) The biology of a calanoid copepod, *Epilabidocera amphitrites*. *Cellule*, **66**, 129–251.

Parker, G. H. (1902) The reactions of copepods to various stimuli and the bearing of this on daily depth-migrations. *Bull. US Fish Comm. Doc.*, **497**, 103–123.

Pohnert, G., Steinke, M. and Tollrian, R. (2007) Chemical cues, defence metabolites and the shaping of pelagic interspecific interactions. *Trends Ecol. Evol.*, **22**, 198–204.

Por, F. D. and Hadel, V. F. (1986) Two new species of *Attheyella* (Copepoda: Harpacticoidea: Canthocamptidae) from Bromeliads of the Serra da Juréia (São Paulo, Brazil). *J. of Crustacean Biol.*, **6**, 777–788.

Poulet, S. A. and Gill, C. W. (1988) Spectral analyses of movements made by the cephalic appendages of copepods. *Mar. Ecol. Prog. Ser.*, **43**, 259–267.

Poulet, S. A. and Marsot, P. (1978) Chemosensory grazing by marine calanoid copepods (Arthropoda: Crustacea). *Science*, **200**, 1403–1405.

Poulet, S. A. and Marsot, P. (1980) Chemosensory feeding and food-gathering by omnivorous marine copepods. In Kerfoot, W. C. (ed.), T*he Evolution and Ecology of Zooplankton Communities*. University Press of New England, Hanover, NH, USA, pp. 198–218.

Poulet, S. A. and Ouellet, G. (1982) The role of amino acids in the chemosensory swarming and feeding of marine copepods. *J. Plankton Res.*, **4**, 341–361.

Preisser, E. L., Bolnick, D. I. and Benard, M. F. (2005) Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology*, **86**, 501–509.

Regnault, M. (1987) Nitrogen excretion in marine and freshwater crustacea. *Biol. Rev.*, **62**, 1–24.

Rengefors, K., Karlsson, I. and Hansson, L.-A. (1998) Algal cyst dormancy: a temporal escape from herbivory. *Proc. R. Soc. Lond. B*, **265**, 1353–1358.

Rittschof, D. and Cohen, J. H. (2004) Crustacean peptide and peptide-like pheromones and kairomones. *Peptides*, **25**, 1503–1516.

Seifried, S. and Dürbaum, J. (2000) First clear case of carnivory in marine Copepoda Harpacticoida. *J. Nat. Hist.*, **34**, 1595–1618.

Selander, E., Fagerberg, T., Wohlrab, S. *et al.* (2012) Fight and flight in marine dinoflagellates?—kinetics of simultaneous grazer induced responses in *Alexandrium tamarense*. *Limnol. Oceanogr.*, **57**, 58–64.

Selander, E., Jakobsen, H. H., Lombard, F. *et al.* (2011) Grazer cues induce stealth behaviour in marine dinoflagellates. *Proc. Natl Acad. Sci. USA*, **108**, 4030–4034. doi:10.1073/pnas.1011870108.

Selander, E., Thor, P., Toth, G. B. *et al.* (2006) Copepods induce paralytic shellfish toxin production in marine dinoflagellates. *Proc. R. Soc. Lond. B*, **273**, 1673–1680.

Seuront, L. (2011) Hydrocarbon contamination decreases mating success in a marine planktonic copepod. *PLoS One*, **6**, e26283. doi:10.1371/journal.pone.0026283.

Seuront, L. (2013) Chemical and hydromechanical components of mate-seeking behaviour in the calanoid copepod *Eurytemora affinis*. *J. Plankton Res.*, **35**, 724–743.

Seuront, L. and Stanley, H. E. (2014) Anomalous diffusion and multifractality enhance mating encounters in the ocean. *Proc. Natl Acad. Sci.*, **111**, 2206–2211.

Slifer, E. (1970) The structure of arthropod chemoreceptors. *Annu Rev Entomol*, **15**, 121–142.

Smith, J. M. and Harper, D. D. (2003) *Animal Signals*. Oxford University Press, New York, USA.

Snell, T. (2010) *Chemical Communication in Crustaceans*. Springer, New York, NY.

Snell, T. and Carmona, M. (1994) Surface glycoproteins in copepods—potential signals for mate recognition. *Hydrobiologia*, **293**, 255–264.

Snell, T. and Morris, P. (1993) Sexual communication in copepods and rotifers. *Hydrobiologia*, **255**, 109–116.

Stearns, D. E. (1986) Copepod grazing behavior in simulated natural light and its relation to nocturnal feeding *Mar. Ecol. Prog. Ser.*, **30**, 65–76.

Stearns, D. E. and Forward, R. B. (1984) Photosensitivity of the calanoid copepod *Acartia tonsa*. *Mar. Biol.*, **82**, 85–89.

Steinke, M., Stefels, J. and Stamhuis, E. (2006) Dimethyl sulfide triggers search behaviour in copepods. *Limnol. Oceanogr.*, **51**, 1925–1930.

Strickler, J. R. (1982) Calanoid copepods, feeding currents, and the role of gravity. *Science*, **218**, 158–160.

Strickler, J. R. and Bal, A. K. (1973) Setae of the first antennae of the copepod *Cyclops scutifer* (Sars): their structure and importance. *Proc. Natl Acad. Sci. USA*, **70**, 2656–2659.

Teegarden, G. J. (1999) Copepod grazing selection and particle discrimination on the basis of PSP toxin content. *Mar. Ecol. Prog. Ser.*, **181**, 163–176.

Thomas, M. L. (2010) Detection of female mating status using chemical signals and cues. *Biol. Rev.*, **86**, 1–13.

Tiselius, P. (1992) Behaviour of *Acartia tonsa* in patchy food environments. *Limnol. Oceanogr.*, **37**, 1640–1651.

Tiselius, P., Saiz, E. and Kiørboe, T. (2013) Sensory capabilities and food capture of two small copepods *Paracalanus parvus* and *Pseudocalanus sp. Limnol. Oceanogr.*, **58**, 1657–1666.

Tranter, D. J., Bulleid, N. C., Campbell, R. *et al*. (1981) Nocturnal movements of phototactic zooplankton in shallow waters. *Mar. Biol.*, **61**, 317–326.

Tsuda, A. and Miller, C. (1998) Mate-finding behaviour in *Calanus marshallae* Frost. *Philos. T. Roy. Soc. B.*, **353**, 713–720.

Turner, J. T. (2004) The importance of small planktonic copepods and their roles in pelagic marine food webs. *Zool. Stud.*, **43**, 255–266.

Uchima, M. (1985) Copulation in the marine copepod *Oithona davisae* Ferrari & Orsi, 1: Mate discrimination. *Bull. Plankton Soc. Japan*, **32**, 23–30.

Uchima, M. and Murano, M. (1988) Mating behaviour of the marine copepod *Oithona davisae*. *Mar. Biol.*, **99**, 39–45.

Vanderploeg, H. A. and Paffenhöfer, G. A. (1985) Modes of algal capture by the freshwater copepod *Diaptomus sicilis* and their relation to food-size selection. *Limnol. Oceanogr.*, **30**, 871–885.

Van Donk, E., Ianora, A. and Vos, M. (2011) Induced defences in marine and freshwater phytoplankton: a review. *Hydrobiologia*, **668**, 3–19.

van Duren, L. A. and Videler, J. J. (1996) The trade-off between feeding, mate seeking and predator avoidance in copepods: behavioural responses to chemical cues. *J. Plankton Res.*, **18**, 805–818.

Van Leeuwen, H. and Maly, E. (1991) Changes in swimming behaviour of male *Diaptomus leptopus* (Copepoda: Calanoida) in response to gravid females. *Limnol. Oceanogr.*, **36**, 1188–1195.

Visser, A. and Jackson, G. A. (2004) Characteristics of the chemical plume behind a sinking particle in a turbulent water column. *Mar. Ecol. Prog. Ser.*, **283**, 55–71.

Visser, A. W. and Kiørboe, T. (2006) Plankton motility patterns and encounter rates. *Oecologia*, **148**, 538–546.

von Vaupel Klein, V. (1982) A taxonomic review of the genus *Euchirella* Giesbrecht, 1888 (Copepoda, Calanoida). II. The type-species, *Euchirella messinensis* (Claus, 1863). A. The female of F. typica. *Zool. Verh., Leiden*, **198**, 1–131.

Watras, C. (1983) Mate location by diaptomid copepods. *J. Plankton Res.*, **5**, 417–423.

Weatherby, T. M. and Lenz, P. H. (2000) Mechanoreceptors in calanoid copepods: designed for high sensitivity. *Arthropod Struct. Dev.*, **29**, 275–288.

Weatherby, T. M., Wong, K. K. and Lenz, P. H. (1994) Fine structure of the distal sensory setae on the first antennae of *Pleuromamma xiphias* Giesbrecht (Copepoda). *J. Crustacean Biol.*, **14**, 670–685.

Webster, D. R. and Weissburg, M. J. (2009) The hydrodynamics of chemical cues among aquatic organisms. *Annu. Rev. Fluid Mech.*, **41**, 73–90.

Weissburg, M., Doall, M. and Yen, J. (1998) Following the invisible trail: kinematic analysis of mate-tracking in the copepod *Temora longicornis*. *Philos. T. Roy. Soc. B.*, **353**, 701–712.

Wohlrab, S., Iversen, M. H. and John, U. (2010) A molecular and co-evolutionary context for grazer induced toxin production in *Alexandrium tamarense*. *Plos One*, **5**, e15039.

Woodson, C. B., Webster, D. R., Weissburg, M. J. *et al*. (2007a) The prevalence and implications of copepod behavioral responses to oceanographic gradients and biological patchiness. *Integr. Comp. Biol.*, **47**, 831–846.

Woodson, C. B., Webster, D. R., Weissburg, M. J. *et al*. (2007b) Cue hierarchy and foraging in calanoid copepods: ecological implications of oceanographic structure. *Mar. Ecol. Prog. Ser.*, **330**, 163–177.

Wyatt, T. D. (2009) Fifty years of pheromones. *Nature*, **457**, 262–263.

Yang, I., Selander, E., Pavia, H. *et al*. (2011) Grazer-induced toxin formation in dinoflagellates: a transcriptomic model study. Europ. J. Phyco*logy*, **46**, 66–73.

Yen, J. (1988) Directionality and swimming speeds in predator-prey and male-female interactions of *Euchaeta rimana*, a subtropical marine copepod. *B. Mar. Sci.*, **43**, 395–403.

Yen, J. and Lasley, R. (2010) Chemical communication between copepods: finding the mate in a fluid environment. In Breithaupt, T. and Thiel, M. (eds) *Chemical Communication in Crustaceans*. Springer New York, New York, NY, pp. 177–197.

Yen, J., Lenz, P. H., Gassie, D. V. *et al*. (1992) Mechanoreception in marine copepods: electrophysiological studies on the first antennae. *J. Plankt. Res.*, **14**, 495–512.

Yen, J., Sehn, J. K., Catton, K. *et al*. (2011) Pheromone trail following in three dimensions by the freshwater copepod *Hesperodiaptomus shoshone*. *J. Plankton Res.*, **33**, 907–916.

Yen, J., Weissburg, M. J. and Doall, M. H. (1998) The fluid physics of signal perception by mate-tracking copepods. *Philos. T. R. Soc. B.*, **353**, 787–804.