Ecology and biology of chemoreception in polychaetes

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Abstract

Nervous system and sensory structure morphologies provide useful information for reconstructing phylogenetic relationships among the Polychaeta, Annelida, and Arthropoda. With the more common use of indirect immunocytochemistry and laser scanning confocal microscopy methods, the detailed information available from morphological studies has increased. Despite this wealth of information, developing an integrated understanding of the ecology, physiology, morphology, and molecular mechanisms of sensory systems in polychaetes remains a challenge.

For many marine organisms, including polychaetes, chemical signals and chemoreception mediate numerous ecologically important behaviors including defense, reproduction, recruitment, and feeding, yet the mechanism of chemoreception in polychaetes has not been well described. This review summarizes research on the ecology and biology of polychaete chemoreception, particularly as it mediates reproduction, recruitment, and feeding, discusses the chemosensory structures of polychaetes, and describes recent advances in our understanding of chemoreception mechanisms in polychaetes.

Key words: Annelida, *Capitella*, G-protein, deposit-feeding, larval recruitment, olfaction, pheromones, signal transduction

Introduction

As a group, the polychaetes are equipped with an impressive array of sensory structures with which to gain information about their environment (e.g., review by Purschke 2005). Although studies comparing morphology and development of sensory structures have led to new insights about the possible phylogenetic relationships among polychaete taxa, far fewer studies have demonstrated the physiological function and sensitivities of sensory structures. Indeed, the status of polychaete sensory biology was aptly summed up by Purschke (2005): "To date the function of many sensory structures found in polychaetes is still uncertain or completely unknown." Identification of sensory signal transduction pathways in polychaetes lags considerably behind such research in other invertebrate taxa. In one notable exception, the recent work by Arendt et al. (2004) on photoreceptor proteins in *Platynereis dumerilii* Audouin & Milne-Edwards revealed intriguing similarities to vertebrate visual systems and sheds light on the evolution of vision in the metazoa (Fernald 2006).

Comparative chemoreception has emerged as a rich research area (reviewed by Bargmann 2006), yet in terms of examining the neurobiology and evolution of chemoreception mechanisms, research to date has been largely limited to relatively few "model organisms" that do not include many lophotrochozoan taxa (Table 1; Eisthen 2002). Chemoreception is a general term that refers to the

perception of chemical stimuli and includes both olfaction (smell) and gustation (taste). For many marine organisms, including polychaetes, chemical cues and chemoreception mediate numerous ecologically important behaviors including defense, reproduction, recruitment, and feeding (reviewed by Zimmer & Butman 2000). Despite its ecological importance, the molecular mechanisms of polychaete chemoreception remain relatively unknown.

TABLE 1. Examples of "valuable model organisms" for which much data concerning the neurobiology or molecular mechanisms of chemoreception are available.

Phylum	Class	Number of taxa identified per class	Genus & Species	Common name(s)
Nematoda	Secernentea	1	*Caenorhabditis elegans* Maupas	
Arthropoda	Malacostraca	2	*Panulirus argus* Latreille	Caribbean spiny lobster
	Insecta	6	*Manduca sexta* L.	Tobacco horn worm, hawk moth, sphinx moth
			Drosophila melanogaster Meigen	Fruit fly
Mollusca	Gastropoda	4	*Lymnaea stagnalis* L. [a]	Pond snail
Chordata Subphylum Vertebrata	Actinopterygii	4	*Danio rerio* Hamilton	Zebrafish
			Carassius auratus L.	Goldfish
			Ictalurus punctatus L.	Channel catfish
	Amphibia	4	*Ambystoma tigrinum* Green	Tiger salamander
	Mammalia	8	*Mus musculus domesticus* L.	House mouse
			Rattus norvegicus Berkenhout	Norway rat
			Homo sapiens L.	Human

Adapted from Table 1 in Eisthen (2002).
[a]Eisthen did not include *Lymnaea stagnalis* among the 29 taxa commonly used in neurobiological chemoreception research, but the pond snail may be emerging as a useful gastropod model.

In this paper, I undertake a brief review of the ecology and biology of polychaete chemoreception, particularly as it mediates reproduction, recruitment, and feeding, discuss the chemosensory structures of polychaetes, and describe recent advances in our understanding of chemoreception mechanisms in polychaetes. Because the purpose of this review is to integrate studies of ecology, behavior, morphology, and mechanisms of polychaete chemoreception, its scope in each of these areas is necessarily limited. For example, the use of chemical defenses by polychaetes is mentioned only briefly, because much of this research has focused on the identification of defensive chemical compounds that deter predator feeding (e.g., Gaston & Slattery 2002; Kicklighter et al. 2004) rather than how these chemical signals mediate polychaete behavior (an exception to this will be discussed in the section on larval settlement). Similarly, the importance of fluid dynamics in determining chemical delivery to organisms either in the water column or at the

sediment-water interface has been ably reviewed by others (Weissburg 2000; Zimmer & Butman 2000). In each case considered, I have attempted to summarize the current state of knowledge and to highlight recent research; in some cases relevant older literature will have been subsumed in citations of review papers, and other research is certain to have been unintentionally slighted. Interested readers are encouraged not only to consult the cited reviews, but to delve deeper into the older literature, for many of the observations made by researchers in the late 1960s and the 1970s still represent our best knowledge concerning chemoreception in some polychaete taxa.

Chemical signals and polychaete reproduction

Polychaete reproduction is controlled by environmental and endocrine factors, and further, synchronous spawning and mating behaviors in some species are coordinated through various chemical signals including pheromones (reviewed by Andries 2001; Hardege 1999; Hardege et al. 2004). The coordination of spawning and mating by chemical signals has been best studied in the nereidid polychaetes (Hardege 1999), and for species that swarm and spawn in the water column these behaviors follow several steps that are coordinated by pheromones. First, when heteronereids swarm at the surface, males and females release sex-specific enantiomers of 5-methyl-3heptanone, which induces swimming in circles of decreasing size (Zeeck et al. 1988). *Nereis succinea* (Frey & Leuchart) females also release a second mate recognition pheromone (Beckmann 1996); this mate recognition pheromone has been identified as cysteine-glutathione disulfide (also termed CSSG, or nereithione, Hardege et al. 2004). As the males swim in circles around a female, they release a cloud of sperm and coelomic fluid that contains an egg release pheromone. The female commences a nuptial dance (swimming in narrow high velocity circles), discharges her eggs and with them sperm release pheromone, which causes males to swim with increasing speed and emit large amounts of sperm. The chemical nature of these pheromones and their actions on various nereidids are summarized in Table 2.

An interesting characteristic of the chemical signals that induce nereidid spawning is their heterospecific activity. For example, Watson et al. (2003) found that gonadal and body fluid extracts from echinoderms, herring, and *Arenicola marina* (L.), as well as body fluid and spawning water of *Nereis virens* Sars induced spawning activity in male *Nereis succinea*. Extracts from male herring induced spawning activity in male *Platynereis dumerilii*, as did the cryptomonad *Rhodomonas baltica* Karsten. The active fraction of *R. baltica* was similar to uric acid, which is the natural sperm release pheromone produced by female *P. dumerilii* (Zeeck et al. 1996). Conspecific extracts of spawning water and gonadal material did not induce spawning activity in *A. marina* and *N. virens*. The former result contradicts earlier observations and remains to be clarified, and based on the latter result, the authors suggest that pheromones are not important for the intertidally spawning *N. virens*. The authors also suggested that the heterospecific activity from the invertebrate extracts might be due to the presence of glutathione in the extracts, but this was not determined.

Pheromonal control of spawning is not restricted to mobile semelparous free-spawners, and the lugworm *Arenicola marina* has also received considerable attention. In addition to environmental signals, hormones control egg maturation, sperm activation, and the process of gamete release in *A. marina* (Howie 1961, 1984; Pacey & Bentley 1992; Hardege & Bentley 1997; summarized in Table 2). Briefly, a prostomial maturation hormone induces the production of a coelomic maturation factor (CMF) (Watson & Bentley 1997), which then causes oocytes to proceed from prophase to metaphase of the first meiotic division. The chemical nature of the prostomial hormone and CMF is not known, but CMF appears to be proteinaceous and has a molecular mass >30 kDa (Watson & Bentley 1998).

The fatty acid, 8, 11,14 eicosatrienoic acid activates sperm and induces spawning in males (Pacey & Bentley 1992). Additional waterborne volatile organic substance(s) released by the male induce females to vigorously pump water through their burrows, resulting in sperm entering the burrow where eggs are retained and presumably maximizing the probability of successful fertilization (Hardege et al. 1996; Hardege & Bentley 1997).

TABLE 2. Chemical signals involved in coordinating reproduction in nereidid polychaetes and *Arenicola marina*.

Chemical Signal	Role (species)	Reference(s)
5-Methyl-3-Heptanone	· Released by swarming nereidids and prompts "nuptial dance" (Pd, Ns) · Inhibits spawning (Nv)	Zeeck et al. 1988, 1992; Hardege 1992 as cited in Hardege 1999
3,5 octadiene-2-one	· Induces swarming behavior (Nj)	Bartels-Hardege et al. 1996
Cysteine-glutathione disulfide (CSSG, nereithione)	· Mate recognition & tracking pheromone (Ns) · Sperm-release pheromone (Ns)	Beckmann 1996 as cited in Hardege 1999; Zeeck et al. 1998a; Hardege et al. 2004; Ram et al. 2008
L-Glutamic acid + inosine + L-Glutamine + guanosine	· Egg release pheromone bouquet (Ns males)	Zeeck et al. 1998b
Uric acid	· Sperm-release pheromone (Pd females)	Zeeck et al. 1996, 1998c
Prostomial maturation hormone	· Induces production of coelomic maturation factor (Am)	Watson & Bentley 1997, 1998
Coelomic maturation factor	· Prompts oocyte maturation (Am)	Watson & Bentley 1997, 1998
8,11,14-eicosotrienoic acid	· Sperm maturation factor (Am) · spawning (gamete release) (Am)	Bentley et al. 1990; Pacey & Bentley 1992
Gamete-release pheromone(s)	· Induces sperm release (Am females)	Hardege & Bentley 1997
Volatile organic substance (possibly 2-ethyl-1-hexanol)	· Induces pumping seawater into burrow by female (Am males)	Hardege et al. 1996

Abbreviations: Am, *Arenicola marina*; Nj, *Neanthes japonica*; Ns, *Nereis succinea*; Nv, *Nereis virens*; Pd, *Platynereis dumerilii*

Although research has been most comprehensive in the nereidids and *A. marina*, chemical signals undoubtedly play a role in reproduction of other polychaete species. For example, in spionid polychaetes, females of some species use feeding palps to manipulate spermatophores transferred from males (Rice 1978), and some females can discriminate between spermatophores produced by conspecifics *versus* closely related species (Rice 1978, 1991). Recent research suggests a prostomial hormone coordinates spawning and oogenesis in the scaleworm *Harmothoe imbricata* (L.), and that females produce a waterborne pheromone that attracts males and prompts stereotypical pairing behavior (Watson et al. 2000; Gaudron *et al.* 2007). Voronezhskaya et al. (2008) recently described a novel form of chemical signaling during polychaete reproduction in which adult *Platynereis dumerilii* that have been deprived of food produce a waterborne cue that significantly retards larval development.

In novel work examining how organisms assess environmental information to adjust offspring sex ratio (sex allocation), Schleicherova et al. (2005) demonstrated that the simultaneous hermaphroditic polychaete, *Ophryotrocha diadema* Åkesson, estimates the number of potential reproductive competitors or partners using chemical cues and adaptively shifts sex allocation in the population by suppressing female function. The waterborne chemical cue is species-specific and produced by mature individuals (Schleicherova et al. 2005).

In another example of how chemical signaling during reproduction might influence populations, Sutton et al. (2005) demonstrated that premating isolation observed between *Nereis (Neanthes) acuminata* (Ehlers) populations (Weinberg et al. 1990) is based on chemical cues. Using a behavioral assay of aggression, the researchers found that conditioned seawater taken from worms of various populations induced fighting behavior in individuals from different populations, indicating that the species is capable of chemically based "kin" recognition. Aggression levels within a population were lower than those between different populations, and the authors suggest that the high degree of fighting observed could lead to premating reproductive isolation among the different populations. Weinberg et al. (1990) suggested that differences in sex pheromones might result in the mating behaviors observed in their study, and these recent results (Sutton et al. 2005) confirm that a chemical signal is likely to be involved, but the nature of that chemical has not yet been identified.

Chemical signals and polychaete recruitment

Pawlik (1992) reviewed the chemical ecology of settlement in benthic marine invertebrates, providing an excellent introduction to the topic and perspective from other invertebrate species. Qian (1999) reviewed the factors affecting polychaete larval settlement, focusing primarily on positive chemical cues that induced gregarious settlement in sabellariid, spirorbid and serpulid polychaetes (indeed, these families continue to be among the best studied). A more recent review of the natural chemical cues inducing both settlement and metamorphosis in marine invertebrate larvae is provided by Hadfield & Paul (2001). The potential sources of chemical cues are many, including cues from conspecifics or congenerics, microbial films, sympatric species, food, or habitat. In many cases, the nature of the chemical compounds inducing polychaete settlement has not been fully characterized (Hadfield & Paul 2001). The diversity of chemical constituents demonstrated to induce polychaete larval settlement includes amino acids (Harder & Qian 1999; Jin & Qian 2004); inorganic ions such as K+ ,Cs+, and possibly sulfide (Yool et al. 1986; Pechenik & Qian 1998; Carpizo-Ituarte & Hadfield 1998; Cuomo 1985; Dubilier 1988); juvenile hormones (Biggers & Laufer 1992); free fatty acids (reviewed by Pawlik 1992, but this has been a matter of some debate as discussed by Qian 1999 and Hadfield & Paul 2001), polysaccharides (Kirchman et al. 1982a) and a suite of neurotransmitters (e.g., Jensen & Morse 1990; Pawlik 1990). Recent research has examined which chemical constituents of natural biofilms act as inducers of polychaete larval settlement in fouling communities.

Natural biofilms are complex, and may be comprised of multiple bacterial species as well as diatoms and fungi. Each of these constituents can be a source of chemical signals to settling larvae. For example, researchers comparing polychaete larval settlement on single- and multispecies bacterial films have noted that multispecies films generally induce the most settlement, and some of the component bacterial species induce settlement while others do not (Kirchman et al. 1982a, Unabia & Hadfield 1999). Similarly, Harder et al. (2002a) demonstrated that some diatom species induced settlement of the serpulid *Hydroides elegans* Haswell while others did not. Further research demonstrated that for inductive diatom species, the diatom-derived settlement cue was heat stable,

occurred in close association with the diatom surface, was not water soluble, and might be capsular extracellular polymeric substances (EPS) (Lam et al. 2003). Lam et al. (2005) demonstrated that cell-dissociated EPS fractions from inducing diatoms evoked a settlement response by *H. elegans* similar to that observed with natural monospecies diatom films. Enzymatic degradation to remove proteinaceous components of the EPS fractions did not alter the settlement response, suggesting that large proteins and glycoproteins did not play a significant role in inducing settlement. However, settlement in response to the EPS fractions was not as high as that induced by a mature biofilm including bacteria and diatoms, so the authors suggested multiple cues are likely to be involved.

Investigating the properties of bacterial biofilms that induced *H. elegans* settlement, Lau & Qian (2001) found that formaldehyde and streptomycin treatment of biofilms eliminated or reduced induction of larval settlement, and suggested that the larvae were responding to bacterial metabolites and that these were concentrated in the extracellular polymer matrix of the cells. Harder et al. (2002b) found that the lipophilic fractions of metabolites from two bacterial species, when adsorbed onto charcoal, induced *H. elegans* larval settlement to the same degree as the corresponding monospecies bacterial films. However, when EPS fractions were dissociated from bacterial films, immobilized in hydrogels and presented to *H. elegans*, only the initial stages of settlement were induced (Lau et al. 2003). Taking a different approach, Huang & Hadfield (2003) compared *H. elegans* settlement in response to two strains of the bacterium *Pseudoalteromonas atlantica* that either produced EPS or did not, but no larvae settled on the biofilms of either strain. The researchers found that bacterial density positively correlated with strength of metamorphic induction in single- and multispecies biofilms, but some bacterial strains were strongly inductive at low densities, suggesting that the inductive signal might be due to chemical characteristics of a single bacterial species. Because bacteria display density-dependent intracellular signaling (quorum sensing) and *H. elegans* settlement on biofilms is positively correlated with bacterial density, Huang et al. (2007) recently examined the possibility that chemical signals (acylated homoserine lactone derivatives, AHLs) produced by quorum-sensing bacteria in a biofilm might induce *H. elegans* settlement. At certain concentrations, AHLs elicited only larval behaviors representing the initial stages of settlement, but this topic deserves further study.

Importantly, most of the studies examining the effect of biofilm constituents on polychaete larval settlement have been conducted in still water in the laboratory and have involved only one species, *Hydroides elegans*. While such experiments are very useful for teasing apart potential chemical cues inducing larval settlement, not all polychaete species may respond to the same signals, and natural biofilms occur as part of a fouling community, thus other organisms in the community may influence settlement processes as well. For example, Dahms and colleagues (Dahms et al. 2004a; Dahms & Qian 2005) found that the presence of harpacticoid copepods on biofilms reduced settlement of *H. elegans* via predation, and suggested that the copepods might also indirectly influence settlement by changing the chemical characteristics of the bacterial biofilm. Similarly, although much of the research examining the chemical ecology of polychaete larval settlement has emphasized the role of positive inducers of settlement, chemical cues that inhibit settlement can be equally important (Woodin 1991). Certainly, the practical goal of preventing biofouling has prompted efforts to identify compounds that inhibit settlement (Clare 1996; Rittschof 2001; Dahms et al. 2004b,) and although not all of these compounds may be active in nature (Hadfield & Paul 2001), some probably are (Lee & Qian 2003; Walters et al. 2003; Yang et al. 2007). Some of the best examples of naturally occurring settlement deterrents come from studies of soft-sediment systems.

Woodin et al. (1995) pointed out that negative responses by larvae and juveniles may be evoked by organism-specific or process-specific cues. Organism-specific negative cues include bioactive compounds produced by organisms (presumably to deter predators) such as the halogenated

compounds produced by numerous polychaetes (Fielman et al. 1999). In laboratory experiments, Woodin et al. (1993) found that nereidid larvae rejected sediments inhabited by adult terebellids, *Thelepus crispus* Johnson; this species produces a bromobenzyl alcohol that was interpreted as the rejection cue. Similarly, newly settled *Arenicola cristata* Stimpson juveniles placed on sediments spiked with naturally occurring concentrations of 4-bromophenol, 2,4-dibromophenol, and 2,4,6-tribromophenol produced by the capitellid *Notomastus lobatus* Hartman had significantly longer burrowing times compared to controls (Woodin et al. 1997). Brominated aromatics also inhibited settlement by *Arenicola marina* (L.) (Hardege et al. 1998). Esser et al. (2008) recently found that sediments spiked with 1-chlorononane (a proxy for the predominant halometabolite produced by *Streblospio benedicti* (Webster)) inhibited larval settlement by *S. benedicti*.

Making the case for process-specific recruitment cues, Woodin et al. (1995) noted that the sources of post-settlement mortality for infaunal larvae and juveniles (e.g., predation, erosion, and deposition) all involved alteration of the sediment surface, and proposed that newly settled juveniles should be able to distinguish between disturbed and undisturbed sediments. This study demonstrated that newly settled *Nereis vexillosa* Grube and *Arenicola cristata* either failed to burrow or took significantly longer to do so when presented with disturbed sediments resulting from deposition of subsurface sediments or removal of surface sediments; flume experiments showed that non-burrowing individuals were quickly eroded (Woodin et al. 1995). Because infaunal activity alters sediment geochemical gradients (e.g., Marinelli 1992), subsequent research focused on the possible geochemical constituents of sediment that might provide a signal of disturbance and thus affect recruitment.

Studies pairing behavioral observations with modeling of geochemical processes have demonstrated that elevated ammonium concentrations and depressed oxygen concentrations in surface sediments are associated with sediment rejection by newly settled polychaetes (Woodin et al. 1998; Marinelli & Woodin 2002; Marinelli & Woodin 2004), although the effect of depressed oxygen varied with species. As with experiments identifying the chemical constituents of biofilms that induce settlement by *Hydroides elegans*, these studies examining the geochemical signals that result in habitat rejection have mostly employed still-water assays. Evidence suggests, however, that rejection of disturbed sediments can occur in natural flows. In flume experiments with realistic flow rates, Snelgrove et al. (2001) demonstrated that settlement by *Capitella* sp. I larvae was significantly reduced in sediments that were heavily reworked by adults (i.e., contained abundant fecal pellets).[1] These authors suggested that pelletized sediments may signal larvae that organic matter in the sediments is depleted. Indeed, both quantity and quality of sediment organic matter affects *Capitella* sp. I settlement (Grassle et al. 1992; Thiyagarajan et al. 2005, 2006). Also conducting their research in flumes, Engstrom & Marinelli (2005) used polyacrylamide gels to manipulate ammonium concentrations in surface sediments while keeping variables such as sediment grain size and organic content constant. Consistent with earlier work, they found that retention of *Arenicola cristata* larvae was highest at low ammonium concentrations.

Whether positive or negative, perception of chemical cues by larvae and juveniles occurs within the physical hydrodynamic scene of the water column and benthic boundary layer, and how hydrodynamics affect the delivery of chemical cues to larvae is an important question. Although hydrodynamic influences on larval settlement have been studied (e.g., Butman 1987; Pawlik et al. 1991; Butman & Grassle 1992; Snelgrove et al. 1993), what limits (if any) hydrodynamic regimes place on larval chemical perception warrants further exploration. An example of the integrated studies that will be necessary to address these questions is found in the work of Hadfield, Koehl, and

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1. Note that *Capitella* sp. I is now called *C. teleta* (Blake et al. 2009).

colleagues whose recent studies of larval behavior by the gastropod *Phestilla sibogae* Bergh (Hadfield & Koehl 2004), coupled with detailed characterization of hydrodynamics and distribution of chemical signals above coral reefs (Koehl & Hadfield 2004, Koehl et al. 2007), have resulted in a powerful individual-based model of how these larvae respond to dissolved settlement induction cues in the complex hydrodynamic environment above a coral reef (Koehl et al. 2007).

Chemical signals and polychaete feeding

The feeding behavior and ecology of polychaetes has been studied for many years. In particular, Fauchald & Jumars' (1979) seminal manuscript, "The Diet of Worms," provides an excellent overview of polychaete feeding mechanisms. Chemical-mediated feeding behavior has been reported in numerous polychaete species. For example, Copeland & Wieman (1924) determined that *Nereis virens* emerged from its tube in response to crushed periwinkles and other animal food. Recently, Watson et al. (2005) exploited this feeding behavior to study how chemical signals might mediate predator-prey interactions in *N. virens*, assessing whether extracts of conspecifics, other polychaete prey species, or flatfish muscle (predator), reduced feeding by *N. virens*. Whole-body extracts of conspecifics significantly reduced both the number of *N. virens* individuals feeding and their activity outside the burrow, but extracts of flatfish muscle reduced only the number of worms feeding, and extracts of *Arenicola marina* had no effect on feeding by *N. virens*. The authors concluded that the whole-body extracts of conspecifics acted as an alarm signal to reduce foraging and feeding by *N. virens*. However, whether the chemical signal produced by an injured *N. virens* resembles that extracted from a whole-body homogenate or occurs in a detectable concentration in a natural setting remains to be determined, therefore this question deserves further study.

Mangum and Cox (1971) described the feeding behavior of the onuphid polychaete, *Diopatra cuprea* (Bosc), in response to extracts of 32 marine organisms and numerous other chemical substances including amino acids found in extracts of bivalve flesh. The worms responded to extracts of "almost any organism, including itself." Several sugars elicited feeding currents or mouth opening, as did hemoglobin and fresh blood of other polychaetes. Worms produced feeding currents in response to numerous amino acids, with threshold concentrations that elicited the feeding current of 10^{-5} M to 10^{-8} M for cysteine, methionine, phenylaline, proline, hydroxyproline, and valine. The authors noted that feeding by *D. cuprea* could be attributed to the presence of four to six amino acids found in extracts of two clam species.

Because deposit-feeding polychaetes actively modify the sediment environment as they feed and rates of sediment mobilization depend on food supply, a considerable amount of research has focused on the question of what makes some sediments better food than others (*e.g.*, review by Jumars 1993). Largely absent from this body of research, however, are studies that investigate the cues that initiate ingestion and modulate feeding rates in deposit feeders. Jumars (1993) suggested several stimuli that could operate to regulate ingestion rate: in order, smell, taste, distension of the gut, and internal detection of the absorbed products in body fluids. Chemoreception is implicated in the coordination of feeding by a variety of deposit-feeding polychaetes. For example, fresh fecal material depresses feeding rate in some spionid polychaetes (Miller & Jumars 1986). Phagostimulants are implicated as well. Deposition of fresh phytodetritus prompts rapid behavioral responses by polychaetes and other macrofauna living on the continental slope and in the deep sea (e.g., Levin et al. 1997; Witte et al. 2003). In laboratory experiments, Duchêne & Rosenberg (2001) observed increased activity on the sediment surface by the ampharetid polychaete, *Melinna cristata* (Sars), following addition of a phytoplankton mixture to the sediment surface. When given a choice,

the common deposit-feeding polychaete, *Streblospio benedicti*, fed preferentially on organically enriched sediments *vs.* unaltered sediments (Kihslinger & Woodin 2000).

The specific chemical cues that might modulate deposit-feeding activity have also been investigated. Putting aside phylogenetic discussion of the position of echiurans within the polychaetes, Hughes et al. (2004) tested the hypothesis that deposit feeding by the echiuran *Maxmuelleria lankesteri* (Herdman) would be stimulated by dimethlysulphide (DMS). DMS results from the break-down of dimethylsulphonioproprinate (DMSP) which is produced by some phytoplankton species, and serves as an olfactory cue for some foraging seabirds (Nevitt 2000; Nevitt & Haberman 2003). Although they observed seasonal peaks in DMS+DMSP content of surface sediments, Hughes et al. (2004) found no relationship between these peaks and sediment ejection rate by *M. lankesteri*, nor did experimental addition of DMSP-producing phytoplankton increase surface feeding activity or sediment ejection rates. In contrast, Ferner and Jumars (1999) found that dissolved cues (single amino acids, ADP, and complex mixtures) influenced feeding behavior of *Boccardia proboscidea* Hartman and *Pseudopolydora kempi japonica* Imajima & Hartman (sic). Dissolved taurine, threonine, valine, and glycine acted as phagodepressants while ADP, algal and crustacean extracts, as well as commercial fish food and baby food were phagostimulatory. More recent research has demonstrated that particle-bound amino acids (singly and in mixtures) and sugars stimulated feeding in the spionid polychaetes *Dipolydora quadrilobata* (Jacobi) (Riordan & Lindsay 2002) and *Streblospio benedicti* (Mahon & Dauer 2005).

Polychaete chemosensory structures

The preceding review demonstrates that chemoreception plays a role in ecologically important behaviors of polychaetes. How are the chemicals perceived by worms? In this section, I describe some of the polychaete sensory structures that have been implicated in chemoreception and relevant nervous system connections. Because their sensory modalities have generally not been defined, the numerous solitary ciliated sensory cells found on the body and appendages of many polychaetes are not discussed in detail, but these have been reviewed recently by Purschke (2005).

Larval sensory structures. Annelid trochophore larvae are equipped with a prominent apical tuft of cilia associated with the apical organ, to which a sensory role has generally been ascribed. Lacalli (1981) examined apical organ structure in trochophores of spirorbid and phyllodocid polychaetes and noted that the plexus underlying the apical tuft contained many vesicles and suggested that it played a neural or neurosecretory function. The plexus serves as an initial target for pioneering neurites of the larval nervous system. Marsden (1982) found that either mechanical or chemical stimulation of the apical tuft interrupted ciliary beating in the prototroch of *Galeolaria caespitosa* Lamarck larvae. Examining 3-setiger larvae of *Arenicola cristata*, Marsden & Lacalli (1978) observed paired dorsolateral and lateral masses, each containing an eye and a ciliated sensory structure. The function of these sensory cells was not determined, nor their relationship to other elements of the larval nervous system, but the authors speculated that these cells might be involved in coordinating larval responses (increased muscular activity) to contact with surfaces. Eckelbarger & Chia (1976) described sensory tufts of stiff, immotile cilia arrayed on the body and in longitudinal rows on the dorsal surface of larval tentacles in *Phragmatopoma lapidosa* Kinberg, which play a role during substrate exploration. Amieva et al. (1987) demonstrated that the cilia tufts were produced by primary, bipolar sensory cells whose basal processes extend toward the base of the larval tentacle. Although they did not demonstrate a specific sensory modality of these cells, the authors suggested that they might function in mechano- or chemoreception, particularly contact chemoreception

(Amieva et al. 1987). Developing nuchal organs (see below) have been identified in metatrochophores of various polychaete species (references in Purschke 1997), and no significant changes in their ultrastructure during postembryonic development have been observed (Schlötzer-Schrehardt 1986, 1987, 1991).

Advances in immunohistochemistry and confocal microscopy have improved the experimental identification of polychaete larval nervous systems and sensory structures. For example, Voronezhskaya et al. (2003) described neuronal development in larval *Phyllodoce maculata* (L.), confirming the presence of neurons in the apical organ and their connection to the prototroch nerve. The apical organ in *P. maculata* contains six sertotonergic and seven FMRFamidergic cells. In addition, Nezlin & Voronezhskaya (2003) described a novel unpaired posterior sensory organ (PSO) in trochophore larvae of *P. maculata,* situated at the dorsal midline of the hyposphere and consisting of five bipolar sensory cells. The cells send axons to the cerebral ganglion and the prototroch nerve and dendrites of the cells project to the surface of the larva and are uniciliate; a single neuronal fiber from the apical sensory organ innervates the PSO. The authors noted that the structure is strictly larval, not a rudiment of the nuchal organ, and suggest a chemo- or mechanosensory modality although neither function was demonstrated.

Nuchal organs. Among the polychaetes, nuchal organs are typically considered to function in chemoreception based on histological, ultrastructural, and positional criteria (Storch & Schlötzer-Schrehardt 1988; Rhode 1990; Purschke 1997, 2005; but see Fewou & Dhainaut-Courtois 1995 for a potential osmoregulatory function), although clear physiological evidence of chemoreceptive function has not been demonstrated (Purschke 1997; Rouse & Pleijel 2001). Nevertheless, given Rullier's (1950) demonstration that nereidid polychaetes without nuchal organs failed to feed, a chemoreceptive function seems likely. Purschke (1997) examined the variation in nuchal organ morphology among polychaetes from a phylogenetic perspective, summarizing observations made for 40 species from 23 families. He noted the following general characteristics: (1) nuchal organs typically occur as paired organs found dorsally or dorsolaterally at the posterior margin of the prostomium; (2) they are always ciliated, and most often appear externally as round or oval patches of cilia situated in pits of varying depth, but the external structure can vary significantly; (3) in some taxa (e.g., amphinomids and spionids), they lie on either side of an unpaired sensory lobe, the caruncle, that extends behind the prostomium and over several segments; (4) they are often retractable, equipped with retractor muscles, and although they may be invisible externally when retracted (as in some burrowing species), when everted nuchal organs may appear as flat papillae, more hillock-like or piston shaped structures (Whittle & Zahid 1974; Rhode 1990; Pleijel 1991); and (5) they are usually innervated by paired nerves originating from the posterior part of the brain.

The ultrastructure of nuchal organs is fairly consistent among the polychaete species that have been examined. Purschke (1997) notes that they are comprised of ciliated supporting cells, bipolar primary sensory cells, and a retractor muscle. The ciliated cells rest on an extracellular matrix that is continuous with that of the epidermis. Retractor muscle fibers usually attach to this matrix in the center of the ciliated area. Dendritic processes of the bipolar primary sensory cells are embedded within the ciliated cells and the dendrites terminate in bulbs below the surface of the sensory cells, creating the olfactory chamber (Whittle & Zahid 1974). Both the position and depth of the olfactory chamber varies. In species with highly retractile nuchal organs, the sensory cells often terminate basally at the ciliated area, but may still be surrounded by ciliated supporting cells. Ciliated supporting cells of the nuchal organ secrete cuticle, which along with microvilli, form a protective layer above the sensory cells; the morphology of this protective layers is variable among species (Purschke 1997). The abundant kinocilia of the nuchal organ are presumed to create water currents that allow flushing and the exchange of sensory stimuli (Purschke 1997, 2005).

Species-specific size variation in nuchal organs has been observed, but is not well understood. Von Haffner (1962, as cited in Purschke 1997) and Rhode (1990) found that species with well-developed head appendages had comparatively small nuchal organs and *vice versa*. Purschke (1997) suggested a trend toward reduced nuchal organs in meiofaunal polychaetes, but also noted that numerous meiofaunal species had well-developed nuchal organs relative to their body size. In the serpulids and sabellids, nuchal organs are unpaired and found internally; unpaired nuchal organs also occur in arenicolids and terebellids (Purschke 1997). Nuchal organs appear to be absent in the Oweniidae, Psammodrilidae, Pisionidae, *Magelona*, and Siboglinidae (Purschke 1997; Rouse & Pleijel 2001). Duplicated nuchal organs occur in some dorvilleids and opheliids, but the functional significance of this duplication is not clear (Purschke 1997).

Dorsal and metameric ciliated organs. Because nuchal organs are considered to have a presegmental origin, Jelsing (2002, 2003) studied the distribution and morphology of dorsal ciliated organs (DCO) in 15 species of spionid polychaetes to determine whether these organs, which extend over several anterior segments as either continuous or metameric bands of cilia, were homologous with nuchal organs. Based on their external morphology the dorsal ciliated organs may be assigned to several (non-systematic) groups: paired anterior DCO of different lengths, paired DCO that also occur with sexually dimorphic unpaired metameric DCO (e.g., as in male *Pygospio elegans*), and paired anterior DCO that occur with paired, metameric DCO (Jelsing 2003). Except for the unpaired sexually dimorphic metameric DCO found in male *P. elegans*, the long DCO and metameric DCO displayed ultrastructure similar to nuchal organs, and Jelsing (2003) recommended these structures be considered nuchal organs and metameric nuchal organs.

Parapodial sensory structures. Horridge (1963) described the parapodial cirri of *Harmothoe* as consisting of "little more than groups of bipolar sensory cells with their endings surrounded by supporting tissue." The ventral cirrus contained 500–800 sensory cell bodies, and the dorsal cirrus contained 1000–1200 such cells. Flask-shaped bipolar cells at the base of the ventral and dorsal parapodial cirri had processes that extended into the cirri, and stained with methylene blue (which typically labels nerves). Horridge found that worms usually ignored prodding or pinching of either cirrus, although they rapidly moved away if the bristles of the parapodia were touched. In contrast, dilute acid applied to a cirrus prompted worms to move away, and slight electrical signals were generated in the nerve of an isolated cirrus when a slightly acidic solution of betaine was applied, but these were very difficult to record (Horridge 1963). Based on these results, as well as the appearance of the cirri, and the size and number of axons, Horridge attributed a chemosensory function to the parapodial cirri of *Harmothoe*.

Boilly-Marer (1972a, b, 1973) described the structure of sensory cells on the parapodial cirri of several nereidid polychaetes. She focused on cirri found on the anterior and (for males) posterior parapodia. As the worms mature, the cirri of the first five to seven pairs of anterior parapodia in both sexes swell, and the dorsal cirri of the posterior parapodia become crenellated in males. These changes in morphology of the cirri result from differentiation of organs that consist of sensory cells surrounded by epidermal cells secreting a protein material (Boilly-Marer 1972b, 1973), which she concluded was involved in reception of chemical stimuli emanating from partner of opposite sex. The swelling/crenellated areas of the cirri are also characterized by the presence of ciliated dendritic extensions of bipolar sensory cells, the perikarya of which become enriched with ribosomes as heteronereids form.

Purschke & Hausen (2007) recently examined the lateral organs (or interramal organs) found on parapodia of sedentariate polychaetes; these structures usually appear as densely ciliated areas, pits, or small papillae found between the neuro- and notopodia. They examined specimens representing 10 species in seven families: Orbiniidae, Spionidae, Paraonidae, Poecilochaetidae, Opheliidae,

Maldanidae, and Terebellidae. No data concerning the innervation of the cells was provided, but the authors noted that a retractor muscle attaches basally to the lateral organ. The lateral organs contained two types of uniciliated penetrative sensory cells. The Type 1 cells were typically found in dense arrays, and may even appear to be multiciliated cells; those observed had long ciliary rootlets in contrast to similar sensory cells found outside the lateral organs. Type 2 cells had a circle of strong microvilli, such as those found in collar receptors. Because collar receptors are commonly regarded to be mechanoreceptors (Purschke 2005), the authors attribute a mechanosensory function to the Type 2 cells, although they noted that no definitive experimental evidence demonstrating collar receptor mechanosensitivity has been reported; they therefore did not rule out the possibility that the lateral organs might function in chemoreception or in sensing changes in osmolarity (Purschke & Hausen 2007).

Other putative peripheral chemosensory structures. Following studies demonstrating that different chemicals as well as varying oxygen concentrations modified the irrigation activity of *Arenicola marina* (Kruger 1968 as cited in Jouin et al. 1985; Toulmond et al. 1984), Jouin et al. (1985) examined the fine structure of sensory cells in the caudal epidermis of *A. marina*. Sensory buds of the caudal papillae were composed of supporting cells and two types of receptors (R1 and R2) that were multiciliated primary sensory cells with axons connecting to the basiepidermal nerve plexus. R1 cells had several apical cilia, numerous mitochondria in the apical part of the cell, one basal foot on each basal body, clear cytoplasm, and relatively short ciliary rootlets, which are characteristics of chemosensory cells in vertebrates (Farbman 1992) and in the nuchal organs of polychaetes (Whittle & Zahid 1974). In contrast to the ciliated cells of the nuchal organs, the R1 cells are not protected—they rise up freely into the medium (Jouin et al. 1985). Jouin and colleagues assigned a chemoreceptive function to the R1 cells. The R2 cells were characterized by large ciliary rootlets (such as those found in invertebrate mechanoreceptors, Altner & Prillinger 1980) and a dense fibrillar sheath encircling the ciliary rootlets and apical filaments of the cell. This fibrillar sheath may be comparable, though not necessarily homologous with the scolopale of crustacean mechanosensory organs. The authors proposed a mechanosensitive function for the R2 cells, perhaps in detecting the ventilating current.

Anterior appendages such as palps have also been implicated as chemosensory structures. For example, Dorsett & Hyde (1969) described the compound sense organs found on the prostomial cirri and palps of *Nereis diversicolor*. Small clusters of ciliated sensory cells, with accompanying supporting cells make up these organs; each organ contains between 7 and 15 cells and although the cilia are sheathed, the tip of the sheath appears to be open. The distal processes of the sensory cells contain prominent neurotubules that terminate on or near the basal bodies of the sensory cilia, and the authors noted that similar arrangements are found in the olfactory mucosa of fish. Based on their position on the head, and because the number of organs observed and neurons present was inconsistent with a purely mechanoreceptive function, Dorsett & Hyde (1969) suggested a chemosensory function to these compound sense organs, although they provided no electrophysiological evidence to support this characterization.

The ciliated feeding palps of spionid polychaetes have been the focus of a great deal of research, particularly in terms of defining characters that might be used in taxonomic and phylogenetic studies of the Spionidae. Citing the work of numerous researchers (e.g., Dauer 1984, 1985, 1994, 1997; Eibye-Jacobsen 1997; Qian & Chia 1997; Williams & Radashevsky 1999; Worsae 2001), Worsae (2003) defined 11 palp characters and presented a twelfth character that might be used in such studies; the majority of these characters describe the location and motility of cilia found on the palps. In spionids with a median food groove on the palp, the motile frontal cilia of the food groove are usually a prominent feature and function in transporting captured particles to the base of the palp

(e.g., Dauer et al. 1981). Given behavioral studies described above (Ferner & Jumars 1999; Kihslinger & Woodin 2000; Riordan & Lindsay 2002; Mahon & Dauer 2005) it seems possible that some of the frontal cilia (e.g., the nonmotile cilia) might function as contact chemoreceptors. Nonmotile cilia, or nonmotile cirri *sensu* Dauer (1997), on lateral and abfrontal surfaces of spionid palps have been ascribed a sensory role based on scanning electron microscopy and positional criteria (Dauer 1984, 1987, 1991,1997; Worsaae 2001). Worsaae (2001) also suggested a mechanoreceptor function for motile cirri found on the lateral and abfrontal surfaces of *Dipolydora quadrilobata* palps, speculating that those on the abfrontal surface might help the worms detect the direction of the current in order to orient the palps correctly to intercept suspended food particles. Lindsay et al. (2004) examined the cilia on the palps and prostomium of *D. quadrilobata* and their transmission electron microscopy results supported Worsaae's (2001) characterization of the lateral and abfrontal cells as sensory, revealing cells with numerous apical mitochondria, and short ciliary rootlets characteristic of the caudal chemoreceptor cells described by Jouin et al. (1985). The lateral cells (mislabeled laterofrontal by Lindsay et al. (2004)) found in a row adjacent to the laterofrontal cilia were interspersed with glandular cells and pores. Confocal microscopy revealed axonal processes from the cilia of lateral sensory cells found on the sides of the palps and from abfrontal sensory cilia to the palp nerves.

In a recent investigation, Forest & Lindsay (2008) examined serotonin and FMRFamide-like immunoreactivity of palp sensory structures and the anterior nervous system of four spionid polychaete species, *Dipolydora quadrilobata*, *Pygospio elegans*, *Polydora cornuta* Bosc, and *Streblospio benedicti*. Serotonin immunoreactivity was concentrated in cells underlying the ciliated food groove, the buccal lips of the mouth, in some (but not all) palp nerves, and in the cerebral ganglion. FMRFamide-like immunoreactivity was associated with the cerebral ganglia, nuchal organs, palp nerves, and especially with the perikarya of laterofrontal, lateral, and abfrontal ciliated sensory cells of the palps in *D. quadrilobata* and *P. elegans*. The serotonergic palp cells (SPCs) underlying the food groove in the species studied do not correspond to any known polychaete serotonergic cell type and their function is unknown, although the authors suggested the cells might play a role in feeding by modulating the beat frequency of cilia or controlling mucus secretions (Forest & Lindsay 2008).

Nervous system elements involved in chemosensory behaviors. The morphology of the polychaete nervous system was recently reviewed by Orrhage & Muller (2005), and I will focus only on some components of the nervous system that are likely to be involved in coordinating chemosensory-based behaviors. First, as noted by Bullock & Horridge (1965), the principal structures of the polychaete hindbrain are related to the afferent nerve supply from the nuchal organ. The proximal processes of primary sensory neurons in the nuchal organ enter the hindbrain as nerves, varying in their length and number, and in some cases the bipolar sensory cell bodies lie in clumps, the nuchal ganglia, which may be incorporated into the brain to varying degrees (Bullock & Horridge 1965). Orrhage & Muller (2005) discussed the relationship of nuchal nerves and the nuchal commissure to the cephalic nervous system. Among the Canalipalpata and Scolecida examined, only Orbiniidae have a separate nuchal commissure, which is connected to both dorsal and ventral commissures of the dorsal root and to a nuchal center that in turn is associated with the central neuropile of the brain. Nuchal nerves and nerves to the dorsal organs emanate from the nuchal commissure. This is not the case for other sedentariate families studied (Ampharetidae, Pectinariidae, Terebellidae, Protodrillidae, Nerillidae, Chaetopteridae, Flabelligeridae, Spionidae, Trochochaetidae, Sabellariidae, Sabellidae, Serpulidae, Scalibregmatidae, Poecilochaetidae, Apistobranchidae, and Paraonidae), in which the nuchal nerves attach to the brain directly, but the attachment sites vary considerably. A nuchal commissure is found in nearly all the Aciculata studied

(except Syllidae, Hesionidae and four aphroditacean families), but the position relative to other nerve elements in the brain differs to such a degree among taxa that the authors state "at present a general pattern of the polychaete nuchal system cannot be reconstructed."

Orrhage & Muller (2005) also discussed the innervation of polychaete palps at some length. In general, palps are innervated through two or more nerve roots that emanate from the dorsal root of the circumesophageal connective, the ventral root of the circumesophageal connective, and their commissures. Despite considerable variability in the number and position of nerve roots among taxa, the authors demonstrated by their analysis some striking similarities in innervation patterns. For example, palp nerve roots 6 and 9 are the main roots in Trochochaetidae, Apistobranchidae, Acoetidae, Aphroditidae, Polynoidae, Sigalionidae, Syllidae, Hesionidae, Nereididae and Phyllodocidae. Palp nerve root 9 is also the main root in Protodrillidae, Scalibregmatidae, Glyceridae, and Goniadidae. Palp nerve root 11 is a main root in the Glyceridae and Goniadidae, as well as in the Flabelligeridae, Magelonidae, Poecilochaetidae, Spionidae, Chaetopteridae, and Amphinomidae. Based on these shared innervation patterns, the authors concluded homology among palps of Nereididae and homologous structures in representatives of 24 other families (Orrhage & Muller 2005).

These observations of palp innervation are particularly interesting in light of recent work by Heuer & Loesel (2008) demonstrating significant serotonergic immunoreactivity in nerve fibers running from the palps of *Nereis diversicolor* to the mushroom bodies of the brain. In their discussion of polychaete brain neuroanatomy, Bullock & Horridge (1965) described mushroom-like compact masses of globuli cells occurring with a stalk of finely textured neuropile in the brains of some polychaetes as "corpora pedunculata" and regarded these structures as strongly homologous with similar structures found in arthropods. Heuer & Loesel (2008) referred to the corpora pedunculata of *N. diversicolor* as mushroom bodies because of their similarity to structures in euarthropod and onychophoran brains that are identified as mushroom bodies (Strausfeld et al. 2006). Mushroom bodies in insects, chelicerates, millipedes, centipedes and onychophorans are considered second-order neuropiles of the olfactory pathway, with primary sensory input passing first to olfactory glomeruli (Strausfeld et al. 1995) and then to the mushroom bodies. In *N. diversicolor*, however, Heuer & Loesel (2008) found that the mushroom bodies were directly innervated by the palpal nerve, and observed no olfactory glomeruli. In contrast, Strausfeld et al. (1998) observed olfactory glomeruli associated with mushroom bodies in *Nereis vexillosa* and the polynoid *Arctonoe vittata* (Grube).

As Heuer & Loesel (2008) suggest, a wider sampling of taxa and application of different techniques (e.g., direct dye fills) is much needed to determine the presence of glomeruli in the olfactory pathway and to examine whether direct innervation of mushroom bodies by olfactory receptor fibers represents an ancestral state. Indeed, earlier accounts note that mushroom bodies (i.e., corpora pedunculata) themselves are not present in all families, occurring in the Aphroditidae, Polynoidae, Sigalionidae, Polyodontidae, Nereididae, and Hesionidae but not the Eunicidae, Onuphidae, Lumbrineridae, or Glyceridae; among the sedentary families examined, distinct corpora pedunculata were observed only in the Serpulidae, being absent in the Cirratulidae, Terebellidae, Ampharetidae, Opheliidae, Maldanidae, Scalibregmatidae, and Sabellidae (Bullock & Horridge 1965). Determining the presence/absence of such structures and their innervation could be valuable in interpreting phylogenetic relationships within the polychaetes and among the polychaetes and articulata and may also shed light on the evolution of chemoreceptive pathways.

Polychaete chemoreception: linking structure & function

A recurring theme in the research identifying sensory structures in polychaetes has been the relative dearth of physiological evidence linking particular structures with functions and behavior. Compared to other invertebrate model systems (e.g., nematodes, insects, crustaceans), we know very little about the sensitivity of and signal transduction pathways employed in chemosensation by polychaetes. In this section, I describe research that links presumed chemosensory structures with a chemosensory function, as well as recent progress to identify the molecular basis of chemoreception in polychaetes.

Electrophysiological responses of nereidids to pheromones. Building on earlier work demonstrating that both transformed parapodial cirri and the brain, as well as integrity of the connections between ventral nerve cord and brain, were required to induce the nuptial dance and gamete release in *Platynereis dumerilii* (Boilly-Marer 1974), Boilly-Marer & Lassalle (1978) used suction electrodes to record electrical signals from the brain of *Nereis succinea* L. in response to coelomic fluid of sexually mature conspecifics. The preparation consisted of the head, peristomium, and six anterior segments bearing swelled cirri on the parapodia. The experiments demonstrated that introducing coelomic fluid of sexually mature conspecifics of the opposite sex prompted intense electrical activity in the brain, and suggested that the parapodial cirri were necessary for perception of the stimulus. Similar assays demonstrated electrophysiological responses to sex pheromones of conspecifics and heterospecifics in mature, but not immature, specimens of six nereidid species (Boilly-Marer & Lassalle 1980). In a comprehensive study, Ram et al. (1999) demonstrated both behavioral and physiological responses of *N. succinea* males to nereithione and various glutathione derivatives. This study employed spawning assays and video observations of behavioral responses as well as continuous electrical recordings from suction electrodes applied externally to parapodia at various points along the body from the head to the posterior. Nereithione prompted spawning of *N. succinea* males, and elicited all three components of the male behavior (circling, spawning, and accelerated swimming). Nereithione applied near the head of worms elicited electrophysiological activity from the parapodia in the posterior third of the body, and the duration of the activity depended on the concentration of the nereithione. Although the receptor for nereithione and the molecular mechanism of pheromone signal transduction are as yet uncharacterized, these studies demonstrate that the sensory cells of the parapodial cirri serve a chemosensory function and help mediate the spawning behavior of nereidids in response to a specific chemical signal.

Activity-dependent cell labeling in response to chemical cues. To determine whether putative sensory cells on feeding palps of *Dipolydora quadrilobata* were activated by chemical cues, Lindsay et al. (2004) adapted the method used by Michel and colleagues (1999) to label activated olfactory neurons in zebrafish and spiny lobster. When coupled with known stimulatory cues in solution and perfused over olfactory organs, the guanidinium analog, 1-amino-4-guanidobutane (= agmatine) accumulated in activated odorant receptor neurons (Michel et al. 1999; Steullet et al. 2000). Cells stimulated by a cue accumulated agmatine and could be identified using an anti-agmatine IgG antibody followed by silver intensification labeling (Marc 1995, 1999a,b).

When *Dipolydora quadrilobata* were presented agmatine plus an amino acid mixture that elicited behavioral responses in previous experiments (Riordan & Lindsay 2002), agmatine accumulated in ciliated cells of the palps, particularly the lateral and abfrontal cells (Lindsay et al. 2004). The percentage of peripheral cells that were labeled in the presence of amino acids varied by cell type (3%–14%), and was greatest for the cells located on the lateral and abfrontal surfaces of the palps. This rate of labeling is similar to that observed for olfactory neurons in spiny lobster aesthetascs (0.5%–4.6%, Steullet et al. 2000). Electrophysiological experiments are required to determine whether the lateral, abfrontal, and laterofrontal cells might also function as mechanoreceptors and to

characterize the sensitivity of their responses to various environmental chemical cues. These results represent the first physiological evidence that peripheral sensory cells on spionid feeding palps function as chemoreceptors and suggest a fruitful approach to functional studies of other polychaete sensory structures.

   Polychaete chemosensory signal transduction pathways. Much of our knowledge of chemoreception in marine invertebrates comes from studies of decapod crustaceans such as lobsters and crayfish, which have chemoreceptive cells in the antennules, antennae, legs, or mouthparts. In all cases, these receptor cells are bipolar, modified ciliary cells, with axons that project into the central nervous system (CNS) apparently without forming synapses in the periphery (Ache 1982; Ache & Derby 1985). In most organisms studied, chemosensory signal transduction (Fig. 1) is mediated by
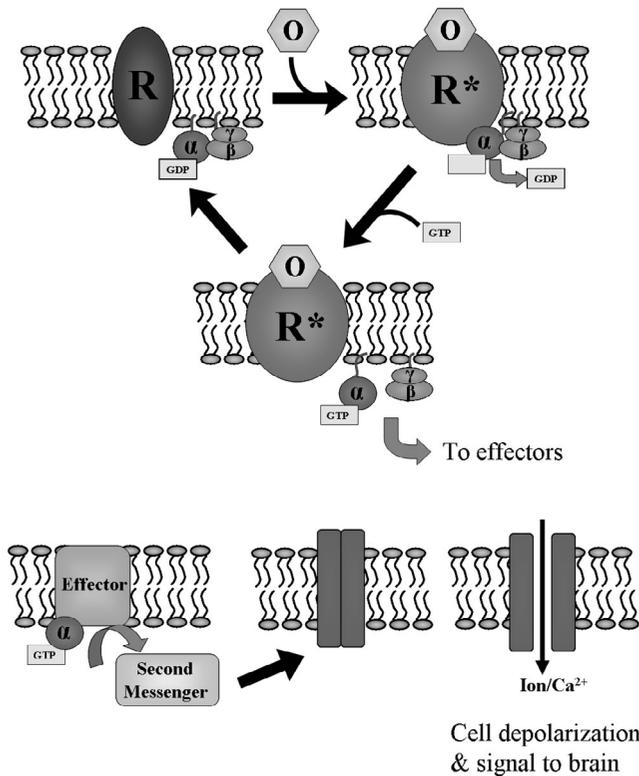
FIGURE 1. Simplified G-protein mediated chemosensory signal transduction pathway. The heterotrimeric G-protein is composed of α, β, and γ subunits. Odorant (O)/chemical signal binding to the membrane-bound receptor (R) causes coupling of the activated receptor (R*) and the intracellular G-protein. The R*-Gprotein interaction promotes exchange of GDP for GTP on the α subunit, and results in dissociation of the Gα-GTP from the Gβγ subunit and the activated receptor. Both Gα-GTP and Gβγ subunits then modulate activity of intracellular effectors. For example, the Gα-GTP might activate the adenylyl cyclase/cyclic-AMP or phospholipase C/inositol 1,4,5-trisphoshate second messenger pathways, causing ion channels in the cell membrane to open, depolarization and signals to the brain. The signal ends when intrinsic GTPase activity in the Gα subunit removes a phosphate from GTP and the Gα-GDP reassociates with the Gβγ subunit (adapted from Cabrera-Vera et al. 2003).

G-proteins that are activated by odorants to initiate a second messenger pathway involving either cyclic AMP (cAMP) or inositol 1,4,5-trisphosphate (IP_3) that subsequently results in activation or modulation of sensory cells (reviews by Anholt 1993; Krieger & Breer 1999; Hildebrand & Shepherd 1997). Both cAMP and IP_3 pathways coexist in the olfactory receptor neurons of lobsters (Hatt & Ache 1994), but different classes of G-proteins are associated with each pathway (McClintock et al. 1997; Xu et al. 1997). Among the polychaetes, however, the chemosensory signal transduction pathway remains largely undescribed, and the evidence for a G-protein mediated pathway involving activation of either the cAMP or IP_3 pathways is contradictory.

Investigating the signal transduction pathway that mediates the induction of *Capitella* sp. I larval settlement in response to juvenile hormones and juvenile hormone-like activity, Biggers & Laufer (1992) found that compounds that elevated intracellular cAMP concentrations did not induce larval metamorphosis and suggested that cAMP did not act as a second messenger in the signal transduction pathway. In subsequent work that included biochemical assays on larval homogenates, as well as behavioral assays run in the presence of various ion channel modulators, Biggers & Laufer (1999) found that juvenile hormone-active compounds induced larval settlement and metamorphosis by activating protein kinase C (PKC) and subsequent modulation of ion channels. PKC was localized to ciliary cells of the prototroch and to isolated apical cells located in the prostomium that had previously been suggested to be chemosensory (Eckelbarger & Grassle 1987). Specifically, Biggers & Laufer (1999) proposed that the lipophilic juvenile hormone-like compounds pass through the membrane of ciliated epithelial chemosensory cells and bind to inactive cytosolic PKC, which then becomes active and is translocated to the membrane where it causes closure of potassium channels. The resulting reduction in potassium ion efflux depolarizes the membrane of the chemoreceptor cell, causing voltage-gated calcium channels to open and the resulting influx of calcium ions possibly resulted in neurotransmitter release.

Studying induction of metamorphosis in *Hydroides elegans*, Holm et al. (1998) assayed larval metamorphosis in the presence of compounds that affected either G-protein activity, the production or activity of cAMP, or the activation of protein kinase C. Their results suggest that neither a G-protein-coupled receptor, nor the adenylate cyclase/cAMP pathway, nor the phosphatidylinositol/diacylglycerol/protein kinase C signal transduction pathway is directly involved in the processing of metamorphic cues, but the researchers noted that calcium and potassium did play a role in metamorphosis of *H. elegans*. Citing the example of abalone larvae (Trapido-Rosenthal & Morse 1985; Baxter & Morse 1987, 1992; Wodicka & Morse 1991), Holm et al. (1998) did not rule out the possibility that G-proteins and the PI/DAG/PKC pathway might transduce signals that *modify* the response of *H. elegans* larvae to the metamorphic signal. Researchers investigating settlement and metamorphosis of the spirorbid *Janua* (*Dexiospira*) *brasiliensis* Grube in response to bacterial EPS have suggested another alternative, that lectins on the larvae might mediate the settlement process by binding to bacterial extracellular components containing glucose, resulting in a settlement signal (Kirchman et al. 1982b; Maki & Mitchell 1985).

In the G-protein-coupled signaling pathway, the α subunit of the heterotrimeric G-protein is particularly important because it interacts with both the membrane-bound receptor and, when activated, downstream effectors (Fig. 1). Gα subunits are characterized into several classes, and among these, Gαq subunits have been demonstrated in the chemoreception signal transduction pathways of other invertebrates (Fadool et al. 1995; Talluri et al. 1995; McClintock et al. 1997; Krieger & Breer 1999). Recently, Tsie et al. (2008) isolated nearly full length sequence for a Gαq protein from the feeding palps of *Dipolydora quadrilobata* and observed Gαq immunoreactivity in nuchal organs, palp tissue, food groove cilia, lateral, and abfrontal palp cilia (Fig 2). Gαq immunoreactivity tended to be greater at the tips of feeding palps, suggesting the possibility of

increased chemosensitivity in this region, which is also the region of the palps involved in "pore-water sniffing" (Ferner & Jumars 1999). As noted previously, spionid polychaetes actively select particles based on their size and organic content when making food choices (Taghon 1982; Self & Jumars 1988; Mahon & Dauer 2005). The significant Gαq immunoreactivity found in the food groove cilia supports the theory that chemoreceptors, or another kind of G-protein-coupled receptor, are located on food groove cilia and that they transduce signals via Gαq.
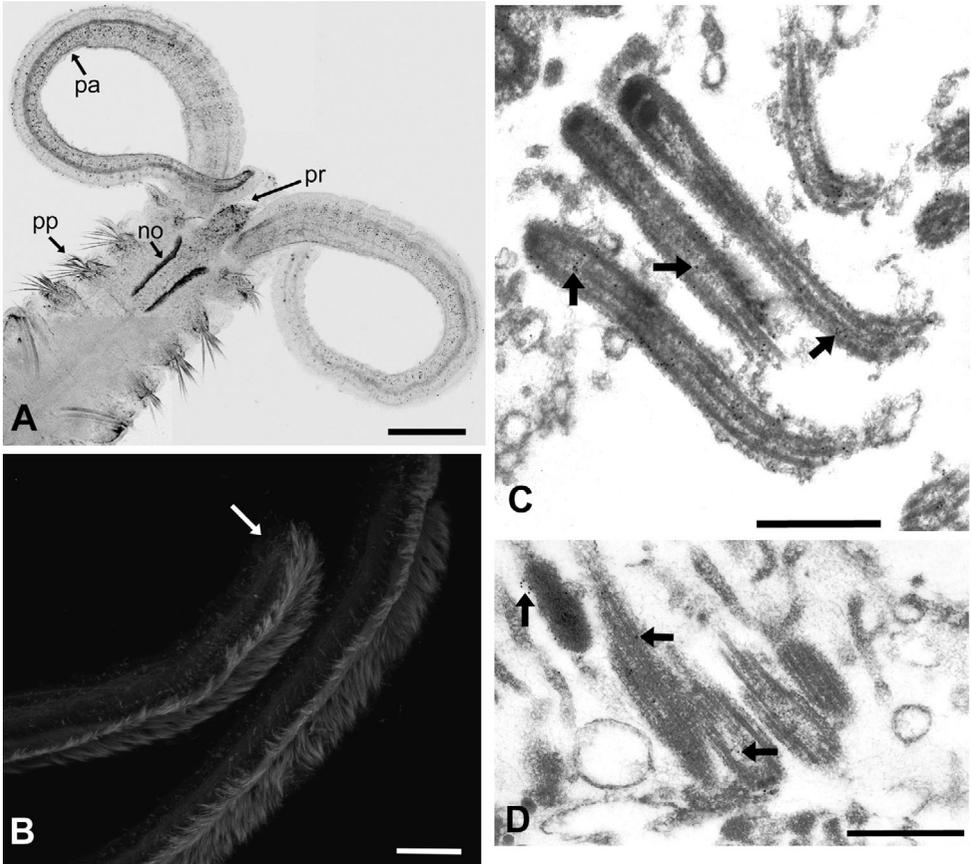
FIGURE 2. Localization of acetylated α-tubulin (B) and Gαq (A–D) antibodies in the anterior of *Dipolydora quadrilobata* revealed by confocal microscopy and TEM; (A) Gαq immunoreactivity (in black) in feeding palps (pa), nuchal organs (no), prostomium (pr), and parapodia (pp). Scale 200 μm, confocal maximum intensity projection, composite image;(B) Co-localization of acetylated αtubulin (green) and Gαq antibodies (blue) in the palps. Gαq immunoreactivity was concentrated in the food groove cilia and in the tip of the palp (arrow), confocal maximum intensity projection, scale 50 μm; (C) immunogold labeling of Gαq in food groove cilia, lateral section, arrows point to single or groups of gold particles, TEM, scale 0.5 μm; (D) gold labeling of Gαq in abfrontal cilia of the palp, TEM, scale 0.5 μm. (Images from Tsie et al. 2008, reproduced with permission from Springer).

The data from these studies of signal transduction pathways in larval and adult polychaetes are contradictory, although it seems possible that different pathways might be involved in larvae and

adults given that larval sensory structures such as the apical organ do not persist following metamorphosis. Clearly, additional work is necessary to determine the chemosensory signal transduction pathways in polychaetes, and the recent publication of the *Capitella* sp. I genome sequence may aid in these efforts.

Summary and conclusions

Chemical signals and chemoreception mediate ecologically important behaviors by polychaetes, including reproduction, larval settlement, metamorphosis, and recruitment, and feeding. Some of the pheromones that coordinate gamete maturation, spawning synchrony, and spawning behaviors have been identified (e.g., nereithione), while others have not. The research on chemically mediated reproduction has focused primarily on the nereidid polychaetes and one sedentariate species, *Arenicola marina*, but chemical signals undoubtedly play a role in reproduction of other species and future research may change our understanding of endocrine and pheromonal control of polychaete reproduction. Among the nereidids, sensory receptors on the modified parapodial cirri of sexually mature individuals are required for the pheromones to be perceived, but the chemosensory cells that detect pheromonal cues in other species are not well described. Although the biochemical identification of chemical signals involved in polychaete reproduction has progressed significantly in the last two decades, identification of pheromone receptor proteins and the pheromonal signal transduction pathway has been elusive.

As researchers have sought to understand the factors that lead to observed spatial patterns of recruitment, studies of the chemical mediation of polychaete larval settlement and recruitment have proliferated. Larval responses to numerous chemical signals from a diversity of sources (e.g., habitat, conspecifics, food, biofilms, etc.) have been described, and both inducers and deterrents to settlement have been demonstrated. The apical organ of polychaete trochophore larvae has been implicated in chemoreception, but it may also serve as a mechanoreceptor. The nature of the chemosensory signal transduction pathway in polychaete larvae is not well understood.

As is true for polychaete reproduction and recruitment, various chemical signals have been demonstrated to influence feeding behavior by polychaetes, including extracts of various prey items, complex mixtures of amino acids, and sugars. Nuchal organs are generally considered the primary chemoreceptive organ in polychaetes, but other putative chemosensory structures have also been described. For example, recent work demonstrates that the feeding palps of spionids function in chemoreception. The same chemical cue that elicited feeding behavior in *Dipolydora quadrilobata* (Riordan & Lindsay 2002) also activated sensory cells of the palps in activity-dependent cell-labeling studies (Lindsay et al. 2004). Although the signal transduction pathway has not been fully described, G-proteins may be involved (Tsie et al. 2008).

More than 50 years ago, Hodgson (1955) reviewed problems in invertebrate chemoreception and identified three priorities for future research, including the basis for selective behavioral responses to chemical stimuli, the fundamental excitation processes in chemoreceptors, and the mechanisms by which impulses from chemoreceptors result in integrated motor activity. Since then, researchers have identified common features of olfactory mechanisms in insects, nematodes, decapod crustaceans, gastropod molluscs, amphibians, and numerous fish and mammalian species. In the last two decades, researchers have made great strides in identifying chemical stimuli that mediate polychaete reproduction and recruitment and have begun to examine the molecular mechanisms underlying polychaete chemoreception. Our knowledge of polychaete neuroanatomy has improved significantly with the advent of confocal microscopy and improved immunohistochemical labeling techniques.

Nonetheless, the questions Hodgson identified remain largely unanswered for polychaetes. Answering them will require an integrated approach, one that includes molecular biological studies to identify and characterize both pheromone-specific and general chemosensory signal transduction pathways, as well as neurophysiological studies to determine the sensitivities of presumed chemosensory structures, in addition to the wealth of behavioral studies demonstrating chemical mediation of ecologically important behaviors. Such studies will be important contributions to our understanding of the evolution of chemoreception mechanisms among the metazoa.

Acknowledgements

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