



SYMPOSIUM

The Neuroecology of Dimethyl Sulfide: A Global-Climate Regulator Turned Marine Infochemical

Gabrielle A. Nevitt¹

Centre for Animal Behavior, Section of Neurobiology, Physiology and Behavior, University of California, Davis, CA 95616, USA

From the symposium “Neuroecology: Neural Determinants of Ecological Processes from Individuals to Ecosystems” presented at the annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2011, at Salt Lake City, Utah.

¹E-mail: ganevitt@ucdavis.edu

Synopsis Information transfer influences food-web dynamics in the marine environment, but infochemicals involved in these processes are only beginning to be understood. Dimethylsulfoniopropionate (DMSP) is produced by phytoplankton and other marine algae, and has been studied primarily in the context of sulfur cycling and regulation of global climate. My laboratory has been investigating DMSP and its breakdown product, dimethyl sulfide as infochemicals associated with trophic interactions in marine habitats, including sub-Antarctic and coral reef ecosystems. Using a neuroecological approach, our work has established that these biogenic sulfur compounds serve as critical signal molecules in marine systems and provides us with a more mechanistic understanding of how climate change may impact information transfer within marine food webs.

Introduction

In the mid-1980s, Robert Charlson, James Lovelock, Meinrat Andreae, and Stephen Warren presented the “CLAW” hypothesis as novel mechanism for the regulation of global climate. In essence, the CLAW hypothesis suggested that primary productivity of the oceans should play a fundamental role in regulating global climate through a negative feedback loop. More specifically, Charlson et al. (1987) proposed that solar radiation would enhance phytoplankton growth, which, in turn, would increase the production of dimethylsulfoniopropionate (DMSP), a common metabolite in marine algae. Once released, they went on to suggest that DMSP would be degraded to dimethyl sulfide (DMS), and other products, and emitted to the atmosphere. Oxidation would lead to the formation of sulfur dioxide and sulfate aerosols, which, in turn, would serve as cloud condensation nuclei (CCN). CCNs would attract water vapor, stimulating cloud formation. Clouds would scatter incoming sunlight, increasing albedo. Growth of phytoplankton would be consequently

down-regulated through reduction in photosynthesis and potentially through lower surface seawater temperatures.

Although the details of this negative feedback loop remain controversial, the contribution of biogenic and anthropogenic sulfur to the regulation of global climate continues to be the subject of much political and scientific interest (Andreae et al. 1995; Lovelock 2006; Vallina et al. 2007). Considerable resources have been directed towards understanding the physical and ecological processes leading to the production and emission of DMS into the atmosphere with an aim towards creating process-oriented predictive climate models. As a result, perhaps more is known about the production and spatio-temporal distribution and characteristics of this scented compound than about any other scented compound on Earth (reviewed by Nevitt 2000).

Using this information, my laboratory established DMS as a signal molecule in the marine environment, with a focus on its use by higher predators, including seabirds and fishes (reviewed by DeBose and Nevitt 2008). Our first investigations established

DMS as a critical infochemical in multi-trophic foraging interactions of seabirds in the sub-Antarctic oceans. These studies were later extended to coral reef fish systems, for which we have shown that DMSP serves as a signal molecule initiating foraging aggregations. In this symposium article, I will briefly summarize these findings, emphasizing how a neuroecological framework informed our approach. I will conclude by synthesizing our major findings, and in so doing bridge the selective adaptation of DMS as an infochemical to its potential function in maintaining algal growth, and by inference, global climate.

DMS as an infochemical for procellariiform seabirds

Procellariiforms are a diverse group of seabird species that share several characteristics (reviewed by Warham 1990, 1996). Species within this order (examples include albatrosses and petrels) are pelagic, and are adapted to forage over hundreds or thousands of square kilometers for patchily distributed prey resources. Procellariiforms also have the largest olfactory bulbs among birds, and olfaction is now known to be critical for behaviors as diverse as foraging, homing, and individual recognition (reviewed by Nevitt 2008). Although procellariiforms have a global distribution, their species diversity is greatest in the Southern Hemisphere, especially in the sub-Antarctic.

Our broader research concerns the sensory ecology of this group with an emphasis on foraging and individual recognition, and interested readers are referred to other more comprehensive reviews (Nevitt 1999a, 2008; Nevitt and Bonadonna 2005a). Pertinent to this discussion, we have shown that several species within this order use DMS as a foraging cue. Our approach exemplifies a neuroecological framework for investigation (Fig. 1; Zimmer and Ferrer 2007), in that we have (1) identified a biologically relevant cue that some species use to find prey, (2) performed detailed behavioral experiments in the field to demonstrate attraction to the cue, (3) performed field-based laboratory experiments to confirm detection ability at concentrations that birds encounter at sea, and (4) begun to examine the evolution of correlated traits pertinent to the use of DMS as a foraging cue. Although the work was not conceived with these four steps in mind, the approach has been curiosity-driven, with each perspective helping to inform and sharpen questions posed by the others.

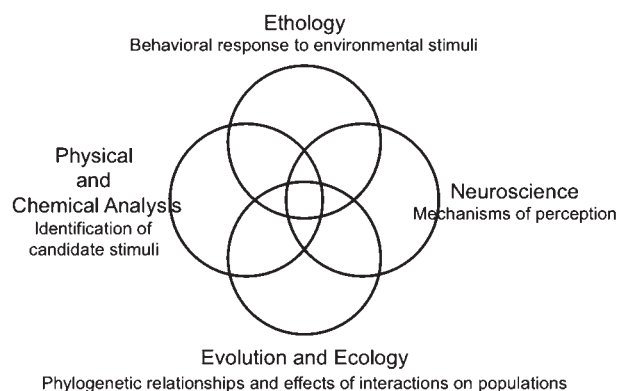


Fig. 1 Schematic of the “neuroecological approach” to investigation (after Zimmer and Ferrer 2007).

Identifying a biologically relevant cue

DMSP is one of the most common metabolites found in marine microalgae, including phytoplankton, in which its function is debated (reviewed by van Alstyne 2008). DMSP is highly soluble in seawater, and is released predominantly following cell lysis, which occurs during senescence or when phytoplankton are crushed during grazing by consumers. Once cells are lysed, DMSP is rapidly catabolized to DMS and acrylic acid by the enzyme DMSP-lyase (Fig. 2).

Since DMS is implicated as a climate regulator, when our investigations were initiated in the early 1990s, there were already considerable data available on the production and distribution of DMS globally, and particularly in the Southern Ocean. It had been established, for example, that DMS tended to be elevated up to five times background levels in productive areas such as those associated with shelf breaks and frontal zones—regions where seabirds and other marine predators tend to forage (see Nevitt 2000 and references therein). It is unusual to have detailed information about any biogenic odor occurring over large (hundreds to thousands of kilometers) spatial scales. Indeed, a lack of quantitative data concerning biogenic odors has been a major stumbling block in investigations of large-scale olfactory navigation in most far-ranging organisms including salmon, sea turtles, and homing pigeons (e.g., Wallraff and Andreae 2000 and references therein). Access to data both on surface seawater and atmospheric DMS thus provided a unique insight into the problem, which led to testable hypotheses. Although appearing “featureless” to the human eye, the open ocean is overlain with an olfactory landscape, which highlights potentially productive foraging areas. A bird arriving at such an area might recognize its

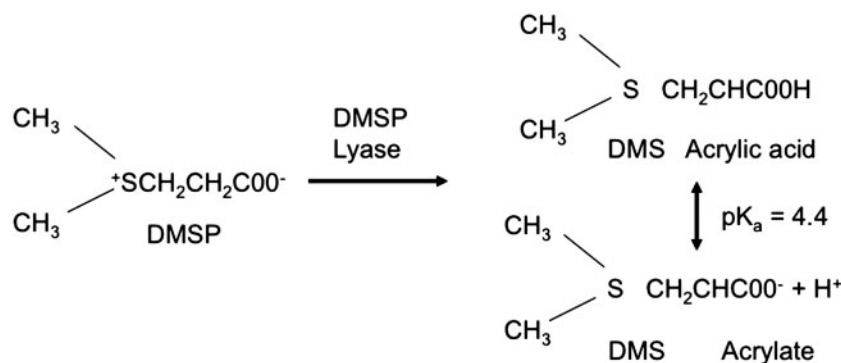


Fig. 2 The enzymatic breakdown of DMSP to DMS and acrylic acid (after van Alstyne 2008).

scent and be triggered to begin an area-restricted search (Nevitt et al. 1995; Nevitt 1999a, 2000).

Field ethology

Initial investigations showed that the abundances of some species of procellariiforms (blue petrels, *Halobaena caerulea*, and prions, *Pachyptila* spp.) were positively correlated with localized elevations in atmospheric DMS (Nevitt 2000). DMS was known to be released during grazing by microzooplankton on marine algae (Dacey and Wakeham 1986, see also Simó 2004). Like many procellariiforms, these species consume substantial numbers of copepods and krill in their diets. Since both copepods and krill are phytoplankton grazers, this suggested that DMS might be a relevant foraging cue for these birds (Nevitt et al. 1995, 2004; Nevitt 1999b).

Subsequent work involved determining whether species could detect DMS at biogenic levels in foraging contexts. We achieved this through a series of multi-year experiments performed at sea, which have been reviewed in detail elsewhere (see Nevitt et al. 1995, 2004; Nevitt 1999a, 1999b). In brief, working from icebreakers, we devised methods of presenting birds with known concentrations of odors as slicks presented on the ocean's surface, and monitored species' responses over brief (10 min) periods. In a related set of experiments, we also presented birds with intermittent scented and unscented aerosols, and then measured turning rate as an indirect measure of scent-tracking behavior.

Experimental results revealed a consistent, species-specific attraction to DMS. From these and other experiments, we concluded that species within the sub-Antarctic seabird assemblage used different sensory strategies to forage (Nevitt et al. 2004). In brief, we found that birds paid attention to odors released in association with trophic interactions. Some species tended to track DMS, a scent that is released as phytoplankton are crushed and eaten,

whereas other species are more attracted to nitrogenous odors released when krill, fish, and squid are crushed, in addition to being attracted by visual cues from other birds.

Physiology

We also investigated physiological sensitivity to DMS to confirm that birds could detect this compound at ambient concentrations at sea. Unconditioned heart-rate response had been previously established as an effective physiological indicator of olfactory perception in other avian species. In combination with behavioral Y-maze experiments, we confirmed that test species could detect DMS at naturally occurring concentrations (picomolar range) (Nevitt and Bonadonna 2005b).

Evolution

In the course of these experiments, we noticed that DMS-responders shared a suite of characteristics (Nevitt et al. 1995). Species that tracked DMS tended to be cryptically colored, suggesting an adaptation for camouflage from potential predators, and they tended to nest in deep, subterranean burrows rather than in above ground crevices or in open nests. This suggested a novel relationship between nesting strategy and the use of olfaction in finding prey. Using phylogenetic methods, we went on to demonstrate a significant relationship between burrow nesting and DMS tracking behavior (van Buskirk and Nevitt 2008). Results suggested that the nesting environment itself may play a role in shaping sensory adaptations for foraging, with implications for olfactory tuning to prey-specific odorants including DMS (see also Nevitt 2008). We have now demonstrated that at least two burrow-nesting species (thin-billed prions *Pachyptila belcheri* and Leach's storm-petrels *Oceanodroma leucorhoa*) can

also learn odors before they leave the nest to forage for the first time (Cunningham and Nevitt 2011; O'Dwyer and Nevitt, unpublished data). Since petrels fledge without parental instruction, this result suggests that odors brought into the nest by parents may play a role in conditioning birds to the scent of foraging hotspots even before they leave the nest.

DMS as a foraging cue in other marine systems?

Our work with procellariiform seabirds (briefly reviewed here) comprises the most complete study to date on the use of DMS as a foraging cue in multi-trophic foraging cascades in the marine habitat. However, since DMSP is a common metabolite of marine phytoplankton, this suggested to us that its role as an infochemical may be more generally applied to other habitats, and that this possibility should be explored.

A logical ecosystem to extend this investigation was in coral reef systems, where DMSP has been studied extensively in other contexts (Jones and Trevena 2005), including pronounced production by coral zooxanthellae (Broadbent and Jones 2002, 2004). There, the potential role that DMSP might play in coordinating fish aggregations was not well worked out (Hay and Kubanek 2002). For example, although it was known that marine fishes can detect free amino acids that are also released during grazing events, Dacey and others had experimentally demonstrated that free amino acids were much less stable than dissolved DMSP, and that they tended to be rapidly consumed by bacteria (Decho et al. 1998; reviewed by DeBose and Nevitt 2008). At the same time, DMSP was known to stimulate the appetite of fishes, and was even used as a flavor enhancer to some commercial fish feeds in Japan. DMSP had previously been shown to stimulate feeding in both freshwater and marine fish species, including a carangid species *Seriola quinqueradiata* (Nakajima et al. 1990). Electrophysiological studies in other species (*Cyprinus carpio*) suggested that detection was via olfaction (Nakajima et al. 1989; reviewed by DeBose and Nevitt 2008). Together, this information pointed to DMSP as a logical candidate for a naturally occurring biogenic compound that could trigger aggregation of fishes. The coral reef system also offered parallels to our investigations of seabirds, in that we could design and implement relatively straightforward field experiments for testing the effects of DMSP on behavior under natural field settings.

DMSP as an infochemical for coral reef fishes

Paralleling our early investigations on seabirds, initial investigations demonstrated a correlation between transient abundance of carangid (jacks) fishes and elevated seawater concentrations of DMSP in coral reef habitats (DeBose and Nevitt 2007, 2008). As predators, carangids consume planktivorous prey, including, shrimp, other invertebrates, and fish. Because these prey species, in turn, are consumers of marine algae, DMSP should be released when either phytoplankton or consumers of phytoplankton are crushed (Iida 1988). This suggested to us that DMSP may be driving foraging cascades in patterns similar to those we had observed with procellariiforms. In this case, we hypothesized that elevated levels of DMSP might trigger either feeding or aggregative behavior in fishes.

To test this idea, (DeBose et al. 2008) conducted a series of “release” experiments in which biogenic concentrations (10^{-7} M) of DMSP were experimentally deployed along a fringing reef off Curaçao, Netherlands Antilles. Coral reef fishes are known to respond to acoustic cues, so the release study was designed to be silent, that is, to release test solutions without the use of pumps. Carboys containing either DMSP (10^{-7} M) or control (distilled water) were suspended mid-water and anchored to the substrate. Release was thus driven by the buoyant force of freshwater, over a period of 1 h, while observers monitored fish behavior and took water measurements for later confirmation of DMSP concentration. As in the seabird experiments, the goal was to produce a down-current DMSP plume approximating concentrations (10^{-7} to 10^{-9} M) that coral reef fish were likely to encounter in nature (Broadbent and Jones 2004; Jones and Trevena 2005).

Results from this field experiment showed that DMSP was significantly attractive to three species of planktivores—brown chromis (*Chromis multilineata*), Creole wrasse (*Clepticus parrae*), and boga (*Inermia vittata*). Although more work needs to be done, these results paralleled the studies of birds in suggesting species-specific patterns, with species that are exclusively planktivores being attracted to DMSP release. Carangid jacks were absent at this experimental site; however, at present, we speculate that they are attracted by a combination of olfactory and visual cues, but data are preliminary (DeBose et al. 2010).

Thus, results from two widely different marine systems suggest that sulfur compounds derived from the algal metabolite DMSP function as

infochemicals for higher predators. This idea has been extended to other marine organisms, including basking sharks *Cetorhinus maximus* (Sims and Quayle 1998), African penguins *Spheniscus demersi* (Cunningham et al. 2008), Northern fur seals *Callorhinus ursinus* (Kowalewsky et al. 2006), and the marine microbial community (Seymour et al. 2010). However, most work is still preliminary and researchers have not yet investigated attraction to DMS or DMSP in experimental foraging contexts under natural conditions. For example, the use of DMS or DMSP as a biogenic cue for sharks is inferred by their movements near productive fronts (Sims and Quayle 1998). In penguins, odor presentations were tested in breeding colonies rather than at sea (Cunningham et al. 2008), and in seals, zoo animals were trained to perform a task in response to DMS presentations. Interestingly, recent laboratory-based work has shown that DMS and DMSP serve as signal molecules in marine microbial interactions, and this should be an active area for future research (Seymour et al. 2010). Further studies would benefit from applying a more comprehensive neuroecological framework.

DMS as an infochemical: relevance to regulation of global climate

Why have biogenic sulfur compounds evolved as signal molecules in marine systems? A better question might be: how does the production of DMS benefit marine algae? DMSP-lyase is thought to have evolved multiple times in marine algae (reviewed by van Alstyne 2008), suggesting intense selection pressure to degrade DMSP to DMS and acrylic acid, even after algal cells have died. The function of acrylic acid has been well studied as an anti-microbial agent and deterrent to algal grazing by protozoans (reviewed by Wolfe 2000), and it is generally assumed that this benefit has been the major selective pressure for DMSP-lyase (but see also Steinke et al. 2002). Our work has also shown, however, that DMS functions as a key infochemical for top predators. Could this function benefit marine algae?

We have produced convincing evidence in two different marine systems that DMS and DMSP function as signal molecules in multi-trophic interactions. Hypotheses that have been proposed to explain this adaptation suggest that phytoplankton produce infochemicals that draw in predators to phytoplankton grazers which, in turn, eliminate the grazers. While this hypothesis may be more tractable to test in the context of planktonic food webs (reviewed by

Pohnert 2007), foraging interactions among marine predators are complex, and the impact that higher predators have on grazers or on the longevity of phytoplankton is not easily quantifiable. Phytoplankton tend to occur in areas of convergence, where sea-surface nutrients are highest, but it is interesting to speculate that trace nutrients delivered by predators through excreta may also contribute to phytoplankton growth. This is an area that is largely unexplored, but offers promise in understanding the inter-relationships between higher predators and phytoplankton-driven processes.

For example, iron is well established as a limiting micro-nutrient in the Southern oceans (Smetacek and Naqvi 2008). Recent experiments have demonstrated that phytoplankton blooms can be induced by fertilizing surface seawater with soluble iron. Nicol et al. (2010) have recently proposed that soluble iron is naturally recycled by phytoplankton consumers, some of which serve as previously unrecognized reservoirs for free iron in surface seawater. They have shown that free iron in the feces of at least one class of krill consumer (four species of baleen whales) is 10 million times that of Antarctic surface seawater. They have gone on to show that Antarctic krill (*Euphausia superba*) alone contains 24% of the free iron in surface seawater where this species occurs. Depending on how it is packaged and released, free iron will either stay at the surface or sink to depths where it is not available to phytoplankton. This presents the interesting possibility that an overlooked selective advantage for producing DMSP-lyase, and by inference DMS, is to recirculate, by way of predators, micronutrients that are otherwise limited to algal producers in surface seawater.

The demonstration that DMS serves as an infochemical thus adds another layer of complexity to the role higher predators play in food-web interactions. Given our current state of knowledge, this is particularly relevant in the Southern Oceans where food-web dynamics are relatively simple compared to other marine and terrestrial ecosystems, and highly dependent on a few keystone species (most notably *Pheocystis* sp. and krill *Euphausia* sp.). The potential role that higher predators play in sulfur cycling (Fig. 3) has been largely ignored by marine microbial biologists interested in ecological processes driving sulfur cycling relative to regulation of climate (Strom 2008). At the same time, it has been well established in terrestrial systems, for example, that birds that utilize island habitat for nesting also play a critical role in delivering nutrients to insular flora (reviewed by Hay and Kubanek 2002; Hay 2009). Although recent data have been collected on

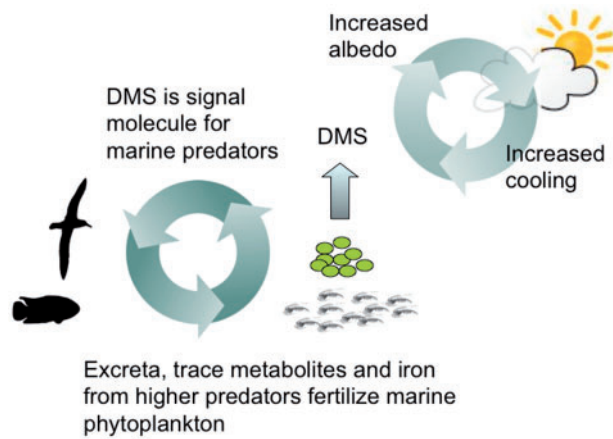


Fig. 3 The potential role that higher predators play in the cycling of sulfur. DMS and DMSP (not shown) are involved in the regulation of global climate, and are released when algae lyse during senescence and during grazing by zooplankton (see text). These compounds serve as infochemicals, attracting marine predators that forage on grazers. Marine algae may benefit by the recirculation of trace nutrients delivered through the predators' excreta.

micronutrients available to phytoplankton via mammalian excreta, similar studies have not been carried out for far-ranging seabirds.

If higher predators are found to play a similar role in the redistribution of micronutrients, such as free iron, to algal producers, then the removal of these predators through over-fishing or other anthropogenic activities may have implications for algal health. This, in turn, could impact production of sulfurous or other biogenically derived aerosols. Given the growing awareness that geochemical cycling, ecosystem health, and climate are not mutually exclusive, this area of research certainly warrants further investigation and highlights the need for increased communication and intellectual exchange between community ecologists and microbial ecologists.

In summary, this project started out as a modest attempt to better understand the foraging strategies of a mixed-species feeding assemblage in the Southern Ocean. While this review is not intended to be a comprehensive overview of the various roles biogenic sulfur compounds play in the infochemistry of the marine ecosystem, my hope is that this work will encourage others to incorporate a neuroecological perspective into their own studies.

Acknowledgments

I thank Drs Charles Derby and Richard Zimmer for organizing and inviting me to participate in this symposium on "Neuroecology". Marcel Losekoot

and Dr Eric Woehler kindly provided editorial assistance and proofread the article. The thoughtful comments of both the editor and two anonymous reviewers improved the article, for which I am very grateful.

Funding

National Science Foundation (IOS 0922640 to G.A.N.).

References

- Andreae MO, Elbert W, de Mora SJ. 1995. Biogenic sulfur emissions and aerosols over the tropical South Atlantic 3. Atmospheric dimethylsulfide, aerosols and cloud condensation nuclei. *J Geophys Res* 100:11335–56.
- Broadbent A, Jones G. 2002. DMSP in corals and benthic algae from the Great Barrier Reef. *Estuarine, Coastal Shelf Sci* 55:547–55.
- Broadbent A, Jones G. 2004. DMS and DMSP in mucus ropes, coral mucus, surface films and sediment pore waters from coral reefs in the Great Barrier Reef. *Mar Freshw Res* 55:849–55.
- Charlson RJ, Lovelock JE, Andreae MO, Warren SG. 1987. Oceanic phytoplankton, atmospheric sulphur, cloud albedo and climate. *Nature* 326:655–61.
- Cunningham GB, Nevitt GA. 2011. Evidence for olfactory learning in procellariiform seabird chicks. *J Avian Biol* 42:85–8.
- Cunningham GB, Strauss V, Ryan PG. 2008. African penguins (*Spheniscus demersus*) can detect dimethyl sulphide, a prey-related odour. *J Exp Biol* 211:3123–7.
- Dacey JWH, Wakeham SG. 1986. Oceanic dimethylsulfide: production during zooplankton grazing on phytoplankton. *Science* 233:1314–6.
- DeBose JL, Lema SC, Nevitt GA. 2008. Dimethylsulfoniopropionate as a foraging cue for reef fishes. *Science* 319:1356.
- DeBose JL, Nevitt GA. 2007. Investigating the association between pelagic fish and dimethylsulfoniopropionate in a natural coral reef system. *Mar Freshw Res* 58:720–4.
- DeBose J, Nevitt G. 2008. The use of odors at different spatial scales: comparing birds with fish. *J Chem Ecol* 34:867–81.
- DeBose J, Nevitt G, Dittman A. 2010. Rapid communication: experimental evidence that juvenile pelagic Jacks (Carangidae) respond behaviorally to DMSP. *J Chem Ecol* 36:326–8.
- Decho AW, Browne KA, Zimmer-Faust RK. 1998. Chemical cues: why basic peptides are signal molecules in marine environments. *Limnol Oceanogr* 43:1410–7.
- Hay ME. 2009. Marine chemical ecology: chemical signals and cues structure marine populations, communities, and ecosystems. *Ann Rev Mar Sci* 1:193–212.
- Hay ME, Kubanek J. 2002. Community and ecosystem level consequences of chemical cues in the plankton. *J Chem Ecol* 28:2001–16.
- Iida H. 1988. Studies on the accumulation of dimethyl-beta-propiothetin and the formation of dimethyl sulfide in aquatic organisms. *Bull Tokai Reg Fish Res Lab* 124:35–111.

- Jones GB, Trevena AJ. 2005. The influence of coral reefs on atmospheric dimethylsulphide over the Great Barrier Reef, Coral Sea, Gulf of Papua and Solomon and Bismarck Seas. *Mar Freshw Res* 56:85–93.
- Kowalewsky S, Dambach M, Mauck B, Dehnhardt G. 2006. High olfactory sensitivity for dimethyl sulphide in harbour seals. *Biol Lett* 2:106–9.
- Lovelock J. 2006. *The revenge of Gaia: why the earth is fighting back - and how we can still save humanity*. London: Allen Lane. p. 176.
- Nakajima K, Uchida A, Ishida Y. 1989. A new feeding attractant, dimethyl- β -propiothetin, for freshwater fish. *Nipp Suis Gakk* 55:689–95.
- Nakajima K, Uchida A, Ishida Y. 1990. Effect of a feeding attractant, dimethyl- β -propiothetin, on growth of marine fish. *Nipp Suis Gakk* 56:1151–4.
- Nevitt GA. 1999a. Foraging by seabirds on an olfactory landscape. *Am Sci* 87:46–53.
- Nevitt GA. 1999b. Olfactory foraging in Antarctic seabirds: a species-specific attraction to krill odors. *Mar Ecol Progr Ser* 177:235–41.
- Nevitt GA. 2000. Olfactory foraging by Antarctic procellariiform seabirds: life at high Reynolds numbers. *Biol Bull* 198:245–53.
- Nevitt GA. 2008. Sensory ecology on the high seas: the odor world of the procellariiform seabirds. *J Exp Biol* 211:1706–13.
- Nevitt GA, Bonadonna F. 2005a. Seeing the world through the nose of a bird: new developments in the sensory ecology of procellariiform seabirds. *Mar Ecol Progr Ser* 287:292–5.
- Nevitt GA, Bonadonna F. 2005b. Sensitivity to dimethyl sulphide suggests a mechanism for olfactory navigation by seabirds. *Proc Roy Soc B Lett* 1:303–5.
- Nevitt GA, Reid K, Trathan P. 2004. Testing olfactory foraging strategies in an Antarctic seabird assemblage. *J Exp Biol* 207:3537–44.
- Nevitt GA, Veit RR, Kareiva P. 1995. Dimethyl sulphide as a foraging cue for Antarctic Procellariiform seabirds. *Nature* 376:681–2.
- Nicol S, Bowie A, Jarman S, Lannuzel D, Meiners KM, van der Merwe P. 2010. Southern Ocean iron fertilization by baleen whales and Antarctic krill. *Fish Fisheries* 11:203–9.
- Pohnert G, Steinke M, Tollrian R. 2007. Chemical cues, defence metabolites and the shaping of pelagic interspecific interactions. *Trends Ecol Evol* 22:198–203.
- Seymour JR, Simó R, Ahmed T, Stocker R. 2010. Chemoattraction to dimethyl-sulfoniopropionate throughout the marine microbial food web. *Science* 329:342–5.
- Simó R. 2004. From cells to globe: approaching the dynamics of DMS(P) in the ocean at multiple scales. *Can J Fish Aqu Sci* 61:673–84.
- Sims DW, Quayle VA. 1998. Selective foraging behaviour of basking sharks on zooplankton in a small-scale front. *Nature* 393:460–4.
- Smetacek V, Naqvi SWA. 2008. The next generation of iron fertilization experiments in the Southern Ocean. *Phil Trans Roy Soc A* 366:3947–67.
- Steinke M, Malin G, Liss PS. 2002. Trophic interactions in the sea: an ecological role for climate relevant volatiles. *J Phycol* 38:630–8.
- Strom SL. 2008. Microbial ecology of ocean biogeochemistry: a community perspective. *Science* 320:1043–5.
- Vallina SM, Simó R, Gasso S, de Boyer-Montégut C, del Rio E, Jurado E, Dachs J. 2007. Analysis of a potential “solar radiation dose–dimethylsulfide–cloud condensation nuclei” link from globally mapped seasonal correlations. *Glob Biogeochem Cycles* 21 [Epub ahead of print April 19, 2007; GB2004 doi:10.1029/2006GB002787].
- van Alstyne KL. 2008. Ecological and physiological roles of dimethylsulfoniopropionate and its products in marine macroalgae. In: Amsler CD, editor. *Algal chemical ecology*. Heidelberg, Berlin: Springer. p. 173–94.
- van Buskirk RW, Nevitt GA. 2008. The influence of developmental environment on the evolution of olfactory foraging behaviour in procellariiform seabirds. *J Evol Biol* 21:67–76.
- Wallraff HG, Andreae MO. 2000. Spatial gradients in ratios of atmospheric trace gases: a study stimulated by experiments on bird navigation. *Tellus Ser B: Chem Phys Meteor* 52:1138–56.
- Warham J. 1990. *The petrels: their ecology and breeding systems*. London: Academic Press. p. 440.
- Warham J. 1996. *The behaviour, population biology and physiology of the petrels*. London: Academic Press. p. 613.
- Wolfe GV. 2000. The chemical defense ecology of marine unicellular plankton: constraints, mechanisms, and impacts. *Biol Bull* 198:225–44.
- Zimmer RK, Ferrer RP. 2007. Neuroecology, chemical defense, and the keystone species concept. *Biol Bull* 213:208–25.