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Hermit crabs as model species for investigating the behavioural responses to pollution

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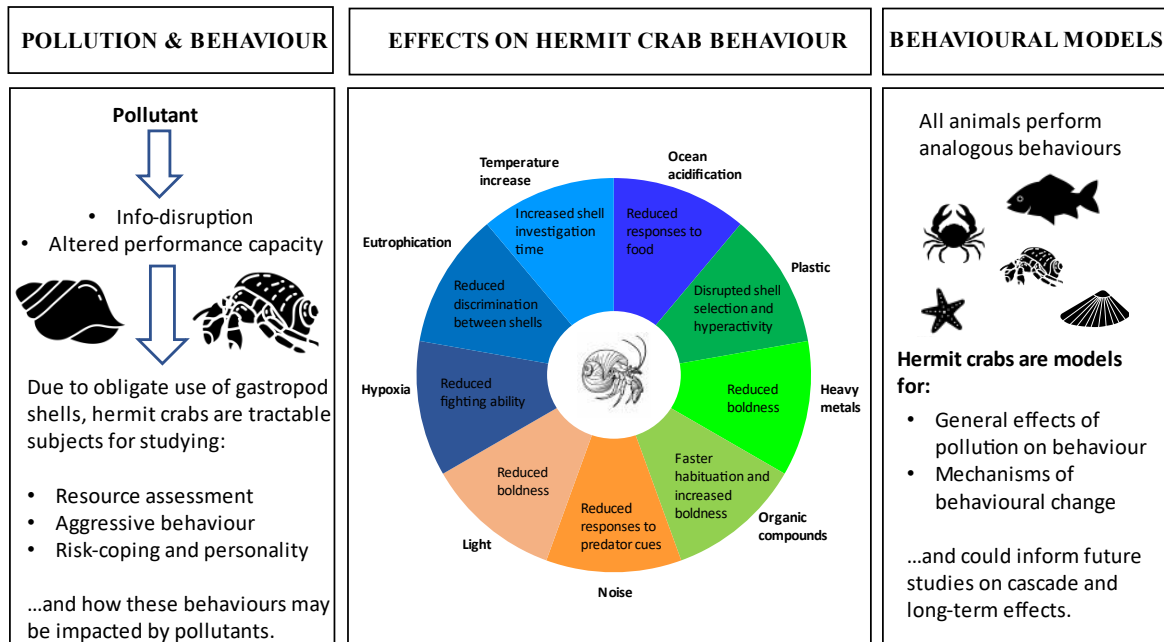
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Graphical abstract

POLLUTION & BEHAVIOUR

Pollutant

- Info-disruption
- Altered performance capacity

Due to obligate use of gastropod shells, hermit crabs are tractable subjects for studying:

- Resource assessment
- Aggressive behaviour
- Risk-coping and personality

…and how these behaviours may be impacted by pollutants.

EFFECTS ON HERMIT CRAB BEHAVIOUR

Temperature increase — Increased shell investigation time

Ocean acidification — Reduced responses to food

Plastic — Disrupted shell selection and hyperactivity

Heavy metals — Reduced boldness

Organic compounds — Faster habituation and increased boldness

Noise — Reduced responses to predator cues

Light — Reduced boldness

Hypoxia — Reduced fighting ability

Eutrophication — Reduced discrimination between shells

BEHAVIOURAL MODELS

All animals perform analogous behaviours

Hermit crabs are models for:

- General effects of pollution on behaviour
- Mechanisms of behavioural change

…and could inform future studies on cascade and long-term effects.

Highlights

- Pollution can impact behaviour directly and by disrupting cognition.
- Individual responses can cascade to populations, communities and ecosystems.
- Hermit crabs provide a globally distributed model for investigating info-disruption
- Hermit crab behaviour is affected by climate change, chemicals, noise and light.
- These effects can be readily studied across a wide range of behavioural contexts.

Abstract

Human impacts on the environment affect organisms at all levels of biological organisation and ultimately can change their phenotype. Over time, phenotypic change may arise due to selection but individual phenotypes are also subject to change via genotype × environment interactions. In animals, behaviour is the most flexible aspect of phenotype, and hence the most liable to change across environmental gradients including exposure to pollution. Here we review current knowledge on the impacts of pollution, broadly defined to include the release of substances, energy, and the effects of carbon emissions, on the behaviour of a highly studied group, the globally distributed hermit crabs. We first show how their obligate association with empty gastropod shells underpins their use as model organisms for the study of resource-assessment, contest, and risk-coping behaviours. Intense study of hermit crabs has advanced our understanding of how animals use information, and we discuss the ways in which pollutants can disrupt cognitive processes involved. We then highlight current studies of hermit crabs, which paint a clear picture of behavioural changes due to multiple pollutants. Impacts on behaviour vary across pollutants and entire suites of behaviours can be influenced by a single pollutant, with the potential for interactive and cascade effects. Hermit crabs offer the opportunity for detailed behavioural analysis, including application of the repeated measures animal-personality framework, and they are highly amenable to experimental manipulations. As such, we show how they now provide a model system for studying the impacts of pollution on behaviour, yielding insights broadly applicable across animal diversity.

1. Introduction

Animal behaviour, expressed by individuals, is fundamental to a broad range of interspecific and intraspecific relationships and thus the structure, function, and stability of ecosystems (Ives & Carpenter, 2007; Rahman & Candolin, 2022). Consumptive behaviour, for example, directly links populations of predators and prey, and these links are further influenced by non-consumptive behaviour such as risk avoidance (Rahman & Candolin, 2022). Intraspecific behavioural interactions are also ecologically relevant due to their contributions to population dynamics, via reproductive behaviour as well as through social behaviour (including aggression), which mediates the flow and distribution of resources through populations. Therefore, any pollutants that alter behaviour are potentially impactful beyond the fitness of exposed individuals. Understanding the causation and nature of pollutant-driven behavioural change, at the level of the individuals under exposure, is thus an essential step towards establishing their potential for wider impacts, beyond the species or individuals effected directly.

1.1 Direct effects and info-disruption

Pollutants can potentially alter animal behaviour through a variety of routes. First, behavioural change can derive from the proximate effects of exposure on organismal health. These might limit activity via impaired energy metabolism, or due to the cost of diverting energy, normally allocated to behaviour, to coping and repair mechanisms such as detoxification pathways (e.g. see Mayrand & Dutil 2008). Second, animals might plastically adjust their behaviour to cope with or avoid or approach pollutants (Araújo et al. 2020). Third, all animal behaviour relies on the acquisition, processing and, in most if not all animals, storing of information, henceforth cognition. Cognition involves both intrinsic information such as neural signals of hunger status,

or injury, and extrinsic information such as a cue of predator presence, or a signal from a potential mate. When pollutants alter any of the components of cognition, they are causing *info-disruption*, which we can categorise into two classes based on their point of action. *Extrinsic info-disruption* occurs when the pollutant changes the external environment in ways that make information harder to acquire. In marine environments, for example, animals rely heavily on chemical information (*info-chemicals*; Hardege et al., 2023) and pollutants and environmental change (e.g. water chemistry changes associated with ocean acidification, discussed in section 2.2) could change the properties of normally informative chemicals, thus impacting signal-receptor interactions (Roggatz et al. 2019a, Porteus et al., 2021). Additionally, pollutants might occlude information, masking it from the perception of animals (Halfwerk & Slabberkoorn 2015). Conversely, pollutants could add novel information, perceived by animals, and thereby distracting them from a more salient source of information (Halfwerk & Slabberkoorn 2015). In addition to extrinsic info-disruption, which only effects information gathering, pollutants might impair cognition at the organismal level, which we refer to as *intrinsic info-disruption*. Here, a pollutant might alter binding sites on chemoreceptive cells (Porteus et al., 2021), or damage sensory organs in other ways, therefore impairing information acquisition. Furthermore, pollutants that are taken up (e.g. via respiration or ingestion) might impair the normal functioning of interneurons and endocrine systems, potentially affecting the ability to process and store information (Halfwerk & Slabberkoorn 2015). Additionally, given the complex and multi-modal nature of information use by animals, behavioural changes may be non-linear with respect to the magnitude of pollutant exposure (Halfwerk & Slabberkoorn 2015).

While the behavioural effects of pollutants have been documented in a variety of species, our understanding of which of these mechanisms are involved is relatively limited. In the following sections we review what is currently known about the causes and nature of

impacts of pollutants on the behaviour of hermit crabs. Further, due to a unique aspect of their biology, their association with empty gastropod shells, we show that they provide a model system for investigating how impacts on behaviour at the individual level might cascade (Rahman & Candolin, 2022) upwards to alter relationships within populations, communities, and ecosystems.

1.2 Hermit crabs as models for behavioural impacts of pollution

Hermit crabs (Figure 1) provide an emerging model for the study of the behavioural impacts of pollution and offer the potential for distinguishing among the different routes by which pollutants may lead to behavioural changes. They are decapod crustaceans of the infraorder Anomura, and are globally distributed through tropical, temperate, and arctic regions (Balazy et al. 2015) with a handful of species accruing in both Pacific and Atlantic sub-Antarctic waters (Lovrich and Thatje 2006). Of the estimated 800 species of hermit crab most are marine (Lancaster 1988) but 12 tropical species are semi-terrestrial s living on land in their post-larval phases and there is a single freshwater species. Marine hermit crabs are found in the intertidal, the sub-littoral and in the deep sea where they form an important part of the benthic biota as opportunistic predators, scavengers, and detritivores (Balazy et al. 2015). A unique aspect of the biology of most hermit crabs is their association with empty gastropod shells, which they use as "portable burrows", in most species. Shell use involves a suite of behaviours, which, since the 1960s (e.g. Hazlett, 1966; Markham, 1968; Reese, 1962), have been intensively studied and meticulously quantified. Recently, there has been a growing interest in using the suite of shell-orientated behaviours as a model to understand how the external environment including the presence of pollutants might influence behaviour. Gastropod shells provide hermit crabs a degree of buffering against desiccation (during emersion), temperature

fluctuation (Taylor, 1981) and fluctuations in other seawater physicochemical variables (e.g. salinity). The primary function, however, is protection of the weakly calcified abdomen from predators and other mechanical damage. When threatened they withdraw tightly into their shell, temporarily protecting the normally exposed appendages and anterior cephalothorax (including the eyes, mouthparts, antennae, and antennules). Hiding in a shelter is an effective way of avoiding a predator but it comes at the cost of reduced activity. Thus, hiding duration in hermit crabs can be used to investigate how animals respond to information on risk and reward (Briffa et al., 2008). Furthermore, hermit crabs deploy a suite of behaviours directed at gathering information about the quality of empty gastropod shells, and they select shells based on shell size, species (see Elwood & Neil, 1992), condition (Rotjan et al., 2004) and colour (Briffa et al., 2008; Rimmer et al., 2021). Adequate shell size, which changes during growth, affects not only survival but also growth rate, fecundity and, in the case of females, protection afforded to developing offspring. On the other hand, larger heavier shells impose greater costs on locomotion (Herreid & Full, 1986) and therefore optimal shell size represents a trade-off between protection and energetic efficiency (Côté et al., 1998; Osorno, 1998). This shell assessment behaviour has been the subject of particularly detailed study, using various species of hermit crab as model systems for the investigation of information acquisition and decision-making in animals (e.g. Elwood & Neil, 1992). A final dimension of shell-orientated behaviour is "shell fighting" where individuals compete aggressively over the ownership of contested shells. Like many examples of aggression (Briffa & Sneddon, 2007), shell fights involve both information-gathering and the accumulation of metabolic costs (Briffa & Elwood, 2004). Further, due to their small size and amenability to manipulative experiments, other classes of behaviour not immediately associated with shell use, such as foraging (e.g. see Laidre 2013) and activity rates, are also well studied in hermit crabs. In the following we outline key aspects of the hermit crab behavioural repertoire, focussing on those that have been investigated in

relation to pollution. Then, in Section 2, we review the current state of knowledge on the effects

of a wide range of pollutants on these behaviours.

1.2.1 Resource assessment

As noted above, gastropod shells represent a key resource linked to survival, growth, and

fecundity and hence fitness (Elwood & Neil, 1992). Hermit crabs utilise a range of behaviours

in assessing the quality of empty shells that they encounter. Initial attraction to the shell is

though vision and distance chemoreception, where the antennules are moved rapidly through

the water in a 'sniffing' response (de la Haye et al. 2011). The first physical contact with the

shell will then usually be with the longer antennae, which are used for contact chemoreception.

Next, the empty shell is grasped and manipulated with the walking legs. Turning the shell this

way enables a tactile inspection of its external surface using the chelipeds. Eventually the shell

is manoeuvred into a position that allows the chelipeds, and sometimes the walking-legs, to be

inserted thought its aperture, enabling the crab to gather tactile information on its internal

features (Reese 1962; Elwood & Neil 1992). In experiments on shell investigation, crabs are

presented with empty shells that can be varied in terms of mass relative to an optimal shell

mass given the mass of the crab (which is typically calculated from shell selection

experiments). Further, the colour and species of shells can be manipulated (e.g. Briffa &

Twyman 2011; Rimmer et al. 2021). Thus, experiments on shell investigation probe the visual,

chemical, and mechanical information that hermit crabs use, and reveal information on how

crabs make the decision of whether to exchange the currently occupied shell for a new one.

1.2.2 Contests

Shell fighting involves both energetically demanding behaviour and information processing on conspecifics and resources (Briffa & Elwood 2004). The sequence of events in a shell fight is described in Elwood & Neil (1992): Briefly an 'attacker' will advance a 'defender' and grasp the defender's shell. The defender usually withdraws tightly into its shell at this point. Holding the defender's shell, the attacker gathers information on its external surface. The attacker may then decide to escalate the fight, by performing vigorous bouts of shell rapping, where it repeatedly strikes the surface of its own shell against the shell of the defender, in a series of bouts of rapping interspersed with pauses (Elwood & Neil, 1992). If the vigour of rapping is sufficient (e.g. a high number of raps per bout and short pauses between bouts;; Briffa et al., 1998, 2003; Briffa & Elwood, 2000a), the defender may then decide to give up, releasing its abdominal grip of the shell's internal structure. In this case, the attacker will evict the defender, pulling it out of the shell through the aperture, thereby winning the fight over the contested shell originally occupied by the defender. Having taken possession of the defender's shell, the attacker can then choose whether to occupy it, and abandon its original shell. The other way a shell fight can end is when the attacker decides to give up, either at the shell-assessment stage prior to escalation, or after it has performed some bouts of shell rapping, this outcome being described as a non-eviction (Elwood & Neil 1992). Shell fights provide insights about the interplay between performance capacities and cognition, and the extrinsic factors that might affect these.

1.2.3 Personality and risk-taking

Animal personality refers to the presence of consistent behavioural differences between individuals (Dingemanse et al., 2010). The study of personality cuts across behavioural

contexts such as resource assessment or contests but a particular focus is on relation to risk-coping strategies, or variation in "boldness". Risk-prone individuals are described as being bold whereas risk-averse individuals are described as shy. Where consistent individual differences are present, however, the different behavioural types rarely fall into a binary distribution of bold versus shy. Rather, we see a continuum of responses, usually referred to as variation along an axis of boldness. The strength of personality in a sample or population is quantified by calculating repeatability (R) from repeated measures data, where each individual in the sample is observed on multiple occasions. R is an intra-class correlation coefficient (Bell et al. 2009) and can be thought of as the effect size for the variation in repeated measures data explained by individual identity – in other words by differences between individuals in their average way of behaving. More formally, R is the proportion of variance in the data due to behavioural differences between individuals (V_{BI}) out of the total variance made up of V_{BI} and variance within individuals (V_{WI}) (Nakagawa & Schielzeth 2010) In addition to variation in their average expression of a given behaviour, individuals might also differ in other ways. First, they might vary in how their behaviour changes in response to extrinsic conditions, showing different behavioural reaction norms, often described as an individual (or genotype) × environment (I × E) interaction effect (Dingemanse et al., 2010). Second, individuals might differ in how predictable their behaviour is, which can be quantified by assessing differences in variance around individual behavioural means within a fixed set of conditions (i.e. variation among individuals in V_{WI}), or variance around individual slopes of reaction when conditions change, or over time ($V_{WI} × E$) (Stamps et al., 2012; Westneat et al., 2015). Studying behaviour at these levels has come to be described as "the animal personality framework" (Figure 2) (e.g. Wolf & Weissing 2010). Animal personality is relevant to the topic of pollution because if individuals differ in their responses to it and if those differences are heritable, then pollution potentially becomes a selective force that could drive behavioural change across generations

10

(i.e. evolution). Hermit crabs are a convenient model in which to study animal personality, including the effects of extrinsic conditions, due to their behaviour of rapidly withdrawing into their shell when disturbed before slowly re-emerging. The duration of these startle responses is readily measured and can be observed repeatedly in the same individuals. By studying startle responses in hermit crabs, we can learn about variation in risk-taking between and within individuals and how individuals differ in their responses to extrinsic conditions such as pollutants, as well as looking at population level average effects. In terms of understanding the behavioural effects of pollution, we can use the animal personality framework to investigate effects at the levels of populations, and between and within individual variation in responses.

2. Review of behavioural impacts of pollution in hermit crabs

We define pollution broadly as the introduction to the environment of substances or energy at a rate that has the potential to impact organisms. We include the effects of anthropogenic climate change (hypoxia, temperature, and ocean acidification) due to the release of carbon in addition to chemical pollutants such as plastic and heavy metals, and energy such as light or noise. This definition corresponds with the concept of Human Induced Rapid Environmental Change (HIREC), a term that has been broadly adopted in the behavioural and evolutionary ecology literature (e.g. Sih et al. 2011). In the following sections we review studies on hermit crabs on the effects of these pollutants across the behavioural contexts associated with gastropod shell use described above, as well as in terms of more general behaviour such as foraging activity rates. Table 1, which groups pollutants into three broad categories (effects of climate change, waste products and release of energy) provides an overview of the studies conducted to date, and of current gaps in knowledge.

2.1 Elevated temperature

Intertidal hermit crabs are adapted to cope with environmental heterogeneity such as spatial and temporal fluctuations in salinity, pH, dissolved oxygen, and temperature. Variation in these physicochemical parameters is naturally higher in tide-pools compared to sublittoral waters due to the effects of the weather on low volumes of water, the tidal cycle and the metabolic activity of other organisms such as respiration in marine algae at night. Nevertheless, due to carbon dioxide emissions, average sea-surface temperatures are rising, and these effects can be magnified in coastal waters and the intertidal, especially during extreme temperature events. Therefore, intertidal animals like hermit crabs will be impacted by exposure to periods of elevated temperature (and the other parameters that co-vary with temperature, see Sections 2.2 and 2.3) that exceed their usual tolerance ranges (see Helmuth et al. 2006 for a detailed discussion). Dealing with temperature first, we will consider what is currently known about the possible behavioural responses to atmospheric pollution by carbon emissions.

Given their adaptations to the intertidal environment, it is not surprising that hermit crabs are behaviourally responsive to temperature fluctuations. In experiments where individual *Clibanarius erythropus* (named "St. Pirin's hermit crab" following its recent reestablishment in the UK) were allowed to move freely within a thermal gradient, the majority spent most of their time in cooler seawater areas (12-17°C) and avoided higher temperatures up to a maximum of 35°C (Warburg & Shuchman, 1984). This result indicates that these hermit crabs could respond to high temperature via avoidance behaviour, a result found in an *in situ* study of the tropical hermit crab *Diogenes deflectomanus*, which left tide-pools and also showed a distinctive 'shell raising' behaviour during periods of heat stress (Leung et al., 2023). Such temperature driven changes in habitat choice thus have potential consequences for time-allocation within microhabitats and even for broader scale distribution patterns. It has been

suggested, for example, that increased seawater temperatures could be responsible for a range expansion in *Pagurus granosimanus*, bringing individuals of this North Pacific species into greater conflict over gastropod shells with individuals of the congeneric *P. beringanus* (Torjman & Iyengar, 2021). Interestingly, in Warburg & Schuman's (1984) experiment, crabs in groups of 5 or 10 individuals selected higher temperature zones than those observed individually, an effect attributed to the interaction between information on temperature and chemical information on the presence of conspecifics (Warburg & Shuchman, 1984). This result suggests that there are some constraints on avoidance behaviour, and in addition to biotic variables other obvious constraints include physical ones such as the boundaries of tide-pools, which hermit crabs rarely cross. Thus, it is likely that in the context of rising seawater temperatures, intertidal hermit crabs will be exposed to prolonged periods of elevated temperature. As ectothermic animals this is expected to raise their metabolic rate (Thatje et al., 2010) and hence energy demand. An elevated energy demand could lead to a shift in the balance of risks (predation) and rewards (opportunity for foraging) of re-emerging from the shell after encountering a startling stimulus, and hence lead to changes in hiding duration. This hypothesis was tested by comparing startle response durations at 10°C and 15°C in the common European hermit crab *Pagurus bernhardus* (Briffa et al., 2013). In this experiment each individual was observed eight times at each of the two temperatures. To control for potential order effects, a cross-over design was used where half the crabs were observed at the lower temperature first and the remainder received the higher temperature treatment first (Figure 3b). For crabs exposed to 10°C followed by 15°C, average startle responses durations (calculated across all crabs) were lower at the higher temperature, but the opposite pattern was seen in crabs that were exposed to 15°C followed by 10°C. Furthermore, regardless of treatment order, there was a high degree of variation between individuals in how their individual average startle response durations differed between the two temperatures. Thus, contrary to expectations, there

13

was no overall effect of temperature, with mean differences between temperatures is likely due to order effects. While there was no effect of temperature on risk-taking at the sample mean level, there was an effect at the level of V_{WI}, with crabs behaving less predictably at the higher temperature. Since *P. bernhardus* also behave less predictably in the presence of predators (Briffa, 2013a) these less predictable startle responses, rather than shorter ones, at higher temperatures may reflect a strategy to mitigate risks associated with elevated metabolism.

A recent study on a terrestrial hermit crab, however, *Coenobita clypeatus*, demonstrated a clear mean level effect on boldness. Sakich et al. (2023) exposed individuals to a wide range of air temperatures of $15 - 35°C$ and found that at higher temperatures startle response duration was decreased. Similarly to Briffa (2013), they found no effect on overall repeatability although this was not decomposed into its different variance components as in Briffa (2013), so they did not assess the effects of temperature on behavioural predictability. Some of the differences in findings between these studies may be accounted for by different experimental protocols (for example a 30s interval between evoking successive startle responses in the latter study compared to 24h in the earlier study). Nevertheless, these differences highlight that responses to a given pollutant may differ between aquatic and terrestrial species and hermit crabs offer a unique opportunity for comparison given that homologous behaviours can be investigated across animals from different habitats.

The behavioural impacts of elevated temperature discussed this far are likely to derive from direct effects on energetic requirements and avoidance of adverse conditions. There is also evidence that elevated temperature drives behavioural change via info-disruption. Thatje et al. (2010) observed greater rates of antennule wiping in *Pagurus cuanensis* at higher temperatures, indicative of reduced efficiency in chemoreception, but it is unknown whether this results from intrinsic or extrinsic info-disruption. Additionally, Gilliand et al. (2021) found

that long clawed hermit crabs, *Pagurus longicarpus*, took longer to assess the quality of empty *Littorina littorea* shells at high temperatures and were less likely to eventually choose intact over damaged shells, compared with crabs at low temperature. These changes in behaviour were compounded by reduced salinity, another potential consequence of climate change due to the increased incidence of heavy rainfall, demonstrating that different components of pollution can have interactive effects on behaviour.

2.2 Ocean Acidification

Elevated atmospheric carbon dioxide (CO_2) leads to increased absorption by the sea. This is predicted to cause a suite of changes to seawater chemistry including a further reduction in pH of up to 0.37 units, relative to 1995-2014by the end of this century (IPCC 2022) and the problem is thus termed Ocean Acidification (OA). Additionally, more severe localised drops in pH could result near shore, in estuaries where changes in salinity provide additional stress, and due to upwellings and leakage from proposed carbon sequestration schemes. Coastal and estuarine environments represent most of the ecosystems inhabited by hermit crabs, and significant natural pH fluctuations occur between day/night, tidal status as well as seasonality. OA is predicted to increase seasonal pH fluctuations (Landschützer et al. 2018) with night pH in coastal areas averaging below pH 7.4 representing pH extremes (Pacella et al. 2018). These changes could then lead to behavioural changes through different routes. First it could impact behaviour through reduced performance capacities due to hypercapnia. Second it could cause intrinsic info-disruption, by affecting the function of chemo-receptors or neurones, and extrinsic info-disruption by changing the properties of chemical cues and signals (Schirrmacher et al. 2021).

The earliest studies on the effects of OA on behaviour in *P. bernhardus* (de la Haye et al. 2011, 2012) used CO_2 manipulation systems to acidify sea water in a way that mimics the OA process to produce severe treatment levels (pH 6.8), relevant to upwellings of highly affected seawater and CO_2 leakage scenarios. First, resource acquisition was impaired (de la Haye et al. 2011) as hermit crabs held under OA conditions were less likely to change from a suboptimal shell to an improved one and those that did change took longer to make the decision, compared to crabs in normal seawater. A reduced rate of antennule flicking (the crustacean 'sniffing response') indicated that this change could in part be due to reduced information gathering, since hermit crabs use chemical as well as visual cues to detect new shells. A second study (de la Haye et al. 2012) focussed in on this possibility of impaired detection of chemical cues and found that under acidified seawater conditions hermit crabs had a reduced ability to find the location of a food odour source. Interestingly, acidifying the food odour itself had no effect on its detectability. An additional component of this study was analysis of haemolymph and crabs held under OA conditions had a greater concentration of chloride ions than those in the normal seawater treatment. Cl^- however did not correlate with locomotory activity. Incidentally, responses to feeding stimulants in hermit crabs are easily observed using y-shape or football pitch design assays, which are also used in outreach programs with data gathered by the public including school children (Roggatz et al. 2019b). This demonstrates the use of research on hermit crabs as a potential route for promoting public engagement with issues of pollution and climate change.

A subsequent study (Kim et al. 2015) on a deep-sea hermit crab, *P. tanneri*, replicated the results of reduced antennule flicking and lower reactivity to food odour, both at a more moderate OA treatment of pH 7.1. Additionally, they found elevated metabolic rate after three weeks of OA conditions, but this effect had dissipated after eight weeks, suggesting that acclimation had occurred. Furthermore, a study on a south Atlantic hermit crab, *Pagurus*

criniticornis, also showed that moderate pH decline reduced responses to the odour of dead gastropods (a source of food and a potential cue of shell availability) but did not affect avoidance of predatory crab odour (Ragagnin et al. 2018). Furthermore, while calcification was unaffected, OA had an interactive effect with excess shading (which can occur in coastal regions due to the placement of built structures) to reduce growth rate, with lipid stores being reduced by 42% under OA (Turra et al. 2020). These studies collectively provide early but tentative evidence that disruption of information processing and whole-body performance capacities could contribute to OA induced changes in chemo-responsiveness.

As noted above absorption of excess CO_2 by the sea leads to a suite of interlinked chemical changes, the reduction in pH being only one consequence of these. Furthermore, odour cues (such as food, a predator, or a mate) are likely made up of complex 'bouquets' of chemicals (see Fletcher et al. 2022). Therefore, the effects of these components should be disentangled from one another. Schirrmacher et al. (2021) started this process by investigating the responses of *P. bernhardus* to different concentrations of a single chemical compound, 2-phenylethylamine (PEA) (Figure 3d). This is widespread in marine environments was attracting hermit crabs under low pH conditions. Further, by manipulating sea water via addition of hydrochloric acid (HCl), the effects of pH were isolated from all other changes due to carbon chemistry. In contrast to the experiments on food cues, hermit crabs were not attracted to PEA at pH 7.7 but showed a dose-dependent attraction at pH 8.1. The primary effect of increasing the proton concentration of seawater on PEA was to increase the concentration of its protonated form PEAH$^+$. Both forms exist in a mixture of three physical conformations, defined by the angle of an amino side chain relative to the rest of the molecule. Using computational chemistry, Schirrmacher et al. (2021) further showed that the proportions of these confirmations are vastly different for unprotonated and protonated PEA. They used similar computational techniques to assess the affinity of these different confirmations to a

potential receptor binding pocket and found that the most common confirmation at pH 7.7, which is relatively rare at pH 8.1, has the greatest affinity of the three conformations. This study provided evidence that OA could lead to changes in behaviour due to extrinsic as well as intrinsic info-disruption. Additionally, these studies on hermit crabs highlight the potentially complex nature of OA on marine animal behaviour. As well as causing diminished responses to relevant cues, OA could lead to enhanced responses to compounds that hermit crabs are not normally attracted to under current conditions.

2.3 Eutrophication

Eutrophication occurs when excess nutrients from either sewage or agriculture enter coastal waters, and a consequence of eutrophication is elevated growth rates of photosynthetic marine organisms. Elevated growth in algae can increase biological oxygen demand in eutrophic areas (see section 2.4 for a discussion of hypoxia) but another impact is increased blooms of toxic dinoflagellates such as the red bloom caused by *Karenia brevis* (Ball et al., 2023). On exposure to high concentrations of *K. brevis* cell suspensions, the hermit crab *P. longicarpus* took longer to choose between shells and exhibited a loss of their normal preference for intact shells over shells that had been damaged by the drilling of predatory gastropods (Ball et al., 2023). Suggested mechanisms for these changes include impaired cognition due to effects of the brevotoxins on neural function, and reduced performance capacities that impair the ability to carry out the physical manipulation of empty shells during shell investigation (Ball et al., 2023). An additional possibility, since this effect was more marked in individuals that started the experiment without a shell, is that the normal preference for intact shells was traded-off against a greater urgency to obtain any shell under exposure to toxins due to the buffering effect of shells in relation to the physico-chemical environment.

2.4 Hypoxia

Hypoxia, reduced dissolved O_2 (DO), can result from eutrophication due to the elevated oxygen demands from algal respiration. Additionally, this effect can be exacerbated by elevated temperature, which leads to decreased O_2 solubility. Climate change induced incidence of hypoxic conditions (defined as <2mg $O_2 l^{-1}$) has been increasing in coastal waters since the 1950s (see Roman et al., 2019 for a review). Severe hypoxia can cause behavioural stress responses and eventually mortality in any marine animal including hermit crabs (e.g. see Pretterebner et al. 2012) but behaviour might also be impacted indirectly via avoidance of hypoxic zones (Roman et al., 2019). However, in intertidal habitats, where movement is bounded by the margins of tide pools the scope for avoidance can be limited. Côté et al. (1998) showed how unavoidable hypoxia could change shell selection behaviour and shell preferences in *P. bernhardus*. Under hypoxic conditions, crabs spent less time investigating empty gastropod shells and ultimately chose to occupy shells that were on average more than 50% lighter than their optimal shell size under normoxic conditions (see Figure 3c in Côté et al., 1998). It seems likely that this change in behaviour is due to the ability of hermit crabs to trade-off protection and scope for growth against their capacity to meet the energetic costs of shell carrying, which is likely to be reduced under hypoxic conditions. This illustrates the role of behavioural plasticity in linking exposure to pollution to changes in behaviour.

Hypoxia will affect the capacity for energetically demanding behaviour such as fighting. Briffa & Elwood (2000b) used a fully orthogonal experiment based on pre-treating attackers and defenders with either hypoxic or normoxic seawater prior to fights (Figure 3a). Attackers exposed to hypoxia rapped with reduced vigour and as a result were less likely to evict the defender compared with attackers that had not been exposed to hypoxia (Briffa & Elwood, 2000b). Additionally, hypoxia in attackers leads to a progressive switch during fights from shell rapping to a less demanding behaviour of shell rocking (Lane & Briffa, 2023). This

decision also seems to be influenced by variation in cognitive abilities among crabs, indicating that while the change in behaviour is underpinned by reduced performance it is driven by a behavioural decision to reduce reliance on demanding activity under hypoxic conditions. Hypoxia also influences the ability of defenders to hinder the performance of attackers because attackers fighting hypoxic defenders can target their raps more accurately on specific regions of the defender's shell, compared with attackers rapping on the shells of defenders that had not been exposed to hypoxia (Lane et al. 2022). Ultimately, however, the ability of defenders to resist eviction appears unaffected by hypoxia, which likely reflects the disparity in energetic demands of the two distinct roles in a shell fight (Briffa & Elwood, 2000b). Taken together, these studies on hypoxia show how pollution can lead to behavioural changes in the absence of obvious info-disruption. Rather, the most likely causes of behavioural change are a combination of direct energetic effects and behavioural plasticity used to mitigate these constraints on performance capacities. Furthermore, it is notable that during shell fights the effects of hypoxia differed between attackers and defenders. This shows that while the impacts of pollutants may differ among individuals, they may also differ between roles adopted in intraspecific interactions and across behaviours, even when those behaviours are closely linked, such as attacking and defending in a fight.

2.5 Heavy metals

Heavy metals such as cadmium, copper, chromium, lead, and zinc reach the sea through routes including drainage from mining, run-off from roads and antifouling paint on vessels (Dos Santos et al., 2022). Even in areas where release rates are controlled, metals have high persistence in sediments and can be released into the water column on disturbance. Heavy metals are thus common pollutants of coastal waters and are readily taken up by crustaceans,

including hermit crabs, to the extent that they could be used as indicator species of these pollutants (Dos Santos et al., 2022). Absorbed metals are known to cause a variety of effects at the cellular level, which collectively increase metabolic load (Dos Santos et al., 2022). This presents a potential constraint on the energy available for allocation to other functions including the performance of demanding activities such as shell fighting. Similar to the experiment on fighting and hypoxia (Figure 3a). White et al. (2013) used an experiment where potential attackers and defenders of *P. bernhardus* were pre-treated with copper prior to staged fights. While copper exposure had minimal impact on the behaviour of defenders, the ability of attackers to evict a defender was clearly impaired by exposure to copper, primarily because they were less likely to initiate a fight than those that had not been treated with copper. For those copper exposed attackers that did initiate fights, the patterns of agonistic behaviour were altered. Surprisingly, the usual pattern (e.g. Briffa et al. 1998) of lower vigour in attackers that failed to evict the defender (compared to fights that ended in an eviction) was reversed. Similarly, when attackers had been exposed to copper, the probability of an eviction declined with increasing disparity in body mass between attackers and defenders, which usually increases the probability of victory. While these results seem counterintuitive, a possible explanation is that copper exposed attackers attempted to compensate for poorer performance in other (unmeasured in this experiment) parameters of shell rapping that influence outcomes, such as power of impact or targeting accuracy, by increasing the number of raps per bout. Despite these unexpected results it is clear that copper exposure differentially affects the ability of hermit crabs to succeed in each of the two distinct roles they can adopt in a fight, and reverses some of the usual correlates of successful agonistic performance. These effects of copper contrast with the effect of microplastics on fighting, where exposure impaired agonistic behaviour of both roles adopted during fights (Cunningham et al. 2021, see section 2.6). These different results suggest different modes of action, with coper possibly exerting toxicity effects

while microplastics might alter olfactory pathways, which also play a role in shell fights (Briffa & Williams 2006).

Another path to behavioural change of increased metabolic load is changes in foraging behaviour and its associated strategies for managing risk. A second study (White & Briffa, 2017) on *P. bernhardus* focussed on the effect of copper exposure on repeatable startle response duration. Here, the effects of repeated observation and time since collection were accounted for by allocating crabs across two treatment groups in a two-phase experiment (Figure 3c). In the first group, five startle responses were collected from each crab while exposed to plain seawater in both phases of the experiment. In the second group, crabs were exposed to plain seawater in the first phase, but copper was added to the seawater in the second phase and again five startle responses were recorded per crab in each phase. Startle responses were, on average, of greater duration in crabs that were exposed to copper in phase two of the experiment, indicating greater risk aversion due to copper exposure. Within these mean level effects, individuals still differed in their trajectories of change in startle response across the ten observations. Some of these differences among individuals can be explained by the effect of copper exposure, as non-exposed crabs were more likely to habituate during this phase, whereas copper exposed crabs were more likely to sensitise. Finally, although there was a weak trend for increased V_{WI} (i.e. less predictable startle response durations) in copper exposed individuals, there was no overall effect on repeatability. Overall, copper exposure made the crabs more risk-averse, which is a surprising result if copper is expected to increase metabolic load as we might expect crabs in this treatment to increase their food intake and hence return to foraging sooner, after being startled by a threatening stimulus. On the other hand, the increased caution may reflect reduced ability to escape from potential predators, a possibility that could also explain the trend for reduced predictability in startle response durations. Clearly acute copper exposure can impact the behaviour of *P. bernhardus* on several levels. Although

we know that hermit crabs take up other heavy metals in addition to copper (e.g. *Pagurus samuelis*, Dos Santos et al. 2022), nothing is yet known about their behavioural impacts, which could be investigated using experimental designs based on those described above for copper.

2.6 Plastic, microplastics and leachates

Plastic has proven a durable, versatile, and useful material, with its production increasing exponentially since the 1950's, and currently exceeding 360 million tonnes per year. Unfortunately, a considerable proportion of plastic, estimated at 4.8 to 12.7 million tonnes, enters the ocean annually (Jambeck et al. 2015). Plastic debris and litter can cause issues with entanglement and ingestion, including hermit crabs becoming attracted to and trapped in plastic bottles (Lavers et al. 2020). However, a particular issue is with plastic particles < 5mm in length or diameter, termed microplastics. These can be primary microplastics, formed as industry made particles, or secondary microplastics, originating from the degradation of larger plastic debris. Microplastics are now ubiquitous in the marine environment and a major source of ocean pollution and threat to marine biodiversity (Auta et al. 2017). In addition, microplastics tend to accumulate in coastal areas, putting littoral organisms such as intertidal hermit crabs at increased risk of exposure. Exposure to microplastics, including ingestion, is known to have a range of physiological effects on crustaceans, including oxidative stress and immune responses (D'Costa 2022). These potentially could affect the capacities to perform energetically demanding behaviours such as fighting, which have been investigated among the studies discussed below. In addition, we will describe experiments that have been conducted to determine whether behaviour could be impacted through effects on cognition, such that microplastics act as info-disruptors.

Several studies have used the hermit crab, *P. bernhardus*, to examine the effects of microplastic exposure on animal behaviour. For example, Crump et al. (2020) exposed female hermit crabs to microplastic particles of polyethylene for five days, at a dose reflective of that found in the wild. Following this exposure period, individuals were transferred to a suboptimal shell that was 50% of their preferred shell weight. After inhabiting this shell for two hours, they were subsequently offered an optimal weight of alternative shell. Compared to unexposed controls, those from the microplastic treatment showed impaired shell selection behaviour. They were less likely to contact or enter the optimal shell, while also taking longer to do so for those that did. Building on this study, Crump et al. (2023) modified the shell selection aspect so that following the microplastic exposure period individuals in suboptimal shells were presented with two vials containing either a better or worse shell compared to that currently inhabited. This setup involves a comparative cognitive assessment and controls for an effect on general activity which could explain results from the earlier study. Those exposed to microplastic were less likely than controls to first contact the vial containing the better-quality shell, while also being slower to make contact, and spending less time investigating this vial. Indeed, they were more likely to make contact with the vial containing the worse shell. These findings indicate an effect of microplastics on hermit crab cognition, impairing information gathering and decision making. Furthermore, McDaid et al. (2023) used the same five-day exposure paradigm to investigate effects on shell selection motivation using both sexes. This was achieved by using single startle response durations (per crab) as a motivational probe (Elwood et al. 1998), with the time taken to resume the previous activity offering a measure of motivation. When individuals in suboptimal shells contacted the high-quality shell, they were startled using visual and auditory stimuli. This approach revealed sex differences in behaviour, with females having longer startle response durations than males, while there was no effect of microplastic exposure. However, there was an interaction effect between microplastic exposure

and sex on the time spent investigating the high quality offered shell. In the control group females spent more time on shell investigation than males but this difference was absent in the microplastic exposed individuals, with females having a similar duration of shell investigation to males. These results are consistent with a sex dependent effect of microplastic exposure on shell selection behaviour.

In addition to shell selection behaviour, the above approach has also been used to examine the effects of microplastic exposure on the shell fights of hermit crabs. Using the orthogonal design where attackers and defenders are pre-exposed prior to fighting (Figure 3a), Cunningham et al. (2021) investigated how microplastics (presence or absence) and contestant role (attacker or defender) influenced shell fighting behaviour in *P. bernhardus*. This revealed a significant interaction between microplastic exposure and contestant role on the number of raps within a bout of shell rapping. Attackers from control conditions used more raps per bout to evict microplastic exposed defenders. This indicated an impaired assessment ability of these defenders, whereby they defended their shell for longer than needed, despite facing a superior (see Briffa et al. 1998, Briffa & Elwood 2004) opponent. Furthermore, there was also an interaction between microplastic exposure and contestant role for the duration of rapping bouts. This was driven by microplastic exposed attackers engaging in longer durations of rapping bouts when facing defenders from the control group. The increased rapping duration of these attackers was not accompanied by more raps, indicating a slower and impaired rapping ability resulting from microplastic exposure. This study thus revealed that congruent with the effects of hypoxia on fighting (Briffa & Elwood 2000b), but in contrast to the effect of copper exposure (White & Briffa, 2017), both contestant roles were influenced by microplastic exposure. Given the importance of shell contests in the life history of hermit crabs, these findings suggest microplastic exposure could have important fitness consequences.

The above studies comprised relatively large sizes of microplastics to avoid ingestion as a route of action, but recent evidence shows that this route may be important. Plastics usually contain a range of additives that allow their properties to be tailored to specific applications. These additives can leach out of plastics in seawater and one additive, oleamide, a so-called slipping agent, has been shown to induce hyperactivity and to over-stimulate feeding behaviour in *P. bernhardus*, and thus encourage the ingestion of microplastic particles (Greenshields et al. 2021). This effect could be explained by the structural similarities between oleamide and oleic acid, a compound associated with animal death and part of prey odour (Dernekbasi et al. 2015) for scavengers. Field evidence also shows that ingestion could be an important route of action, with gut content analysis of field sampled *Pagurus pubescens* showing that 26% of individuals had ingested microplastics (see Gebruk et al. 2021). Nanninga et al. (2020) investigated the effects of laboratory exposure to polyethylene spheres of 10–29 μm, where ingestion could also be a possibility. The aim of this study was to assess the effects of microplastics on individual differences in behaviour and thus the effects of exposure on repeated startle response durations were assessed using a similar experimental design to that of White et al.'s (2013) study on the effects of copper exposure on boldness. Crabs were exposed individually to one of three concentrations of microplastic spheres, (1) control (0 mg l−1), (2) low (0.1 mg l−1, ∼2 ×10^4 parts l^{-1}), and (3) high (1 mg l−1, ∼2 ×10^5 parts l^{-1}), and under these conditions a sequence of five startle responses was obtained for each individual. On average, startle response duration declined with microplastic concentration, meaning that crabs behaved more boldly (i.e. they were more risk-prone) when exposed to this pollutant. Additionally, within-individual variance (V_{WI}) over the five startle responses was lower at the highest concentration compared with the low concentration and control treatments. Thus, microplastic exposure had the effect not only of making crabs more risk-prone on average, but of making their behaviour more predictable. Further studies of hermit crabs and their predators are thus

clearly warranted to establish whether these behavioural changes would translate into elevated predation rates.

These studies serve as a starting point to understand the implications of microplastic exposure for animal behaviour. However, further research is needed to establish which proximate mechanisms are affected and how alterations of these drive the behavioural changes observed. Research from a range of other species indicates that microplastic exposure can have wide ranging toxicology effects, influencing a range of physiological mechanisms (D'Costa 2022, Jewett et al. 2022) but these mechanisms remain to be investigated in hermit crabs.

2.7 Organic pollutants

Organic pollutants include chemicals such as pesticides, antimicrobials and other pharmaceuticals that alter biological processes in exposed organisms. Pharmaceutical pollution is a significant problem in aquatic and coastal environments, with an estimated 4000 pharmaceutically active substances being administered to humans alone (Argaluza et al. 2021). The life cycle of a drug once administered to an organism follows a sequence of liberation, absorption, distribution, metabolism and finally excretion (LADME) of the drug's metabolic products, or indeed excretion of a significant proportion of the dosage itself in unaltered form (Argaluza et al. 2021). These excreted products are ultimately transported to aquatic environments. This vast array of organic pollutants are known to impact many organisms, but to date only a single study has been conducted on the effects of a pharmaceutical on the behaviour of hermit crabs. Sumra and Stahlman (2019) utilised the startle response of the terrestrial hermit crab *Coenobita clypeatus* to determine the effect of methysergide on a simple form of learning, habituation, i.e. the sequential reduction in behavioural response to a potentially threatening stimulus that is revealed to be non-dangerous over repeated exposures,

and seen in many animal taxa. Thie primary aim was to gain insights into the role of the neurotransmitter serotonin (5-HT) in habituation as methysergide is a 5-HT antagonist. Nevertheless, this substance is also used pharmaceutically as a treatment for migraine and is thus a potential pollutant via the route described above. Sumra and Stahlman (2019) found that *C. clypeatus* habituated (i.e. stopped showing the typical startle response), on average, after seven exposures to a simulated predator vocalisation when it was played loudly and after five exposures when it was played quietly. In the presence of methysergide, however, the difference in habituation rate was no longer present, with crabs taking just three exposures to habituate regardless of sound intensity. This increased rate of habituation could have consequences for the trapabililily of exposed hermit crabs, potentially increasing their vulnerability to predators. Furthermore, Sumra and Stahlman's experiment serves as a case study highlighting the suitability of hermit crabs as models to investigate the behavioural impacts of organic pollutants.

2.8 Light

Natural patterns of seasonal, monthly, and diurnal of light and darkness play a central role in the regulation of many biological processes including the timing of specific behaviours and fluctuations in general activity patterns. For example, in the terrestrial hermit crab *Coenobita rugosus*, spawning is coordinated by the lunar cycle (Osaka & Takemura, 2019). The phenomenon of anthropogenic light at night (ALAN) has therefore become the focus of much recent attention due to its disruptive effects on light-sensitive behaviour such as this. Although the problem of ALAN may seem to be particularly relevant to terrestrial environments it is also known to impact marine systems, particularly coastal habitats in proximity to urban development or other infrastructure (Marangoni et al., 2022). Using a cross-over experiment

with repeated measures (see Figure 3b) Velasque et al. (2023) demonstrated that *P. bernhardus* exposed to constant light over 24h for a period of 20 days showed, on average, reduced daytime boldness (i.e. longer startle response durations on disturbance), compared to those maintained on a standard 12:12h light/dark regime. Surprisingly though, there was no difference in night-time boldness between the two light regimes. Startle response duration was significantly repeatable for both treatments during day-time (0700-1900) and night-time (1900-0700) observations, and there were no differences in repeatability between light regime treatments or between day-time and night-time. The change in behaviour was associated with physiological responses to changing light regimes, with elevated metabolic rate in crabs held under constant light (Velasque et al., 2023). In general, boldness is expected to increase with metabolic rate as the trade-off between hiding and foraging would shift in favour of foraging due to elevated energy demands (Careau & Garland, 2012; Mathot & Frankenhuis, 2018; Réale et al., 2010; but also see Royauté et al., 2018). Crabs in this study showed the opposite pattern, so the shift in behaviour cannot be explained by changes in performance capacity in this case. One explanation is that crabs under constant light perceived a greater predation risk and thus were less bold during the following daylight period. However, startle responses are known to become less predictable under predation risk (Briffa, 2013a) but when exposed to constant light, the usual pattern of diurnal variation in predictability, with less predictable behaviour at night, was absent (Velasque et al., 2023). Given that constant light on the one hand decreases boldness, which should reduce predation risk, and on the other hand reduces the predictability of startle responses, which should expose the crabs to greater risk, it is difficult to find an explanation for these behavioural changes that is based on adaptive behavioural plasticity. An alternative explanation is that constant light disrupts the normal adaptive behaviour of hermit crabs, with the potential for impaired fitness. Indeed, coupling analysis of metabolic rate with analysis of behavioural effects revealed a potential multiplicative effect of night-time light on fitness in

hermit crabs: Longer startle responses imply less time available for food acquisition, while elevated metabolic rate in constantly illuminated crabs will lead to increased energy demand.

2.9 Noise

Noise pollution is similar to light pollution as both are examples of pollution through energy release and, therefore, will have zero persistence in the environment once the releasing activity (e.g. an electric light or a running engine) ceases. Crustaceans can detect noise via sensitive mechanoreceptive hairs that are distributed over the body. Noise consists of two components, a pressure wave and particle motion, and the latter interacts with these mechanoreceptors through two routes, substrate borne vibrations (Roberts et al., 2016) and particle motion in the water column in marine species (Tidau & Briffa, 2016). Roberts et al. (2016) used behavioural measures to test the sensitivity of *P. bernhardus* to simulated substrate borne vibrations within the frequency and amplitude ranges of maritime engineering activities. At the onset of exposure to low intensities of vibration hermit crabs quickly exhibited increased movement of the antennae, antennules and mouthparts, behaviours typically involved in information gathering. Additionally, in some crabs these behaviours were accompanied by changes in ongoing locomotor activity – either the cessation of locomotion in crabs that were already walking or a burst of walking in crabs that had been stationary. Using these behavioural indicators, Roberts et al., (2016) determined that the sensitivity threshold of *P. bernhardus* to substrate-borne vibration was within the ranges of disturbance produced by a wide variety of anthropogenic activities, including pile driving and boring, while drilling and dredging would likely be below the detection threshold. Interestingly, the crabs became less sensitive to noise with time held in the laboratory prior to the beginning of trials. This suggests that crabs may become sensitised to anthropogenic noise when they are exposed to it in their natural environment. Taken together

these results show that *P. bernhardus* not only detect noise of this type, but also actively attend to it potentially distracting their attention from other salient information.

As well as underwater noise, airborne noise pollution impacts the behaviour of the semi-terrestrial Caribbean hermit crab *Coenobita clypeatus*. In the presence of playbacks of motorboat noise, a model predator could be moved closer to the hermit crabs before they responded by withdrawing into their shells, compared to the longer approach distances in the absence of noise (Chan et al., 2010a). Rather than masking the visual predator cue, it appeared that playback of motorboat noise distracted attention from the approaching threat. This effect was enhanced when the noise treatment was supplemented by additional flashing lights (Chan et al., 2010a), and when the duration and amplitude of the anthropogenic noise was increased (Chan et al., 2010b). Such attentional effects, which increase hiding latency (i.e. the time taken before the crabs retracted into their shells), clearly have the potential to reduce survival as they interfere with risk-coping strategies. Another way in which noise can elevate predation risk for hermit crabs is by disrupting their usual pattern of resource assessment. Walsh et al. (2017) found that in the presence of white noise, *P. bernhardus* would investigate empty shells more superficially, choosing and entering shells more quickly than usual. Given that assessment time was reduced this might represent a 'fear' response to noise rather than distraction, as we would expect distracted individuals to take longer to complete the shell assessment task. A subsequent experiment on *P. bernhardus* shows that the extent to which noise disrupts shell-assessment depends on both the difficulty of the task and the immediate level of risk. Tidau and Briffa (2019a) demonstrated that when the decision to swap from an original shell in to a new one is easy, due to a large disparity in shell quality, decisions are made more quickly in the presence of noise compared to its absence. However, this effect of noise only occurred when a visual predator cue (a model of the shore crab *Carcinus maenas*) was also present. In contrast, when the disparity in quality between the two shells is relatively low then the decision should be

harder to make. Under these conditions the effect of noise on shell investigation speed was absent in the presence of a predator, but when the predator cue was present crabs spent more time on shell assessment when exposed to ship noise. The effects of noise on shell selection behaviour can be dependent on other conditions, indicating that a range of sensory mechanisms could be impacted. Solé et al (2023) investigated the effects of noise exposure on the statocyst of the Medeteranian red hermit crab *Dardanus calidus*. This organ is involved in balance and the perception of vibration, and so might be implicated in the sensory disruption underlying behavioural changes in response to noise. Exposure to artificial noise at 157 dB for 2h was enough to damage the statocyst organs, which showed lesions following exposure. While this noise exposure had no effect on mean startle response duration, Solé et al. (2023) detected an increase in among-individual variance in startle response durations, even though their observations were censored to a maximum observation time of 120s. This result highlights the possibility that individuals are likely to respond differently to the same pollutant, reinforcing the utility of an animal personality framework in future studies.

Thus far, we have considered how noise can impact individual behaviours in hermit crabs but we have also seen how pollutants can alter social behaviour such as fighting, which is impaired by hypoxia and heavy metals. Another form of social behaviour in *P. bernhardus* is their tendency to aggregate, potentially driven by access to shells either through aggression, as discussed above, or through vacancy chains (Briffa, 2013b; Briffa & Austin, 2009; Lewis & Rotjan, 2009; Osorno, 1998; Rotjan et al., 2010; Weissburg et al., 1991). Additional factors that might contribute to this tendency to aggregate, are the presence of other resources such as food, and the dilution effect, which reduces the vulnerability of individuals to predators. In *P. bernhardus* crabs in optimal shells were more likely to join groups than remain solitary, while individuals in suboptimal shells avoided conspecific groups (Tidau & Briffa, 2019b). This indicates that the possibility of acquiring a new shell does not drive grouping in this species

and for crabs in shells that are too small, the costs of joining a group, such as elevated risks of cannibalism, may outbalance the benefits. This pattern was reversed, however, in the presence of ship noise playbacks, with crabs in suboptimal shells now being the more likely to join a group. The mechanism of this change in social behaviour is unknown but potential explanations are that the distracting effect of the noise interfered with optimal decision making, or that they perceived the noise itself as a threat, which outbalanced the risks of joining a group (Tidau & Briffa, 2019b). Taken together these studies on noise pollution show that pollutants can impact both individual and social behaviour across sensory channels, with the presence of noise, altering responses to tactile, visual and chemical cues. The most likely explanation in each case is that the pollutant distracted the attention of the crabs from other, more salient, cues.

3. Conclusions and future directions

"the careful study of one of the commonest and most insignificant of animals, leads us, step by step, from everyday knowledge to the widest generalisations of the most difficult problems in zoology; and indeed, of biological science in general"

- T. H. Huxley, 1888

In the preface to his classic work on the biology crayfish, Huxley made an early argument for intensive study of a model system, from as many perspectives as possible. Here, we have shown how another decapod taxon, the hermit crabs, has the potential to provide a model for understanding the behavioural consequences of marine pollution, in large part due to their heavily studied behavioural associations with empty gastropod shells, although other behaviours have been studied in relation to pollution as well. Further, due to the long history of detailed behavioural studies on hermit crabs, and the evidence for impacts from pollutants already available, we could develop their use as sentinel species for human induced behavioural

change. From efforts so far, it is possible to draw the following conclusions from studies on the effects of pollutants on hermit crab behaviour:

(1) Acute exposure to pollution alters behaviour across a range of contexts, including resource acquisition, aggression, movement, and risk-coping.

(2) Effects have been demonstrated from a wide array of pollutants including the effects of climate change, chemical pollutants, plastics and sound and light energy.

(3) In most cases pollutants have a suppressive effect on behaviour, by reducing responsiveness to cues.

(4) In some cases, pollutants have an excitatory effect, by increasing responsiveness to specific cues.

(5) Pollutants can have cross-modal effects in terms of the information channels involved in a given behaviour. For example, noise can reduce responses to visual and chemical shell cues.

(6) Pollutants affect behaviour at different levels of variation – effects seen at the sample mean level can also encompass changes at the levels of among- and within-individual variation.

(7) Although only a few studies have investigated the mechanisms underlying behavioural change a variety of mechanisms, both physiological (e.g. elevated metabolic rate) and cognitive (e.g. distraction) have been identified.

(8) There is evidence for info-disruption, which may occur both as a result of effects at the organismal level and due to the direct effects of a pollutant in altering the cue itself (e.g. protonation of PEA).

(9) All these changes, regardless of direction, disrupt normal behavioural patterns in ways that seem likely to have negative effects on hermit crab survival, and ultimately fitness. Impacted individuals may be less responsive to relevant cues about resources (e.g. empty gastropod shells), and more responsive to novel cues leading to elevated interactions with inappropriate or potentially harmful items such as microplastics.

3.1 Generalizing insights from hermit crab studies

Model organisms are widely used in biology. They can be thought of as organisms where the traits of interest (behaviour in this case) are well understood and are highly amenable for probing broadly relevant questions that extend beyond the study system itself. In the opening section of this review, we discussed the behaviour of hermit crabs, showing how they are especially well-suited to addressing questions about how (a) cognition and (b) performance capacities underpin animal behaviour. We then demonstrated how they have therefore provided a system that can produce highly resolved insights about behavioural change due to pollutant exposure via info-disruption and direct physiological effects. Although hermit crabs are particularly amenable to such studies, the behavioural contexts investigated are common across all animals that might be exposed to pollutants. For example, contest behaviour is ubiquitous across animal taxa (Hardy & Briffa 2013), and all animals must assess resources, assess the potential exposure to risk when gathering resources and make decisions accordingly (e.g. Danchin et al. 2008). Indeed, risk-coping is increasingly studied within an animal personality framework, which we have emphasised here, and animal personality is present in diverse taxa (e.g. Bell et al. 2009, Kralj-Fišer & Schuett 2014). Bivalves such as clams and mussels, for example, have been used as models for studying the biological effects of pollutants (e.g. Beyer et al. 2017) and, like hermit crabs, exhibit personality variation in boldness that is sensitive to

elevated temperature (Clements et al. 2021). Thus, insights about behavioural impacts of pollutants revealed through studies on tractable models such as hermit crabs are also likely to be relevant to other animals, most obviously other crustaceans that share conserved elements of the nervous system, but also to animals in disparate taxa that must perform equivalent behavioural tasks based on an overlapping set of environmental cues.

Another way in which insights from a model such as hermit crabs can be broadly relevant is to consider how the behavioural effects that have been demonstrated might cascade to drive wider ecological impacts (Rahman & Candolin, 2022). As noted above, most pollutants studied thus far act to suppress behaviours associated with survival, i.e. responses to food cues and cues for adequate shelter (shells). Since marine hermit crabs are largely detritivores, reduced feeding could impact nutrient cycling in coastal sediments. Similarly, we may hypothesise that impaired shell selection would increase predation risk and thus affect populations of the predators of hermit crabs, such as brachyuran crabs, fishes, and avian predators. Finally, since pollutants such as heavy metals accumulate in the tissues of crustaceans and then, via predators that consume crustaceans, through the higher trophic levels of marine food webs (Dos Santos et al. 2022) increased susceptibility to predation might lead to elevated rates of bioaccumulation through increased consumption. As noted above, the behaviour of other animals will also likely be impacted by pollutants and therefore cascade effects will not be restricted to those initiated by behavioural change in hermit crabs. We suggest that due to the advantages offered by using hermit crabs as a model system they would also be ideal components of mesocosm experiments that could be used to test hypotheses about the cascading effects of behavioural impairment such as those reviewed here.

3.2 Future directions

The studies to date, have been carried out independently by different groups of researchers. As a result, while many of the approaches have been well-aligned in terms of experimental design (Figure 3) and have collectively shown how pollutants disrupt behaviour across multiple contexts, studies to date have not been conducted in a coordinated way. Indeed, while most of the studies were conceived specifically to test for effects of pollution, some of them were originally conceived with other questions in mind, for example using hypoxia to understand the energetic constraints on fighting (Briffa & Elwood 2000b). The net result is an emerging picture of how anthropogenic pollutants impact the behaviour of hermit crabs but one that is incomplete in two senses. First, knowledge gaps remain in the matrix of pollutants and behaviour studied (Table 1). While it would be unrealistic to expect that every potential pollutant (e.g. each of the many organic pollutants that are likely present), or level of pollution (e.g. different levels of noise pollution), released into marine and coastal environments could be tested for behavioural effects, we suggest that at least one example of each pollutant-type (represented by the rows in Table 1) could be assessed for each class of behaviour (represented by columns in Table 1, see below for further discussion). Perhaps surprisingly, noise is the most studied pollutant and light is among the least studied. Undoubtably, there will also be both pollutants (e.g., more pharmaceuticals, additional heavy metals) and relevant behaviours that have yet to be studied in hermit crabs, such that additional rows and columns need to be added into our matrix. In the case of behaviours that could be impacted, reproduction is of obvious importance, and we already know that development reproductive physiology in crustaceans can be impacted by a variety of pollutants (e.g. see Rodruíguez et al. 2007 for a review). However, little is known about the effects of pollutants on reproductive behaviour (e.g. courtship, mate guarding) and investigating this in hermit crabs represents an obvious priority. Second, details of methodologies lack standardisation. For example, we know about

the effects of relatively large microplastic particles on resource assessment and fighting, but for personality we know only about the effects of very small particles, and the two sizes are likely to have different modes of action. In the case of ocean acidification, sophisticated chemical ecology has revealed a potential mechanism of info-disruption, but different suites of behavioural measures have been used compared with work on other pollutants. Thus, even where cells in the matrix (Table 1) have been filled, the current picture lacks balance. A focus for future work should therefore be a coordinated effort to fill key knowledge gaps and attain a well-balanced body of knowledge by standardisation of approaches. Reviewing Table 1, it also apparent that the most studied species is *P. bernhardus*, the European hermit crab. Clearly there would be benefits to filling knowledge gaps with respect to a single species (in the first instance) and given the amount of work already conducted, *P. bernhardus* seems like the obvious candidate. Given the diversity of hermit crabs, however, we expect information will continue to emerge across different species, and eventually this could lead to a phylogenetic comparison of the behavioural impacts of pollutants within the Anomura. Thus, as well as providing an array of model species, the hermit crabs could in time prove to be a model taxon.

In overview, different pollutants can affect the same behaviour in opposite directions (summarised in the graphical abstract). Therefore, in parallel to efforts to fill gaps and standardise approaches, we also need to design experiments involving multiple stressors (e.g. Ragagnin et al. 2018) and their interactions, and to incorporate longitudinal studies that could also reveal the scope for individuals to recover from acute pollutant exposure, and even multi-generational approaches. These will allow us to understand when hermit crabs might be most vulnerable to behavioural disruption and its ultimate consequences for populations (see Southward & Southward 1988 for a potential example). Conversely such approaches would also enable us to understand the conditions where they may be resistant to behavioural changes, considering the possibility that their shells (which as we have seen can be manipulated) can

buffer against environmental extremes (Taylor 1981). We hope that the studies reviewed here highlight the utility of hermit crabs as a model system and that we have made a convincing case that such efforts would be worthwhile.

3.3 Conclusions

Even though our knowledge is still incomplete, hermit crabs already seem to be among the most intensively studied models for the effects of pollution on behaviour, certainly when we consider the granularity of behavioural data obtained. For example, for copper, temperature and microplastics the application of the animal personality framework has allowed their effects on behavioural variance to be decomposed into mean level effects, among individual variation, within individual variation and differences in behavioural reaction norm. By focussing in on these different levels of variation it will be possible to estimate the level of exposure to selection for suites of behaviour under polluted environments. Animal personality is now known to exist in a broad range of taxa, and quantifying this type of behavioural variation can tell us about its exposure to selection, hence the possibility of evolutionary responses to environmental pollutants. While aspects of the behaviours studied are unique to hermit in the sense that they derive from their associations with empty gastropod shells, they are all of broad relevance to animals in general. Resource assessment, communication, aggression, and foraging can be readily quantified in hermit crabs, but all animals must perform these activities, while using information to balance costs and benefits and to manage risk. Here we have shown how studies of hermit crabs provide model systems for determining how these behaviours can be altered by pollution.

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Table 1: Matrix of classes of pollutants and behavioural context, studied in different species of hermit crab. The blue section indicates pollutants associated with climate change, green indicates waste products and yellow indicates the release of energy. Blank cells indicate no studies to date.

(Table on next page)

Table 1:

	Resource assessment	Contests and social behaviour	Personality and risk-taking	General activity, foraging
Hypoxia	*Pagurus bernhardus* Cote et al. 1998	*Pagurus bernhardus* Briffa & Elwood 2000b Briffa & Lane 2022 Lane & Briffa 2023		*Paguristes eremita* Pretterbner et al. 2012
Temperature	*Pagurus longicarpus* Gilliand et al. 2021		*Pagurus bernhardus* Briffa et al. 2013 *Coenobita clypeatus* Sakich et al. 2023	*Pagurus cuanensis* Thatje et al 2010 *Pagurus beringanus* *Pagurus granosimanus* Torjman 2022 *Diogenes deflectomanus* Leung et al 2023
Ocean acidification	*Pagurus bernhardus* de la Haye et al. 2011		*Pagurus tanneri* Won Kim et al. 2016 *Pagurus criniticornis* Turra et al. 2020	*Pagurus bernhardus* de la Haye et al 2012 Shirrmacher et al 2021 Ragagnin et al. 2018
Eutrophication	*Pagurus longicarpus* Ball et al. 2022			
Heavy metals		*Pagurus bernhardus* White et al. 2013	*Pagurus bernhardus* White & Briffa 2017	
Plastic, microplastic and leachates	*Pagurus bernhardus* Crump et al. 2020, 2023 McDaid et al. 2023	*Pagurus bernhardus* Cunningham et al. 2021	*Pagurus bernhardus* Nanninga et al. 2020	*Coenobita perlatus* Lavers et al. 2020 *Pagurus bernhardus* Greenshields et al 2021
Pharmaceuticals			*Coenobita clypeatus* Sumra & Stahlman 2019	
Light			*Pagurus bernhardus* Velasque et al. 2023	
Noise	*Pagurus bernhardus* Tidau & Briffa 2019a Walsh et al. 2017 *Pagurus acadianus* Roberts & Laidre 2019	*Pagurus bernhardus* Tidau & Briffa 2019b	*Coenobita clypeatus* Chan et al. 2010a Chan et al. 2010b *Dardanus calidus* Solé et al. 2023	*Pagurus bernhardus* Roberts et al. 2016

Figure 1: A common European hermit crab, *Pagurus bernhardus*, re-emerging from its Littorina littorea shell after being startled in a laboratory observation. Photo credit: Mark Briffa.
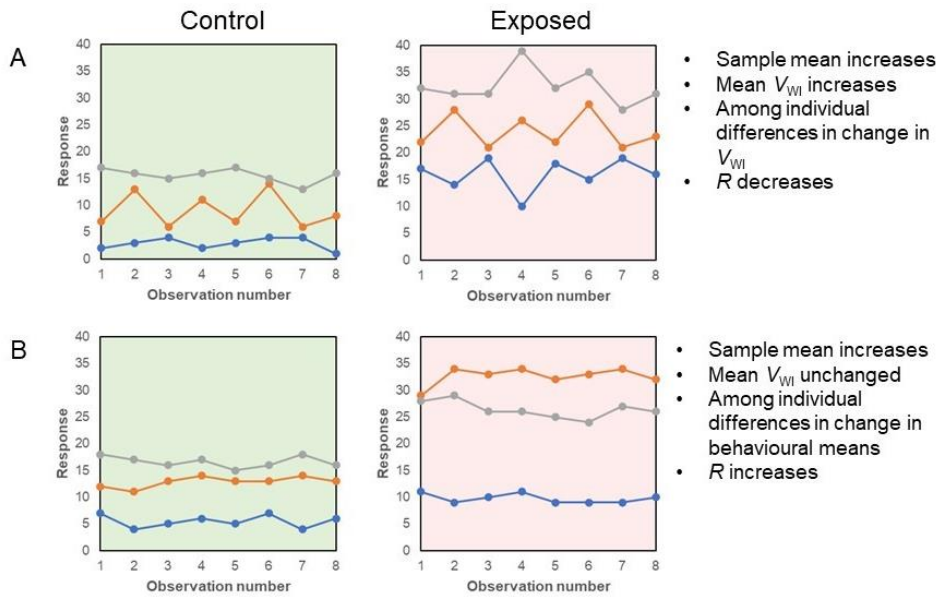
Figure 2: Overview of levels of analysis for the effects of pollution on behaviour studied within the animal personality framework, illustrated with hypothetical data from two experiments A and B. Dots joined by lines show datapoints collected repeatedly from three individuals denoted by different colours. Green plots denote control treatments and pink plots denote exposure to a pollutant. In both cases, each individual is exposed to both conditions – see Figure 3 (b and c) for examples of experimental designs needed to control for chronological effects in such experiments. In scenario A, during the control treatment the orange individual shows greater V_{WI} compared to the grey and blue individuals. When exposed to a pollutant the sample mean behavioural response is greater compared with the control. Additionally, the sample mean of V_{WI} has increased but this increase has been more marked in the grey and blue individuals compared with the orange individual. As a consequence of net elevation in V_{WI}, repeatability (R), is reduced under exposure to the pollutant. In scenario B, R is greater under control conditions compared with the data collected under control conditions during experiment A. This is due to the lower V_{WI} under control conditions in experiment B. V_{WI} does not change under exposure to the pollutant but the sample mean response has again increased. However, there is significant variation among individuals in how the pollutant affects their behaviour, such that they show different behavioural reaction norms (BRN). The orange individual has increased its response by a large amount, the grey individual by a moderate amount and the responses of the blue individual are largely unchanged. Additionally, while V_{WI} is unchanged, V_{BI} has increased, leading to an increase in R.
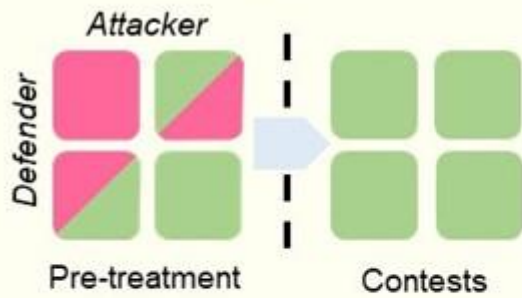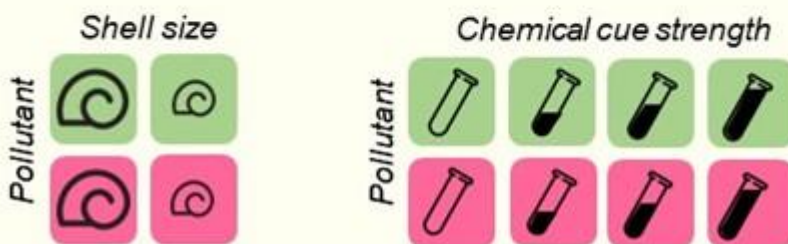
Figure 3: Some core experimental designs used to test for the effects of pollutants on the behaviour of hermit crabs. Green boxes represent control treatments where pollutants are absent and magenta boxes indicate treatments where crabs are exposed to pollutants. Where relevant, blue shading represents the chronology of the experiment. Where this is absent, data were collected simultaneously across treatment groups. Note that some details (e.g. number of repeated measures) vary across studies.