Sentience in decapod crustaceans:
A general framework and review of the evidence

Andrew Crump
Centre for Philosophy of Natural and Social Science,
London School of Economics and Political Science

Heather Browning
Centre for Philosophy of Natural and Social Science,
London School of Economics and Political Science

Alexandra Schnell
Department of Psychology, University of Cambridge

Charlotte Burn
Animal Welfare Science and Ethics, Royal Veterinary College

Jonathan Birch
Centre for Philosophy of Natural and Social Science,
London School of Economics and Political Science

Abstract: We outline a framework for evaluating scientific evidence of sentience, focusing on pain experience. It includes eight neural and cognitive-behavioural criteria, with confidence levels for each criterion reflecting the reliability and quality of the evidence. We outline the rationale for each criterion and apply our framework to a controversial sentience candidate: decapod crustaceans. We have either high or very high confidence that true crabs (infraorder Brachyura) satisfy five criteria, amounting to strong evidence of sentience. Moreover, we have high confidence that both anomuran crabs (infraorder Anomura) and astacid lobsters/crayfish (infraorder Astacidea) meet three criteria—substantial evidence of sentience. The case is, as yet, weaker for other infraorders, such as penaeid shrimps, highlighting important research gaps. Having demonstrated our framework's application to decapod crustaceans, we hope that future research will apply it to other taxa.

Andrew Crump, Research Officer, LSE, works on the Foundations of Animal Sentience project and specializes in invertebrate sentience. He previously completed a PhD in Biological Sciences at Queen's University Belfast. **Website**

Heather Browning, Research Officer, LSE, works on the Foundations of Animal Sentience project and specializes in animal welfare. She previously completed a PhD in Philosophy at the Australian National University. Alongside her academic career, Browning has worked as a zookeeper and animal welfare officer. **Website**

Alexandra Schnell, Research Fellow, Darwin College, University of Cambridge, focuses on comparing cognitive abilities, such as learning and memory, in diverse taxa including cephalopods and corvids. **Website**

Charlotte Burn, Associate Professor, RVC, specializes in the mechanisms and motivations behind animal behaviour, animal perceptual abilities, and how to make concrete improvements to animal welfare. She is also Deputy Head of the RVC's Animal Welfare Science and Ethics Group. **Website**

Jonathan Birch, Associate Professor, LSE, is the Principal Investigator on the Foundations of Animal Sentience project, a five-year Horizon 2020 project investigating animal sentience. **Website**

1. Introduction

Sentience is the capacity to feel. Understood broadly, sentience encompasses all felt experiences, including sensory experiences (e.g. visual, auditory, tactile, olfactory) as well as (for example) feelings of warmth, comfort, fatigue, hunger, thirst, boredom, excitement, distress, anxiety, pain, pleasure and joy. This capacity to feel should be distinguished from other, related capacities: a sentient being might not be able to reflect on its feelings or to understand others' feelings. Although sentience, in a broad sense of the term, includes sensory experiences as well as positively and negatively valenced feelings such as pleasure and pain (see Boissy et al., 2007), we will focus here on negative states. This is not because other aspects of sentience are unimportant, but because pain, distress and harm have special significance for animal welfare policy.

The international scientific community increasingly recognises sentience in at least some invertebrates (Birch, 2020; Feinberg & Mallatt, 2016; Low et al., 2012;

Mikhalevich & Powell, 2020). There are, however, major obstacles to determining whether and which invertebrates are sentient (Birch et al. 2022). Even in humans, we cannot directly observe private experiences and must rely on indirect indicators, such as verbal report, to identify the neural basis of experience (LeDoux 2019; Frith 2021; Seth 2022). Animal brain mechanisms homologous with those linked to sentience in humans (e.g., the known brain substrates underlying the feeling of pain) can be evidence for sentience (Panksepp, 2005). The difficulty is that invertebrate brains differ radically from those of vertebrates, seriously limiting this approach (Feinberg & Mallatt, 2016).

We cannot conclude that invertebrates are non-sentient simply because their brains are organised differently. As an analogy, crustacean eyes are very different from mammalian eyes, but crustaceans can still see. Multiple neurological routes may produce the same result ("multiple realizability"; Mallatt & Feinberg, 2021; Putnam, 1967). Even the dichotomy of homology versus analogy in evolution can be oversimplistic, with 'deep homologies' existing in parallel across evolutionarily distant species (De Waal and Ferrari, 2010). In principle, nervous systems structurally different from, but functionally similar to, vertebrate brains could achieve sentience (e.g., Sherwin, 2001; Edelman & Seth, 2009; Feinberg & Mallatt, 2016; Ginsburg & Jablonka, 2019).

To address questions of invertebrate sentience, we must rely (at least partly) on behavioural and cognitive markers, coupled with our knowledge about the animal's nervous system (e.g., Smith & Boyd, 1991; Bateson, 1991; AHAW, 2005; Varner, 2012; Sneddon et al., 2014; Broom, 2014). Hypotheses about what sentience does—its adaptive value—can guide the choice of markers (Lindahl, 1997). Sentience in humans plausibly facilitates flexible cognitive functions to maximise benefits (e.g., when associated pleasure motivates reward-acquisition behaviour) and minimise harms (e.g., when pain or anxiety motivate punishment-avoidance behaviour). By integrating information across the animal's whole nervous system to generate evaluations, sentience also plausibly facilitates flexible decision-making and new forms of associative learning (Griffin, 1998; Ginsburg & Jablonka, 2019; Birch et al., 2020a). A related idea is that sentience may provide a 'common currency' for decision-making (Cabanac, 1992), allowing an animal to combine and compare information across different modalities and times. Sentience would thereby enable the animal to prioritise its most urgent needs, leading to beneficial motivational trade-offs in novel situations (e.g., Rial et al., 2007; Solms 2021).

Despite the plausibility of a link between sentience and learning, some presumably non-sentient systems can perform relatively simple forms of associative learning and motivational trade-offs (e.g., rat spinal cords disconnected from the brain: Allen et al. 2009). Such findings call for more research into which forms of associative learning and motivational trade-offs are facilitated by sentience (Birch et al. 2020a,b). We accept that any set of behavioural, cognitive and neuroscientific patterns could conceivably be achieved without sentience (e.g., Dawkins, 2001; Karin-D'Arcy, 2005). This, along with the 'private' nature of sentience, is why we cannot resolve the question of invertebrate sentience with certainty. But demanding certainty is inappropriate. If severe welfare risks are present, then (for ethical reasons) we must act on evidence that strongly supports attributions of sentience without providing certainty (Bateson 1991; Bradshaw, 1998; Birch, 2017).

This review introduces a framework for evaluating evidence of animal sentience, focussing on pain as an aspect of sentience with particular ethical significance. We then apply our framework to a controversial candidate for sentience: decapod crustaceans. Although we concentrate on decapods, the framework is general enough to facilitate

future evaluations of sentience in other taxa. Further detail on our framework, and an additional application to cephalopod molluscs, can be found in Birch et al. (2021).

2. A Framework for Evaluating Evidence of Animal Sentience

2.1. The Smith & Boyd (1991) criteria. In 1991, a Working Party of the Institute of Medical Ethics produced seven influential criteria for pain experience (Smith & Boyd, 1991):

1. Possession of receptors sensitive to noxious stimuli, located in functionally useful positions on or in the body, and connected by nervous pathways to the lower parts of a central nervous system.
2. Possession of brain centres which are higher in the sense of having a higher level of integration of brain processing (especially a structure analogous to the human cerebral cortex).
3. Possession of nervous pathways connecting the nociceptive system to the higher brain centres.
4. Existence of receptors for opioid substances in the central nervous system, especially the brain.
5. Evidence that analgesics modify an animal's response to stimuli that would be painful for a human.
6. Functional similarity of an animal's response to the human response to stimuli that would be painful for a human (i.e., the animal responds so as to avoid or minimise damage to its body).
7. Persistence of an animal's behavioural response to a painful procedure, with the animal showing an unwillingness to resubmit and an ability to learn to associate apparently non-painful events with apparently painful events.

These criteria are a good starting point. However, two main issues necessitate modified and updated criteria.

First, the Smith & Boyd criteria (especially the neurobiological criteria) are in some respects too narrow, having been designed to assess vertebrates. For example, Criterion 4 assumes that opioids are the type of neurotransmitters that modulate aversive experiences. Many other endogenous neurotransmitters may modulate aversive experiences, however, so this assumption might not hold for invertebrates. Whilst homology with human emotional biology can offer evidence for animal sentience, analogous systems that are functionally equivalent could also produce sentience (Edelman and Seth, 2009), as noted above. Therefore, in our view, what matters is that threatened or actual noxious stimuli can cause neurotransmitters to modulate the animal's decision-making in a way consistent with experiences of pain, distress or harm. The Smith & Boyd criteria attach too much significance to opioids, rather than allowing for this potential diversity.

Second, the Smith & Boyd criteria are in some respects too easy to satisfy, especially the behavioural criteria (6 and 7). Regarding Criterion 6, a response "functionally similar to the human response" is overly vague. When we touch a hot stove, we withdraw our hand immediately, but this is just a reflex (Campbell et al., 1991). Even though we also experience pain, nociception (rather than pain) causes hand withdrawal: pain is felt *after* the hand has begun to withdraw. So, a similar reflex in an animal would not indicate pain. We need more refined criteria to pinpoint the precise

behavioural/cognitive functions that indicate negative affective states. These functions must go beyond mere reflexes to implicate centralised, integrative information processing about threatened or actual noxious stimuli.

Regarding Criterion 7, persistent responses and unwillingness to resubmit to a procedure may indicate sensitisation (increased sensitivity to a previously encountered stimulus), rather than associative learning. But sensitisation is found in animals with no central nervous system, such as cnidarians (jellyfish and sea anemones) (Ginsburg & Jablonka, 2019, pp. 279-287), which presumably cannot integrate information and produce sentience. Rigorous behavioural/cognitive criteria for sentience must instead identify abilities requiring centralised, integrative processing. Criteria satisfied by animals that are unlikely to be sentient (because they have no central nervous system) are not well-motivated.

2.2. Our criteria. Our framework consists of eight proposed criteria for sentience, focusing on pain experience:

1. **Nociception**. The animal possesses receptors sensitive to noxious (i.e., harmful, damaging) stimuli (nociceptors).
2. **Sensory integration**. The animal possesses brain regions capable of integrating information from **different sensory sources.**
3. **Integrated nociception.** The animal possesses neural pathways connecting the nociceptors to the integrative brain regions.
4. **Analgesia.** The animal's behavioural response to a noxious stimulus is modulated by chemical compounds affecting the nervous system in either or both of the following ways:
   a) The animal possesses an endogenous neurotransmitter system that modulates (in a way consistent with the experience of pain, distress or harm) its responses to threatened or actual noxious stimuli.
   b) Putative local anaesthetics, analgesics (such as opioids), anxiolytics or anti-depressants modify an animal's responses to threatened or actual noxious stimuli in a way consistent with the hypothesis that these compounds attenuate the experience of pain, distress or harm.
5. **Motivational trade-offs.** The animal shows motivational trade-offs, in which the negative value of a noxious or threatening stimulus is weighed (traded-off) against the positive value of an opportunity for reward, leading to flexible decision-making. Enough flexibility must be shown to indicate centralized, integrative processing of information involving an common measure of value.
6. **Flexible self-protection.** The animal shows flexible self-protective behaviour (e.g., wound-tending, guarding, grooming, rubbing) of a type likely to involve representing the bodily location of a noxious stimulus.
7. **Associative Learning.** The animal shows associative learning in which noxious stimuli become associated with neutral stimuli, or in which novel ways of avoiding noxious stimuli are learned through reinforcement. Note: habituation and sensitisation are not sufficient to meet this criterion.
8. **Analgesia preference.** Animals can show that they value a putative analgesic or anaesthetic when injured in one or more of the following ways:
   a) The animal learns to self-administer putative analgesics or anaesthetics when injured.

b) The animal learns to prefer, when injured, a location at which analgesics or anaesthetics can be accessed.

c) The animal prioritises obtaining these compounds over other needs (such as food) when injured.

Our criteria revise and update Smith & Boyd's (1991) criteria, addressing the problems we have identified. Although behavioural and cognitive criteria (criteria 5-8) are especially important for invertebrates, we have still included neurobiological criteria (criteria 1-4) to balance neurobiological and cognitive/behavioural evidence (Crump & Birch 2022; Edelman et al., 2005; Edelman & Seth, 2009; Paul et al., 2020). Our criteria also build on Sneddon et al.'s (2014) criteria for animal pain, which include fewer neurobiological than behavioural criteria, and, we think, contain some redundancies (discussed below) that we have combined into fewer criteria.

By themselves, none of our criteria provide conclusive evidence of sentience. None is a "smoking gun". This is especially true for Criterion 1, which a non-sentient animal could easily satisfy. However, as part of the mechanism for detecting noxious stimuli (which also underlies the feeling of pain in humans), the presence of nociceptors slightly raises the probability of a capacity for pain—just as the presence of eyes raises the probability of a capacity for conscious vision. Criterion 1 cannot directly distinguish between nociception and pain, but Criteria 2 and 3 address this task. Every criterion is relevant to the strength of the overall case for sentience.

Criteria 1-3 are based on Smith & Boyd's (1991) criteria, but we replace "higher" and "lower" brain regions with an emphasis on integrative brain regions. There is widespread agreement in consciousness science that, in humans and other mammals, sentience depends on brain regions that integrate information from many sources (Frith 2021; Seth 2022). This agreement exists despite significant disagreement about which specific brain regions are important (Crump and Birch 2022). Hence sentience is more likely in species with integrative brain regions. Moreover, as explained earlier, a plausible adaptive function of sentience is to integrate different information sources, and thus enable animals to coordinate appropriate behavioural responses.

Smith & Boyd's (1991) criteria 4 and 5 are closely related, since analgesics normally work by substituting for endogenous neurotransmitters, exploiting the same mechanisms. We have replaced them with one criterion (our Criterion 4) that can be satisfied in two ways. Instead of focusing on opioids, our Criterion 4 counts various forms of responsiveness to endogenous compounds or drugs as evidence of sentience. These compounds must modulate the animal's behaviour in ways that would be expected on the hypothesis that they alter experiences of pain, distress or harm.

Some simpler responses to endogenous compounds or drugs, especially those that act peripherally, may not distinguish between nociception and pain, because they could merely dampen the responsiveness of nociceptors. Even these could contribute evidence for homology with human pain mechanisms, if the same analgesics work for both humans and other animals. More complex responses, or responses to compounds that act via the integrative brain regions, can provide more compelling evidence for pain beyond nociception. Responses must be specific to suggest that the animal's perception of the potentially noxious stimulus has been altered, rather than being a more general alteration of behaviour, such as reduced activity levels.

We have replaced Smith & Boyd's (1991) behavioural criteria (criteria 6 and 7) with much more detailed and rigorous cognitive and behavioural criteria (our criteria 5-8) that align with all plausible views about the adaptive value of sentience, without

committing to any specific view. These identify four main types of behavioural and cognitive abilities likely to require negatively valenced affective states: motivational trade-offs, flexible self-protective behaviour, associative learning, and behaviour suggesting value is being accorded to analgesics or anaesthetics when injured (as shown by self-administration, conditioned place preference or prioritisation).

Whilst our behavioural criteria are more concrete than Smith & Boyd's (1991), they are less extensive than those listed by Sneddon et al. (2014). This avoids treating very similar behaviours as independent lines of evidence. For example, Sneddon et al. separately list "Self-administration of analgesia" and "Pay cost to access analgesia". Our Criterion 8 regards these as different ways to satisfy the same criterion. Our criteria also distinguish more explicitly between nociceptive and pain-related behaviours. For example, a nociceptive reflex could easily achieve Sneddon et al.'s "Movement away from noxious stimuli" (Campbell et al., 1991).

Our behavioural criteria deliberately leave room for interpreting empirical evidence on a case-by-case basis. Rather than attempting to address all possible ambiguities in this section, as we go through the application of the framework to decapods, we will explain how each criterion is tested against the evidence. We will, however, clarify two important points.

First, "flexibility" does not imply a capacity for planning ahead or reflection—only that the animal can respond to the same noxious stimulus in different ways, depending on its situation. The animal may show sensitivity to the efficacy of each response, trying something else if a set of responses is ineffective. There may also be individual differences within the species in the types or sequences of responses produced. Flexibility in this sense can be contrasted with fixed, reflexive behaviour that is species- and context-specific.

A difficulty here is that even animals without a central nervous system, such as sea anemones, show some flexibility: they have reflexes that another stimulus, such as a conspecific, can inhibit (Haag and Dyson, 2014). Criteria 5 and 6 accordingly emphasize specific types of flexibility likely to implicate centralized, integrative information processing. Criterion 5 highlights the devaluing of threat and the valuing of reward in a common currency. We are looking here for a level of sophistication that cannot be explained parsimoniously as another stimulus directly inhibiting a reflex. Criterion 6 emphasizes location-specific self-protective behaviour, likely reflecting an internal representation of the location of the aversive stimulus. Here, we require a level of sophistication that exceeds a reflex response to injury, such as a range of different responses that may differ between individuals and may be altered if ineffective.

The second point concerns associative learning (Criterion 7). Sentience could facilitate this by allowing animals to 'label' previously neutral stimuli or behaviours with valenced information, so that the animal can learn to behave more beneficially when faced with similar situations in future. However, simple forms of associative learning appear to occur unconsciously in humans (Greenwald and De Houwer, 2017), leading to ongoing debate about which kinds of associative learning are linked to sentience and why (Birch 2020; Birch et al., 2020a). Instrumental learning (Skora et al., 2021), reversal learning (Travers et al., 2018), learning "incongruent" spatial relationships (Ben-Haim et al., 2021), and learning across temporal gaps between stimuli ("trace conditioning"; Clark et al., 2002) are more complex and more strongly linked to sentience than classical conditioning involving two stimuli presented simultaneously. Given the ongoing debate on this issue, we regard any evidence of associative learning as relevant for discussion,

although it is only part of the overall picture, and some examples will be more convincing than others.

Outside our criteria, other lines of evidence for animal sentience have been proposed. Of particular relevance, Sneddon et al. (2014) nominated physiological stress responses to noxious stimuli. Elwood and Adams (2015) showed that, compared to non-shocked controls, shore crabs (*Carcinus maenas*) exposed to electric shocks had higher haemolymph lactate levels – a physiological measure of stress. This effect persisted when only crabs exhibiting similar behaviour were compared, ruling out treatment differences in activity. Ultimately, though, we decided against including a stress-based criterion, on the grounds that physiological stress is neither necessary for pain nor always associated with pain (Stevens et al. 2016). A caveat here is that sometimes inducing stress can be a way of exploring other criteria, as in, for example, Fossat et al. (2014), where a stress response is used as a way of investigating the effects of anxiolytic drugs.

Our criteria are not unreasonably demanding—they do not require certainty. For example, well-researched mammals, such as lab rats (*Rattus norvegicus*), would satisfy them all (Navratilova et al., 2013). At the same time, the criteria are rigorous and robust. To our knowledge, current evidence suggests that animals unlikely to be sentient, such as cnidarians (jellyfish and sea anemones), would not convincingly satisfy any of them. We have found two reports of associative learning in sea anemones (Ross, 1965; Hodgson, 1981), and one detailed study (Haralson et al., 1975), but nothing that could allow more than medium confidence in any single criterion. Sea anemones exhibit some behavioural flexibility (Haag & Dyson, 2014) but not of a type that satisfies Criterion 5. In sum, our criteria are rigorous and robust, without being unreasonably demanding.

2.3. Our grading system. How do our eight criteria lead to a judgement about the overall strength of evidence? It would be unreasonable to demand unequivocal satisfaction of all eight criteria before attributing sentience to an animal, especially in species that have been relatively little researched. If we are confident an animal satisfies several criteria, then the possibility of sentience should be taken seriously, and welfare risks should be considered. We have implemented a simple, practical grading scheme that relates the number of satisfied criteria to the strength of evidence for sentience.

A grading scheme can only ever provide approximate guidance, and evaluations must be sensitive to individual cases. For example, extra caution may be warranted if many indicators are uncertain rather than demonstrably absent, or if the animal exceeds an indicator's minimal requirements (e.g., satisfying criteria 4 or 8 in multiple ways). Moreover, the criteria are not equal. Criterion 8 provides compelling evidence in its own right, whereas Criterion 1 could only ever form a small part of a wider case for sentience, because nociceptors may detect noxious stimuli without any associated experience or feeling. Nonetheless, a grading scheme helpfully organises our thinking about sentience.

We use confidence levels to communicate the strength of evidence that an animal satisfies or fails each criterion. The possible confidence levels are "very high confidence", "high confidence", "medium confidence", "low confidence", "very low confidence", and "no confidence". Confidence levels consider both the amount of evidence and its reliability and quality.

We use "very high confidence" when the weight of scientific evidence leaves no scope for reasonable doubt. We use "high confidence" when we are convinced that the animals satisfy/fail the criterion, even though scope for reasonable doubt remains. We use "medium confidence" when concerns about the evidence's reliability/quality prevent us from having high confidence. We use "low confidence" when there is little evidence

that an animal satisfies or fails the criterion; "very low" when the evidence is seriously inadequate; and "no confidence" when it is non-existent. To be clear, "low confidence" does not necessarily mean sentience is unlikely or disproven. It can mean that the evidence either way is thin, low-quality, or both, rendering the animal's sentience unknown.

With this in mind, we apply the following approximate grading scheme:

1. High or very high confidence that 7-8 criteria are satisfied: Very strong evidence of sentience. Welfare protection clearly merited. No urgent need for further research into sentience in this taxon.
2. High or very high confidence that 5-6 criteria are satisfied: Strong evidence of sentience. If remaining indicators are uncertain rather than shown absent, further sentience research is advisable. However, these animals should be regarded as sentient in the context of animal welfare legislation.
3. High or very high confidence that 3-4 criteria are satisfied: Substantial evidence of sentience. If remaining indicators are uncertain rather than shown absent, further research is strongly recommended. Despite the scientific uncertainty regarding these animals, it might still be reasonable to include them within the scope of animal welfare legislation, e.g., if they are closely related to animals that have been more extensively studied and for which the evidence is stronger.
4. High or very high confidence that 2 criteria are satisfied: Some evidence of sentience. Sentience should not be ruled out. If remaining indicators are uncertain rather than shown absent, further research might provide insight.
5. High or very high confidence that 0-1 criteria are satisfied: Sentience unknown or unlikely. If remaining indicators are uncertain rather than shown absent, sentience is simply unknown. However, if high-quality scientific work shows the other indicators to be absent, sentience is unlikely.

This scheme does not give the final word on the strength of evidence. It is a rule-of-thumb and can be updated in response to new evidence or understanding. In applying our framework, one must consider the overall evidential picture, and the differences between criteria. We think an approximate grading scheme is ultimately more helpful than a scoring scheme giving each criterion a numerical weight, since these weights would be arbitrary.

2.4. The question of generalization. When using our grading scheme, separate assessments must not be demanded for every individual species. For example, very few of the 15,000 decapod species have been studied scientifically in relation to any of these sentience indicators. Thus, if we graded every decapod separately, most would fall into the "sentience unknown or unlikely" category, but this would be a misapplication of our framework. Many mammalian species have never been studied in relation to sentience (a great deal of the evidence for mammals comes from the lab rat, *R. norvegicus*), but that does not mean their sentience is unknown. It is a widely accepted principle in animal welfare science and policy that we can make reasonable generalizations from well-studied laboratory species to less-studied but related species.

3. Evidence of Sentience in Decapod Crustaceans

In this section, we apply our framework to a taxon where sentience is controversial, decapod crustaceans, and review all the evidence that bears on our eight criteria. Other relevant post-2000 reviews on this topic include Sherwin (2001), AHAW (2005), Elwood et al. (2009), Gherardi (2009), Broom (2014), Sneddon et al. (2014), Sneddon (2015), Burrell (2017), Walters (2018), Diggles (2019), Elwood (2019a, b, 2021), and Passantino et al. (2021).

We will use De Grave et al.'s (2009) taxonomy, which divides decapods in two suborders (Pleocyemata, including crabs, lobsters, crayfish, and caridean shrimp, and Dendrobrachiata, including penaeid shrimp), with the Pleocyemata further divided into ten infraorders. Molecular evidence supports this classification (Wolfe et al., 2019). Sentience research has focussed on the Brachyura (true crabs), with some work on the Anomura (anomuran crabs, including hermit crabs), the Astacidea (astacid lobsters and crayfish), the Achelata (spiny lobsters) and the Caridea (caridean shrimps). But there is limited research on other infraorders, including the commercially farmed penaeid shrimps (Table 1).

Table 1. A summary of the evidence of sentience in decapods. The colours and letters represent our confidence level that the order (or orders) of animals in question (row) satisfies the criterion in question (column). VH (dark green) indicates very high confidence, H (light green) indicates high confidence, M (dark yellow) indicates medium confidence, and L (light yellow) represents low confidence. Since we have not found evidence to support Criterion 8 in any decapod, we have used the category of very low confidence (VL, light grey) in this case. Importantly, low/very low confidence implies only that the scientific evidence one way or the other is weak, not that the animal fails or is likely to fail the criterion. Reproduced from Birch et al. (2021).

Criterion	1	2	3	4	5	6	7	8
True crabs (Brachyura)	H	VH	L	VH	L	VH	H	VL
Anomuran crabs (Anomura)	H	VH	L	L	M	H	L	VL
Astacid lobsters/crayfish (Astacidea)	H	VH	L	VH	L	L	M	VL
Spiny lobsters (Achelata)	H	VH	L	L	L	L	M	VL
Caridean shrimps (Caridea)	H	VH	L	M	L	M	L	VL
Penaeid shrimps (Penaeidae)	H	L	L	M	L	L	L	VL

3.1. Criterion 1*: The animal possesses receptors sensitive to noxious stimuli (nociceptors).*

A nociceptor is "a high-threshold sensory receptor of the peripheral somatosensory nervous system that is capable of transducing and encoding noxious stimuli" (International Association for the Study of Pain, 2017). The most direct method of detecting nociceptors is identifying peripheral sensory neurons with altered electrical activity in response to potentially noxious stimulation. So far, these methods have not conclusively demonstrated the presence of nociceptors in decapods (Sneddon et al., 2014; Walters, 2018).

We have only found two electrophysiological studies explicitly exploring nociception in decapod crustaceans. To assess nociceptive responses to extreme pH, Puri and Faulkes (2010) severed the second of two antennae pairs in Louisiana red swamp crayfish (*Procambarus clarkii*) and took extracellular recordings from the nerve tip of each. The nerves' electrical activity was compared when the antennae were washed or swabbed with sodium hydroxide (NaOH; alkaline), hydrochloric acid (HCl), benzocaine (a local anaesthetic in vertebrates) and the control solution (saline). Electrical responses differed greatly between individual antennae, showing no consistent increases or decreases in spike frequency between the different stimuli. Thus, the study yielded no evidence of nociceptors that respond to extreme pH in crayfish antennae (Puri & Faulkes, 2010). However, the conclusions are limited as extreme pH is just one possible stimulus that a nociceptor may respond to.

A follow-up experiment used the same procedure to investigate P. clarkii responses to extreme heat (60 °C water), control saline, capsaicin (the 'hot' chemical in chilli peppers, dissolved in ethanol), isothiocyanate (the 'hot' chemical in wasabi, dissolved in ethanol), or control ethanol solution (Puri & Faulkes, 2015). Hot water induced significantly more electrical activity than the control saline. No consistent differences in electrical activity were observed between capsaicin, isothiocyanate, and ethanol, although statistical analyses of this were not reported. These findings provide tentative evidence for antennal nociceptors specialised for extreme heat. However, it is unclear whether the receptors also respond to moderate heat, because a range of temperatures was not tested, and because the room-temperature saline bathing the antennae would have rapidly cooled the small volume of hot water. If the receptors respond to moderate heat, they would be thermoreceptors rather than nociceptors. It is, therefore, necessary to investigate nociception using stimuli ranging from mild to increasing intensities/frequencies/durations, as well as across a range of stimulus types (e.g., see Ashley et al., 2007 on rainbow trout; *Oncorhynchus mykiss*).

Another electrophysiological study (not intended to discover nociceptors) investigated the electrical responsivity to stimulation of sensory receptors on the inner edges of the pereiopod chelae (claws of a walking leg) in stone crayfish (*Austropotamobius torrentium*) (Altner et al., 1983). Despite not claiming to find nociceptors, the authors noted mechanoreceptors associated with external setae (bristles) that only responded to "strong mechanical stimuli". They did not quantify how strong, but if it was strong enough to cause avoidance behaviour, they may be mechanical nociceptors.

Molecular research provides indirect evidence for nociception in decapods. Transcriptomics can reveal which genes are being expressed as messenger RNA (mRNA) in an animal's tissue, thereby causing specific proteins to be produced. The

transcriptomes of Caribbean spiny lobster (*Panulirus argus*), clawed lobster (*Homarus americanus*), red swamp crayfish (*Procambarus clarkii*), and blue crab (*Callinectes sapidus*) all express Transient Receptor Potential A (TRPA) channels (Kozma et al., 2020). Some variants of the TRPA subfamily of ion channels can function as aversive stimulus receptors. For example, the four decapods express homologues to TRPA1, which detects various potentially noxious stimuli across many animal species, from flatworms (Arenas et al., 2017) to humans (Kádková et al., 2017). The decapods additionally expressed a homologue to the TRPA channel known as "painless", so-called because knocking it out stops fruit flies (*Drosophila melanogaster*) from avoiding noxious thermal, mechanical or chemical stimuli (Tracey et al., 2003; Im & Galko, 2012).

Overall, the decapods expressed four to five TRPA homologues with other species, and two distinct TRPA channels with no insect homologues. They also expressed TRPV1 (Kozma et al., 2020), another highly conserved ion channel involved in polymodal nociception in mammals (Smith & Lewin, 2009). P. clarkii antennae, limbs and brains also expressed these ion channels to varying degrees (Kozma et al., 2018). These transcriptome data provide relevant evidence but are insufficient for very high confidence that nociceptors are present, because the same proteins can have different functions in different species and different tissues within the same animal.

Finally, nociceptors are widespread across the animal kingdom. As well as in vertebrates, they have been found in annelid worms, nematode worms, gastropod molluscs and insects (Smith & Lewin, 2009; Walters, 2018). Crustaceans are a sister group to hexapods (insects), and both shared a common ancestor with nematodes (Halanych, 2004). It is unclear whether nociceptors evolved once and have been widely conserved since, or whether they evolved independently via convergent evolution (Walters, 2018). If they evolved in a crustacean-hexapod common ancestor, it seems unlikely that crustaceans would later have lost them, because nociceptors have clear survival value.

To summarise, the ion channel families involved in nociception are highly conserved evolutionarily, and crabs and lobsters express several homologous proteins. Nociceptors are also present in other arthropods, such as insects. This indirect evidence, together with the behavioural evidence considered later, allows high confidence that decapods satisfy Criterion 1. Direct neurophysiological evidence would be needed for very high confidence.

3.2. Criterion 2: *The animal possesses brain regions capable of integrating information from different sensory sources.*

Much remains to be discovered about crustacean brains, and there is enormous variation across species (Sandeman et al., 2014; Strausfeld et al., 2020). Nonetheless, crustaceans can integrate different kinds of information, with the three main brain regions (protocerebrum, deutocerebrum, and tritocerebrum; reviewed in Sandeman et al., 2014) extensively linked via an elaborate central complex (Utting et al., 2000).

Specific structures also integrate information, with the hemiellipsoid body perhaps the best understood. Hemiellipsoid bodies are likely homologous with insect mushroom bodies, which also have integrative functions (Brown & Wolff, 2012; Sayre & Strausfeld, 2019). For example, Strausfeld et al.'s (2020) study of nineteen decapods (and a stomatopod) found a protein in the hemiellipsoid bodies crucial for learning and memory in fruit flies (Skoulakis et al., 1993).

In the crab *Neohelice granulata* (Maza et al., 2016), hemiellipsoid bodies could be stained with antibodies to proteins associated with memory processes (known as 'p-CaMKII-α'), and with antibodies to a different protein (5-bromo-2′-deoxyuridine, or 'BrdU') produced by proliferating cells (production of new brain cells underlies learning and memory). Crabs were presented with a repeated 'threatening' visual stimulus, which initially caused them to attempt escape and caused corresponding activity (a calcium cascade) in the hemiellipsoid bodies, with the crabs' response to the repeated stimulus gradually stopping. Maza et al. (2016) showed the crabs the stimulus again after a short interval, either in the same environment as before or with a different visual background. Crabs with the familiar background continued to ignore the cascade, but those with the new background reacted with renewed behavioural and hemiellipsoid activity. The authors, therefore, implicated the hemiellipsoid bodies in learning and memory (Maza et al., 2016), although the type of learning here was probably habituation, not associative learning (see Criterion 7).

One mechanism by which decapod hemiellipsoid bodies can integrate information involves interneurons known as 'parasol cells'. Located within the hemiellipsoid body, these cells can integrate sensory information across modalities, with the ability to amplify signals (DeForest Mellon, 2003), and might play a role in decision-making and prioritisation. Without stimulation, they show consistent, synchronised pulses of activity. In crayfish, at least, individual parasol cells can receive either odour information from the olfactory lobe, visual information from the optical ganglion, or tactile, odour and visual information from the accessory lobe. When a strong stimulus activates any parasol cell, there is a burst of enhanced activity in that cell and neighbouring cells, even neighbours that did not receive the original stimulus input (DeForest Mellon, 2003). This cellular community-level activity may amplify important signals, enabling important information to be prioritised. Neural mechanisms such as this could allow whole-organism perception, learning and decision-making about potential harms.

Some decapods have more developed hemiellipsoid bodies than others. Across 19 decapods studied, the groups having proportionately the largest hemiellipsoid bodies were true crabs (Brachyura), followed by anomuran crabs (Anomura), followed by various caridean shrimps (Alpheidae and Thoridae) (Strausfeld et al., 2020), and hydrothermal vent shrimps (exemplified by *Rimicaris exoculate*; Figure 1) (Machon et al., 2019).

Decapods with relatively reduced hemiellipsoid bodies, such as crayfish and lobsters (Astacidea), may use a different brain region to integrate information. Specifically, the accessory lobe in the deutocerebrum is relatively large in astacids, and it can integrate multisensory information (Sandeman et al., 2014). In Australian freshwater crayfish (*Cherax destructor*), the accessory lobes receive input from deutocerebral interneurons that convey visual and tactile information from the hemiellipsoid bodies in the protocerebrum, as well as olfactory and other information from the deuto- and tritocerebra (Sandeman et al., 1995). The accessory lobe then projects information back up to the protocerebrum. Large and well-connected accessory lobes have also been found in the spiny lobster (*P. argus*, infraorder Achelata) (Wachowiak et al., 1996), freshwater crayfish (*P. clarkii* and *Orconectes rusticus*), and American clawed lobster (*Homarus americanus*).

The astacid combination of relatively small hemiellipsoid bodies with large accessory lobes contrasts with the opposite found in other decapods. For example, coconut crabs (*Birgus latro*, infraorder Anomura) have a very large hemiellipsoid body but an extremely small accessory lobe that is seemingly little connected with the rest of

the brain (Krieger et al., 2010). It is possible that information integration can be achieved either primarily in the hemiellipsoid bodies, as in crabs and some shrimp species, or primarily in the accessory lobe, as in crayfish and lobsters (Sandeman et al., 2014).
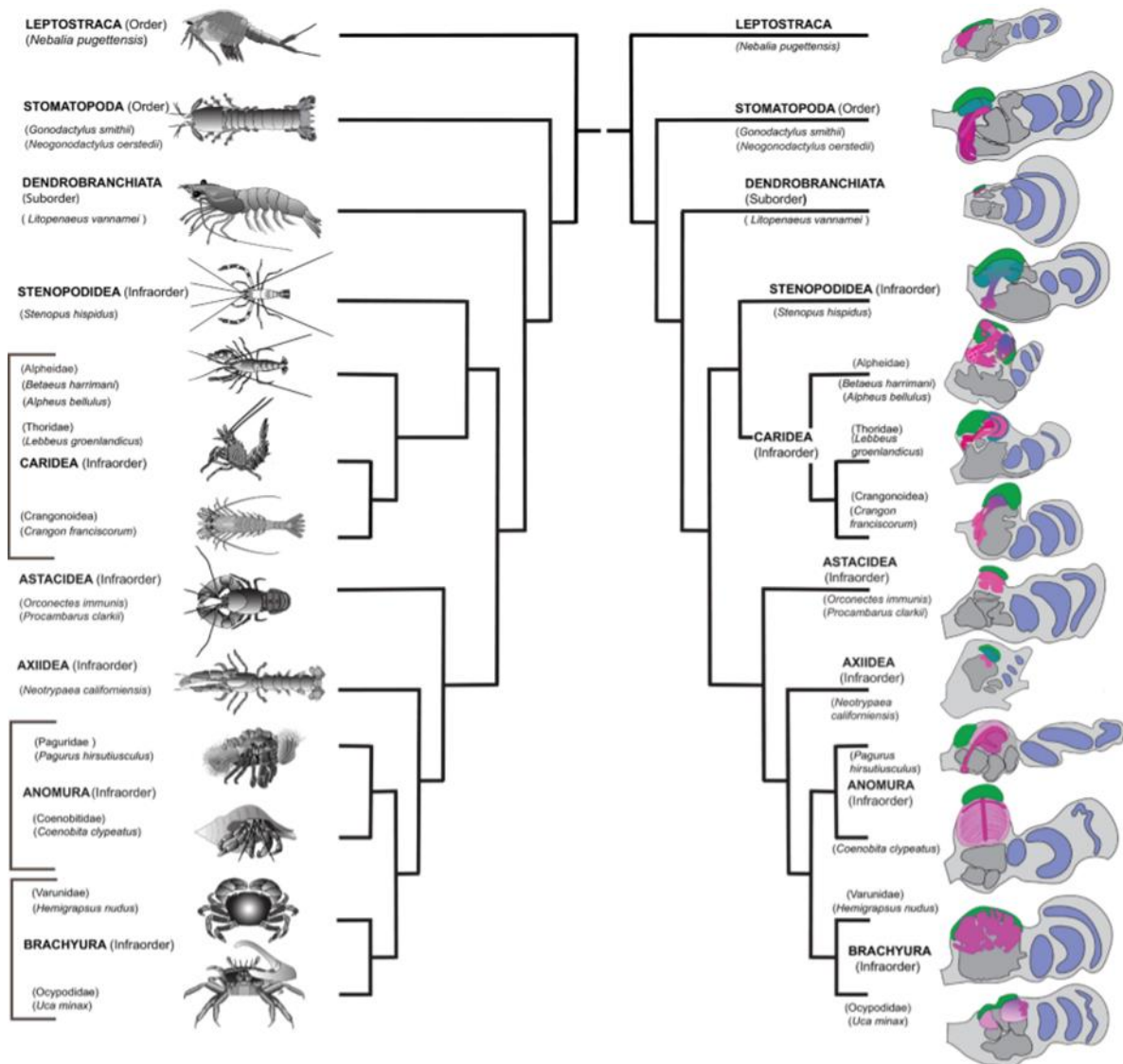

Figure 1. A key figure from Strausfeld et al. (2020). Pink regions indicate an integrative brain region associated with learning and memory (the hemiellipsoid body) in various species of crustacean, as identified using an immunostaining technique (N.B. Leptostraca and Stomatopoda are not decapods). This figure is © Strausfeld et al. 2020 / CC-BY-4.0 licensed. See the original source for full details of the technique used.

In conclusion, the central complex, hemiellipsoid bodies, and accessory lobes integrate information from different sensory sources. True crabs (infraorder Brachyura) and anomuran crabs (Anomura) have proportionally the largest and most developed hemiellipsoid bodies studied so far, followed by caridean shrimps (Caridea). Lobsters and crayfish (Astacidea, Achelata) have relatively small hemiellipsoid bodies, but integrate information using relatively large accessory lobes. We therefore have very high confidence that true crabs (infraorder Brachyura), anomuran crabs (Anomura), lobsters and crayfish (Astacidea, Achelata) and caridean shrimps (Caridea) satisfy Criterion 2. Other infraorders may satisfy this criterion, but many have not been studied in detail.

3.3. Criterion 3: *The animal possesses neural pathways connecting the nociceptors to the integrative brain regions.*

Given our high confidence that decapods have nociceptors and very high confidence that they have integrative brain regions, we must now ask whether neural pathways connect the two. Decapod sensory receptors are usually connected to the integrative brain regions (Sandeman et al., 2014), so it is plausible that nociceptors would also be connected. However, we have found no neurological evidence of the specific pathways transmitting nociceptive information. We therefore have low confidence that decapods satisfy Criterion 3. To be clear, our assessment is based on the absence of high-quality evidence one way or the other—not on evidence against nociceptors connecting to the integrative brain regions. This is an important evidence gap.

3.4 Criterion 4: *The animal's behavioural response to a noxious stimulus is modulated by chemical compounds affecting the nervous system in either or both of the following ways: (a) The animal possesses an endogenous neurotransmitter system that modulates (in a way consistent with the experience of pain, distress or harm) its responses to threatened or actual noxious stimuli; or (b) putative local anaesthetics, analgesics (such as opioids), anxiolytics or anti-depressants modify an animal's responses to threatened or actual noxious stimuli in a way consistent with the hypothesis that these compounds attenuate the experience of pain, distress or harm.*

Decapod crustaceans have endogenous neurotransmitter systems, including endogenous opioid, serotonergic, dopaminergic and octopaminergic systems (see Harlıoğlu et al., 2020 for a recent review). But do these compounds modulate responses to noxious stimuli?

True crabs (infraorder Brachyura). In a series of experiments, Hector Maldonado and colleagues studied the effect of opioids on responses to danger and noxious stimuli in the crab *Neohelice granulatus* (formerly *Chasmagnathus granulatus*). Injecting crabs with naloxone, an opioid blocker, prevented habituation to a danger stimulus (a shadow passing overhead), suggesting a role for endogenous opioids in habituation (Romano et al., 1990, Valeggia et al., 1989). Morphine inhibited crabs' defensive response (extending the claws and raising itself on its legs) to electric shock (Lozada et al., 1988) in a dose-dependent manner, as well as reducing escape responses to the danger stimulus (Maldonado et al., 1989). In both studies, naloxone administration eliminated the effect. Replacing morphine with a synthetic analogue of the opioid met-enkephalin produced a similar result (Godoy & Maldonado, 1995).

Do opioids attenuate an aversive "pain-like" or "fear-like" state, or generally inhibit stimulus responsiveness? Tomsic and Maldonado (1990) investigated whether morphine impaired crabs' motor actions (optokinetic responses) unrelated to danger, relative to controls injected with saline (n = 20 × 75 µg/g morphine, 20 × 100 µg/g, 20 × saline). They reported no effect of morphine on these behaviours, although it is unclear whether the experimenters were blind to treatment. Moreover, Tomsic et al. (1991) compared morphine with a neurotransmitter that impairs motor responses, gamma-Aminobutyric acid (GABA). Only morphine impaired long-term habituation to the danger stimulus. Together, these studies suggest that morphine is specific to danger responses.

Barr and Elwood (2011), however, reported different results. They placed shore crabs (*Carcinus maenas*) in a light area near a dark shelter. Light aversion motivated crabs to enter the shelter, but some crabs received an electric shock on entering. Would

administering morphine make the crabs more likely to enter the shelter despite the shock risk? In fact, morphine reduced the likelihood that crabs would enter the shelter, suggesting a general reduction in responsiveness. Crabs injected with morphine "appeared limp and could not move their appendages in a normal manner" (2011, p. 342), a report conflicting with Tomsic and Maldonado (1990). It is possible that responses to opioids differ between crab species. Indeed, Tomsic et al. (1993) could not replicate their morphine and naloxone results with another crab species, *Pachygrapsus marmoratus*.

The overall message is that opioids may mediate responses to noxious stimuli in both *N. granulatus* and *C. maenas*. However, current evidence does not reveal whether they attenuate aversive experiences or reduce general responsiveness. Variation in different species' response to opioids also remain poorly understood.

There is limited evidence concerning the effects of other drugs on threat responses in true crabs. Serotonin can have both anxiolytic and anxiogenic effects in humans and other mammals, depending on the animal's developmental stage and the brain area affected (Gordon and Hen, 2004). When Maldonado's lab administered serotonin to *N. granulatus* instead of opioids, the crabs sensitised to the danger stimulus, consistent with serotonin producing an anxiety-like state (Aggio et al., 1996). Furthermore, administering fluoxetine, a selective serotonin reuptake inhibitor (antidepressant), eliminated preference for dark areas over light areas in the striped shore crab *Pachygrapsus crassipes* (Hamilton et al., 2016). Combined with evidence from crayfish (see below), these findings indicate that serotonin modulates decapod responses to threatening and aversive stimuli, suggesting homology with mammalian systems.

Kaczer and Maldonado (2009) found that octopamine, the invertebrate analogue of noradrenaline (norepinephrine), improves appetitive (reward-based) learning and impairs aversive learning in *N. granulatus*. This is consistent with octopamine facilitating reward experiences but attenuating aversive experiences (see also Kaczer et al., 2011). Klappenbach et al. (2012) reported that dopamine plays approximately the opposite role to octopamine. It impaired appetitive learning and improved aversive learning in *N. granulatus*, consistent with dopamine attenuating positive experiences and facilitating aversive experiences. This differs from dopamine's role in the vertebrate brain but at least partially corresponds with evidence from other invertebrate taxa, such as insects (Riemensperger et al., 2005).

Other decapods. In shrimp aquaculture, eyestalk ablation involves removing one or both eyestalks of a mature broodstock female prawn. After eyestalk ablation, whiteleg shrimp (*Litopenaeus vannamei*) that received the topical anaesthetic lidocaine swam less erratically, with much less spiralling, than non-anaesthetised shrimp (Taylor et al., 2004). In a similar study, applying lidocaine before eyestalk ablation significantly reduced tail-flicking in the caridean shrimp *Macrobrachium americanum* (Diarte-Plata et al., 2012). These studies, like those above, cannot answer whether the anaesthetic attenuates a valenced state or just inhibits responsiveness. Nevertheless, they imply some degree of homology in human and shrimp nociceptive modulation.

Barr et al. (2008) studied antennae grooming and rubbing behaviour in prawns (*Palaemon elegans*). Applying acetic acid or sodium hydroxide (NaOH) to one antenna induced grooming of that antenna with the small claws on the walking legs and rubbing that antenna against the wall of the tank (see also Criterion 6). Unexpectedly, the local anaesthetic benzocaine also triggered grooming and tail-flipping (a defensive behaviour), suggesting it is strongly aversive. When benzocaine-treated animals were subsequently given acetic acid or NaOH, they were less likely to rub or tail-flip than controls. Depleted energy levels following an aversive reaction to benzocaine probably did not underlie this

effect, because the Benzocaine and water groups did not differ in general activity levels (number of lines crossed). Instead, an anaesthetic effect is the most plausible explanation.

In a high-profile study, Fossat et al. (2014) studied "anxiety-like" behaviour in crayfish (*P. clarkii*, infraorder Astacidea). The crayfish could explore both light and dark arms of a maze. When exposed to repeated electrical fields to induce stress, crayfish spent a lower proportion of time in the light arms. Crucially, endogenous serotonin mediated the effect. The stressed animals' brains contained significantly higher serotonin levels than the unstressed animals' brains. Moreover, injecting unstressed animals with (exogenous) serotonin significantly increased light avoidance compared to controls injected with saline. Administering an anxiolytic (anti-anxiety) drug, chlordiazepoxide, restored the stressed crayfishes' willingness to explore the light arms, relative to a saline control group.

A potential issue with this study is that electromagnetic fields can attract edible crabs (*Cancer pagurus*), before causing immobility and physiological stress (Scott et al. 2018). This attraction followed by harm makes the valence difficult to ascertain. Nonetheless, Fossat et al.'s (2014) "stress" treatment also induced tail-flips and increased blood glucose levels—indicators of an aversive response.

Fossat et al. (2015) further showed a positive correlation between brain serotonin levels and light avoidance, and again demonstrated that administering chlordiazepoxide abolished light avoidance.

Similar findings were observed when conspecific aggression induced the light avoidance behaviour: stressed animals had significantly higher brain serotonin levels and displayed significantly greater light avoidance (Bacqué-Cazenave et al., 2017). Administering chlordiazepoxide again abolished the effect. Perrot-Minnot at al. (2017) found consilient results for an amphipod crustacean. Although amphipods are not decapods, this suggests that the mechanisms involved are not unique to crayfish.

In sum, decapod crustaceans have endogenous neurotransmitter systems, including endogenous opioid, serotonergic, dopaminergic and octopaminergic systems. Decapods, therefore, have mechanisms for responding to noxious stimuli that are both homologous and analogous to those of humans. For true crabs (infraorder Brachyura), opioids may mediate responsiveness to threatening stimuli and electric shocks. They may either attenuate aversive experiences or reduce general responsiveness. Dopamine and octopamine also appear to mediate learning from aversive and attractive stimuli, respectively. In both true crabs and astacids, there is high-quality evidence that serotonin mediates stress responses, and that antidepressant or anxiolytic drugs modulate the response. Lidocaine may also modulate responses to injury in caridean and penaeid shrimps (Caridea, Penaeidae). Thus, we have very high confidence that true crabs (infraorder Brachyura) and astacid lobsters/crayfish (Astacidea) satisfy Criterion 4, and medium confidence for caridean (Caridea) and penaeid shrimps (family Penaeidae). For other taxa, there is insufficient evidence to allow medium confidence.

3.5. Criterion 5: *The animal shows motivational trade-offs, in which the negative value of a noxious or threatening stimulus is weighed (traded off) against the positive value of an opportunity for reward, leading to flexible decision-making. Enough flexibility must be shown to indicate centralized, integrative processing of information involving an evaluative common currency.*

For this criterion, we are seeking evidence that decapods weigh different motivations against one another: a plausible evolutionary function of sentience. This would suggest

that the behavioural responses are not fixed reflexes, but instead vary flexibly on the basis of competing requirements.

Robert Elwood and colleagues' work on hermit crabs (*Pagurus bernhardus*) is especially relevant to this criterion. Hermit crabs live in shells produced by other animals. They prefer some shell types and will swap a low-quality shell for a high-quality shell (Elwood et al., 1979; Elwood, 1995). Appel & Elwood (2009a) asked: if hermit crabs receive electric shocks in their shells, will they leave regardless of shell quality, or will they leave high-quality shells more reluctantly than low-quality shells? The latter would suggest that the disvalue of a noxious stimulus is weighed against other preferences. The mean voltage to induce a hermit crab to leave a high-quality *Littorina* shell was 17.7V, compared with 15.0V for a low-quality *Gibbula* shell. However, the reported *p*-value ($P = 0.0465$; Appel & Elwood, 2009a, p. 122) was achieved with a one-tailed Mann-Whitney U test (based on the probability of an outcome in the predicted direction). Two-tailed tests (based on the probability of an outcome in either direction) would have given $P = 0.093$. This result would not normally be considered significant. Nonetheless, a separate study using a constant 8V also found that hermit crabs were significantly less likely to evacuate high-quality *Littorina* shells than low-quality *Gibbula* shells (Elwood & Appel, 2009).

A possible confound in these studies is that *Littorina* and *Gibbula* shells differ in shape, potentially affecting electric shock transmission. Magee and Elwood (2016a) accordingly asked: will hermit crabs trade-off shock avoidance with predator avoidance? In particular, will hermit crabs be less likely to leave a shell when shocked if the surrounding water contains predator odour (a shore crab)? There was no difference in evacuation voltage between hermit crabs exposed to this predator odour and controls. This is an unsuccessful conceptual replication (but not a direct replication) of Appel and Elwood (2009a). Nonetheless, hermit crabs exposed to a predator odour were substantially more likely to remain in their shells than those exposed to no odour or a low-concentration odour of a potential food source (a mussel), even when given 25V shocks. Curiously, an undiluted, high-concentration mussel odour produced the same effect as the predator odour (Magee & Elwood, 2016a, Table 1). Thus, there is no convincing trade-off between shock avoidance and predator avoidance for two main reasons: the effect of a non-predator control odour (albeit well above natural concentrations), and the lack of trade-off between shock voltage and odour concentration. It is unclear whether the presence of a strong odour reduced activity generally, or was evaluated in a manner likely to require sentience. Based on these experiments, we only have medium confidence that hermit crabs satisfy Criterion 5.

Fossat and colleagues' (2014) study of "anxiety-like" behaviour in crayfish (*P. clarkii*) is also relevant here (for further discussion, see Criterion 4). As explained above, when electrical fields induced physiological stress in crayfish, they avoided the light arms of a maze. Follow-up studies have replicated the effect of stress on behaviour (Fossat et al., 2015; Bacqué-Cazenave et al., 2017), showing that threat tolerance depends on internal state. A similar phenomenon occurs in the nematode worm *Caenorhabditis elegans*, which tolerates threats more when hungry (Ghosh et al., 2016). In *C. elegans*, the simple mechanism achieving this trade-off was a specific interneuron (Ghosh et al., 2016). A similar mechanism, in which physiological stress increases sensitivity to threat, could likewise explain Fossat et al.'s (2014) results. So, while this is compelling evidence for Criterion 4, it is not compelling regarding Criterion 5.

Finally, certain natural behaviours may constitute motivational trade-offs, such as hermit crab (*Pagurus bernhardus*) shell selection. To protect their soft abdomens, hermit crabs inhabit empty gastropod shells. Optimal shell size depends on the size of the hermit

crab, so individuals must swap shells as they grow (Elwood et al. 1979). The decision to swap shells is based on a comparison between current and potential shell quality, and underpinned by visual, olfactory, and tactile assessments (Elwood & Neil 1992). Contests over shells add even more variables, as attackers must weigh shell value against potential contest costs. Some authors suggest that sentience plausibly underpins such complex multimodal trade-offs and decision-making (Elwood 2022, Irvine 2020). This may include positive experiences relating to shell value, as well as the negative states we have focused on. Alternatively, such ecologically relevant behaviours could be instinctive (albeit more complex than a set of reflexes), because they do not necessarily require learning anything novel.

To conclude, odour and shell type modulate hermit crab responses to electric shock. However, it is unclear that *predator* odour and shell *quality* mediate responses, giving us only medium confidence that hermit crabs (infraorder Anomura) can trade-off motivations. Likewise, there is high-quality evidence that crayfish threat tolerance depends on physiological stress, but this does not necessarily demonstrate a centralised decision-making system which weighs different needs against each other.

3.6. Criterion 6: *The animal shows flexible self-protective behaviour (e.g., wound-tending, guarding, grooming, rubbing) of a type likely to involve internal representation of the bodily location of a noxious stimulus.*

Here, we are looking for robust evidence of self-protective behaviours that go beyond reflexes—another plausible evolutionary function of sentience. To meet this criterion, the animal should target its response according to where on the body the noxious stimulus was administered, varying the response as if trying different solutions to the problem.

Elwood et al. (2017) showed that applying acetic acid to the mouths of shore crabs (*Carcinus maenas*) caused the crabs to move their mouthparts, scratch at their mouth with their claws, and 'attempt escape' significantly more than a control group. The same responses were found when the acid was applied to one eye, and the withdrawal of the affected eye for longer than the other eye was also observed.

The mouth part responses were (presumably) because the shore crab eye socket has a groove that leads down to the mouth area, causing acid to reach the mouthparts. The specific eye brushed with acetic acid was nonetheless withdrawn, and mouthparts were rubbed when acid was applied but not when capsaicin, oil or water were applied. Hence this study provides some evidence that shore crabs flexibly target their response to the location where a noxious stimulus is applied. However, more controlled aversive treatments (e.g., which precisely affect either the eyes or mouth) would improve on this experimental design.

McCambridge et al. (2016) compared edible crabs (*Cancer pagurus*) that had either been manually declawed or induced to autotomise (self-remove) a cheliped (claw-bearing limb). Manually declawed crabs were significantly more likely than autotomised crabs to touch the wound with the remaining claw or front walking legs. This is some evidence of wound-tending behaviour. The authors also witnessed manually declawed crabs "shuddering" when they touched the wound, and some "shielded" it with their remaining claw. No quantitative data were collected on these observations, but they are credible anecdotal reports from qualified experts.

Dyuizen et al. (2012) injected formalin into shore crab (*Hemigrapsus sanguineus*) chelipeds to study effects on the nitric oxide system. Actively rubbing the affected claw with the other claw was far more common than in crabs injected with saline solution.

Furthermore, in the three minutes after injection, formalin-treated crabs strongly preferred the uninjured cheliped when walking. The researchers also observed that the injured crabs "seemed to press their injured cheliped closer to the carapace compared with the intact cheliped until the end of the experiment" (Dyuizen et al., 2012, p. 2670), but no quantitative data were collected on this.

Another shore crab (*H. sanguineus*) study, also involving formalin injection, reported that "control and experimental crabs showed a sharp decrease in general activity within the first 3-5 s after injection: they came to a standstill, pressing the injured cheliped against the carapace. Later, crabs from experimental groups (formaldehyde injection) were hyperactive throughout the observation period; they made many movements of bending, unbending, and shaking the injured cheliped" (Kotsyuba et al., 2010, p. 203). No quantitative data on these behaviours were collected. Although the observed behaviours are not identical to those reported by Dyuizen et al. (2012), both report that shore crabs target varied self-protective behaviours at the injured limb, rather than protecting all limbs equally.

In two of their electric shock studies (see Criterion 5), Elwood and Appel noted one hermit crab (*P. bernhardus*) in each study grooming its abdomen after a shock (Appel & Elwood, 2009a; Elwood & Appel 2009). However, in a third study (Appel & Elwood 2009b), which used a different method of shock, 31/61 crabs that evacuated their shells demonstrated this behaviour. This is further credible observational evidence of targeted self-protective behaviour, this time in hermit crabs (Anomura). As the authors speculate, the dramatic difference between studies may reflect the third study's more effective shock procedure.

Diarte-Plata et al. (2012) investigated responses to eyestalk ablation in the caridean shrimp *Macrobrachium americanum* (see Criterion 4). A substantial majority rubbed the wound site, provided it was uncovered. Only a few shrimp rubbed wounds that were covered to prevent bleeding.

Barr et al. (2008) applied acetic acid, sodium hydroxide, gentle force, or a saline control to one antenna of another caridean shrimp species, *Palaemon elegans* (for further discussion, see Criterion 4). The noxious stimuli caused the shrimp to groom and rub the affected antenna. Unexpectedly, the anaesthetic benzocaine also triggered grooming behaviour. However, an attempted replication on three other decapod species, white shrimp (*Litopenaeus setiferus*), grass shrimp (*Palaemonetes* sp.), and Louisiana red swamp crayfish (*P. clarkii*), failed to record any grooming or rubbing behaviour in response to extreme pH (Puri & Faulkes 2010). One possible reason is that this study used hydrochloric acid, rather than the acetic acid applied by Barr et al. (2008).

In total, five studies indicate that true crabs (infraorder Brachyura) can target self-protective behaviours towards the site of a noxious stimulus. While none would be fully convincing in isolation, they give us very high confidence when taken together. There are also credible reports of targeted grooming behaviour in hermit crabs (Anomura), allowing high confidence that anomurans satisfy Criterion 6. We have medium confidence that caridean shrimps (Caridea) direct self-protective behaviour towards their antennae.

3.7 Criterion 7: *The animal learns associations between noxious stimuli and neutral stimuli and/or novel ways of avoiding noxious stimuli through reinforcement.*

There are two ways to satisfy this criterion: an animal can learn to associate a noxious stimulus with a neutral stimulus, such as a particular place or otherwise neutral odour (Pavlovian or classical conditioning), and/or the animal can learn a novel behaviour

(distinct from any pre-existing reflex responses) to avoid a noxious stimulus (instrumental conditioning). In both cases, the main rationale is that sentience has a plausible function in enabling previously neutral stimuli or behaviours to be re-evaluated and associated with negative (or positive) valence.

True crabs (infraorder Brachyura). First, some unconvincing evidence. Dunn and Barnes (1981a) claimed that decerebrate shore crabs (*C. maenas*), in which the brain and thoracic nervous system were separated, could learn to lift their leg to avoid electric shocks. If avoidance learning were achievable using the thoracic nervous system alone, this would cast doubt on the relevance of Criterion 7 to questions of sentience, because the isolated thoracic nervous system is presumably not sentient. However, Dunn & Barnes did not analyse 40% of their data because, "when data from all experiments were included, no significant differences between experimental (P) and control (R) animals emerged" (Dunn & Barnes, 1981a, p. 72). They also calculated twenty individual *p*-values for separate minutes of the experiment, with three barely significant values (0.04) and one < 0.01 (Dunn & Barnes, 1981a, pp. 73-4). Moreover, the researchers used a very high number of trials, so even a conclusive finding could never be described as rapid avoidance learning, which may provide evidence of sentience. A follow-up study used a problematic control procedure (Dunn & Barnes, 1981b), and a similar investigation of decerebrate ghost crabs (*Ocypode ceratophthalm*) did not even attempt statistical analysis (Hoyle, 1976). We do not regard these studies as providing robust evidence.

Punzo (1983) studied shock-avoidance learning in intact (i.e. non-decerebrate) mud crabs (*Eurypanopeus depressus*). The experimental animals apparently learnt swiftly and reliably to hold their leg out of the water, and retained this behaviour after an hour. However, the control procedures are not clearly described, making it difficult to distinguish between effects due to learning and effects due to the shock itself.

In the late 1980s, Abramson, Feinman and collaborators investigated associative learning using the shore crab's (*C. maenas*) eye withdrawal reflex (Abramson and Feinman 1987, 1988; Abramson et al., 1988; Feinman et al., 1990). Abramson and Feinman (1988) paired a carapace vibration (presumed neutral) with an air-puff aimed at the eye (presumed aversive). Experimental crabs were significantly more likely to retract the eye following a vibration alone than the five control groups, which were exposed to various different control conditions (including an "unpaired" control group, which received the same stimuli but in a random order with no pairing, and a "blank" control group which received no stimuli at all). An avoidance learning procedure, where retracting the eye prevented the air puff altogether, produced the same conditioned response (Abramson et al., 1988). One caveat is that carapace vibration may be aversive, so sensitisation to a doubly aversive stimulus (air-puff plus carapace vibration) could explain the results.

In three notable studies, Hector Maldonado and colleagues explored associative learning in the crab *N. granulatus*. Denti et al. (1988) showed that crabs who received an electric shock in a light chamber subsequently took longer to enter that chamber. However, physiologically stressed crabs may have been less likely to explore the light chamber, so this is not itself compelling evidence of avoidance learning.

To eliminate this alternative explanation, Fernandez-Duque et al. (1992) used "yoked" control crabs which remained in the dark chamber but received the exact same shocks as crabs in the light chamber. In general, a "yoked" control is an animal that receives the exact same aversive stimuli as an animal in the test group, but unpaired with any neutral stimulus. Comparing a test group to yoked controls is particularly useful for ruling out explanations based on sensitization to aversive stimuli or reduction of

exploratory behaviour, since the controls have received exactly the same aversive stimuli, but without any pairing with a neutral stimulus. Twenty-four hours later, crabs shocked in the light chamber took significantly longer to re-enter it than the yoked controls.

Dimant and Maldonado (1992) obtained similar results using food (a positive reinforcer) instead of electric shocks (a negative reinforcer). Compared to control crabs that received food in the dark chamber, crabs given food in the light chamber were significantly quicker to enter it after 24 hours. Taken together, these studies are good evidence of associative learning in *N. granulatus*.

Orlosk et al. (2011) trained shore crabs (*C. maenas*) to associate light with food and to search for food within a light beam shone on an arbitrary location. 21/30 crabs learned successfully. However, this study appears not to have used any control group or attempted to rule out habituation overriding the crabs' light aversion.

Magee and Elwood (2013) let shore crabs (*C. maenas*) choose between two shelters and recorded whether they learned to avoid a shelter where shocks were administered ("shock shelter"). Crabs that entered the shock shelter in the first trial did not switch shelters in the following trial, but choosing the shock shelter in the second trial did increase the likelihood of subsequently switching shelters. Magee and Elwood (2013, p. 357) argue that this design is better than Maldonado and colleagues' latency-based design, since a general reduction in activity cannot influence a forced choice. But a limitation is that crabs could move between shelters within a trial. The results could hence be explained by crabs often moving from the shock shelter to the non-shock shelter after a shock (i.e., within trials) and then returning to their most recent shelter at the beginning of each new trial (site fidelity). So, whilst the shock was aversive and site fidelity necessitates remembering the most recent shelter, the increased use of the non-shock shelter might not have been due to associative learning reinforced by shocks (as criterion 7 requires).

Magee and Elwood (2016b) addressed this drawback by partitioning the two shelters with an opaque screen. During training, the crabs (*C. maenas*) were placed on either side of the partition in alternate trials, so only one shelter was available per trial. One shelter was randomly selected as the shock shelter. Magee and Elwood asked: will this training, in which the shock and non-shock shelters were experienced sequentially, cause the crabs to avoid the shock shelter later, when given a free choice of shelters (with the shocking mechanism now switched off)?

This setup could have provided rigorous evidence of avoidance learning, but gave a null result: 36/66 crabs initially chose the former non-shock shelter and 30/66 chose the former shock shelter, which was not a statistically significant difference (Magee & Elwood, 2016b, p. 885). Offered the same choice again but some with visual cues switched around, 29/61 chose the former non-shock shelter and 32/61 chose the former shock shelter, which was again not a significant difference (Magee & Elwood, 2016b, p. 885).

Owing to all the usual difficulties associated with drawing conclusions from non-significant results this null result is not strong evidence *against* avoidance learning. It is possible that the crabs could not learn the information expected, but equally some feature of the experiment may have masked this ability. For example, removing the partition could have disrupted crabs' recognition of the area, or the forced inter-trial removal from both shelters might have been distracting. The task was also relatively difficult. In honeybees (*Apis mellifera*), learning from sequential stimuli is harder than learning from simultaneous stimuli (Dyer & Neumayer, 2005). Nonetheless, this is the kind of associative learning we consider most likely to indicate sentience, so a better-supported null result would be informative.

Taken together, the above experiments show the challenges of demonstrating associative learning, but also some ingenious solutions. The Maldonado group's studies provide good evidence of associative learning in *C. granulatus*, and the Elwood group's offer some positive evidence of associative learning in *C. maenas*, as well as a notable null result.

Other decapods. Fine-Levy et al. (1988) investigated associative learning in spiny lobsters (*P. argus*). They asked: can the animal associate an initially attractive odour (shrimp) with an aversive stimulus (a dark, fast-approaching object), so the odour triggers avoidance behaviours? They observed significant pre- to post-conditioning changes in grabbing, searching and active avoidance behaviours. However, 14 different behaviours were separately analysed, with only 5 of the changes reaching statistical significance.

We also consider it a limitation of the approach that the analysis compared pre- and post-conditioning animals but did not compare a conditioned group to a control group. When considering the same animals, before and after conditioning, it is challenging to disentangle genuine conditioning from other behavioural changes produced by repeated exposure to an aversive stimulus. As noted earlier, evidence for associative learning is stronger when there is a "yoked" control group that has received the exact same aversive stimuli unpaired with a neutral stimulus, and when animals in that group do not display the same behavioural changes.

Kawai et al. (2004) asked whether crayfish (*P. clarkii*) could learn to avoid mild (6.5V) electric shocks by moving to another compartment when a warning light was displayed. Responsiveness to the warning light significantly increased over many repeated trials, but sensitization cannot be ruled out, especially given the numerous shocks involved (20 trials per day for 32 days). Kawai et al. (2004) attempted to address this with follow-up experiments, but did not compare the test group to a yoked control group, which is one good way to rule out sensitization.

In an experiment on *O. rusticus*, Bhimani and Huber (2016) did compare an experimental group to a yoked control group. Crayfish in the test group received mild (6V) electric shocks whenever they entered an area with different substrate, and the controls received the same shocks as the masters (regardless of their own location). Masters soon avoided the shock-inducing substrate, whereas the yoked controls did not (as one would expect, since the shock was unpaired with any substrate for that group).

Is this avoidance learning? An alternative explanation is that shocks triggered an escape response followed by a period of slowed motion, inevitably on the non-shock substrate. Ruling this out would require testing crayfish in a new arena without shocks and with the substrates positioned differently. The study of Datta et al. (2018), which used a similar experimental design with positive reinforcement (amphetamines), had similar limitations.

Tomina and Takahata (2010) tested whether lobsters (*H. americanus*) learned to grip a sensor for food. Training significantly increased gripping behaviour in the four lobsters in the test group (for whom the food reward was paired with the gripping behaviour), but not in the four controls, who received the exact same positive reinforcement (food) unpaired with any gripping.

Okada et al. (2021) performed an associative learning experiment on marbled crayfish (*Procambarus virginalis*). Before training, the crayfish preferred a blue-lit exit to a white-lit exit. They were then trained to associate the blue light with 20 V electric shocks. After training, crayfish were significantly more likely to choose the white-lit exit than the blue-lit exit – a memory retained for at least 48 hours.

In conclusion, Maldonado and colleagues' research permits high confidence that true crabs (infraorder Brachyura) satisfy criterion 7, although there are also several unconvincing studies and a notable null result. Other decapods have received comparatively less attention, although we have medium confidence that lobsters and crayfish learn associatively.

3.8 Criterion 8: *Animals show that they value a putative analgesic or anaesthetic when injured in one or more of the following ways: (a) the animal learns to self-administer putative analgesics or anaesthetics when injured; or (b) the animal learns to prefer, when injured, a location at which analgesics or anaesthetics can be accessed; or (c) the animal prioritises obtaining these compounds over other needs (such as food) when injured.*

This criterion unifies part of Criterion 4b (efficacy of anti-nociceptive agents), with the cognitive Criteria 5 and/or 7. The rationale is that a putative function of pain, as opposed to nociception, is to facilitate specific and novel learning and prioritization. Active preference for analgesics or anaesthetics may also indicate the animal's subjectively perceived aversion to nociceptive inputs, whilst separating this from the other direct effects of physical injury itself (e.g., impaired functioning). As such, this set of behaviours could be quite specific in distinguishing pain from nociception.

Unfortunately, there are no studies to review in this case. Datta et al.'s (2018) procedure for self-administering amphetamines in crayfish (*O. rusticus*) offers a promising method to investigate Criterion 8a. Crook et al. (2021) also successfully tested a conditioned place preference paradigm in Bock's pygmy octopus (*Octopus bocki*)—a potential model for future work on Criterion 8b. However, given the lack of evidence either for or against any decapod satisfying Criterion 8, our confidence level is very low for all infraorders. This is an obvious evidence gap and important direction for future research.

4. Conclusions.

We have developed a framework for evaluating the scientific evidence for animal sentience, with a focus on pain experience. It is based on four neural and four cognitive/behavioural criteria. Although none of these are conclusive in isolation, we consider them all relevant to the overall case. Our "confidence levels" framework communicates the overall strength of evidence regarding each criterion, taking into consideration both the amount of evidence and its reliability/quality. Based on the number of criteria met and our confidence level, our approximate grading scheme converts confidence levels to an overall judgement on the likelihood of sentience.

Applying our framework to decapod crustaceans revealed a complicated evidential picture. The evidence of sentience is strong for true crabs (infraorder Brachyura) and substantial for anomuran crabs, astacids, and caridean shrimps. However, the evidence for a given taxon largely depends on how much sentience-relevant research it has received. True crabs have attracted sustained scientific attention, hence the strong evidence, whereas (for example) penaeid shrimps have barely been studied, resulting in a much weaker case. Nonetheless, there are no cases of either very high or high confidence that a taxon fails a criterion.

Going forward, we hope our framework highlights questions for sentience researchers to address. Criteria 3 and 8, for example, show crucial evidence gaps in the case for decapod sentience. We would accordingly encourage future studies to search for

neural connections between nociceptors and integrative brain regions as well as studies testing whether decapods selectively value putative analgesics or anaesthetics when injured. Another open question concerns when sentience arises during development. For this review, we have focused on adult decapods, which is where most research has been directed, but studies on larval stages are sorely needed.

We have concentrated here on evaluating evidence of sentience, not advising on policy. However, our recent report to the UK government (Birch et al., 2021) recommended including all decapod crustaceans in the scope of animal welfare laws, while also developing enforceable best-practice regulations for commercially important species.

One of our central recommendations was implemented in the recent Animal Welfare (Sentience) Act 2022, which explicitly includes cephalopod molluscs and decapod crustaceans, and places policymakers under a duty to pay "all due regard" for their welfare. In the future, we hope our framework can provide a fair and transparent way to evaluate evidence of sentience in other controversial taxa, such as insects, gastropods, and spiders.

References

Abramson, Charles I.; and Feinman, Richard D. (1987). Operant punishment of eye elevation in the green crab, Carcinus maenas. *Behavioral & Neural Biology*. 48(2): 259-277.

Abramson, Charles I.; and Feinman, Richard D. (1988). Classical conditioning of the eye withdrawal reflex in the green crab. *Journal of Neuroscience.* 8(8): 2907-2912.

Abramson, Charles I.; Armstrong, Philip M.; Feinman, Robin A.; and Feinman, Richard D. (1988). Signaled avoidance in the eye withdrawal reflex of the green crab. *Journal of the Experimental Analysis of Behavior.* 50(3): 483-492.

Aggio, Juan; Rakitín, Ana; and Maldonado, Héctor (1996). Serotonin-induced short- and long-term sensitization in the crab Chasmagnathus. *Pharmacology Biochemistry & Behavior.* 53(2): 441-448.

Allen, Colin; Grau, James W.; and Meagher, Mary W. (2009). The Lower Bounds of Cognition: What Do Spinal Cords Reveal? In: *The Oxford Handbook of Philosophy of Neuroscience* (John Bickle, Ed.). Oxford University Press: 129-142.

Altner, Iris; Hatt, Hanns; and Altner, Helmut (1983). Structural properties of bimodal chemo- and mechanosensitive setae on the pereiopod chelae of the crayfish, Austropotamobius torrentium. *Cell and Tissue Research*. 228(2): 357-374.

Animal Health and Animal Welfare Panel of the European Food Standards Agency [AHAW] (2005). Aspects of the biology and welfare of animals used for experimental and other scientific purposes (EFSA-Q-2004-105). Annex to the *EFSA Journal*. 292: 1-136.

Animal Welfare (Sentience) Act (2022)

Appel, Mirjam; and Elwood, Robert W. (2009a). Motivational trade-offs and potential pain experience in hermit crabs. *Applied Animal Behaviour Science*. 119(1-2): 120-124.

Appel, Mirjam; and Elwood, Robert W. (2009b). Gender differences, responsiveness and memory of a potentially painful event in hermit crabs. *Animal Behaviour, 78*(6), 1373-1379.

Arenas, Oscar M.; Zaharieva, Emanuela E.; Para, Alessia; Vásquez-Doorman, Constanza; Petersen, Christian P.; and Gallio, Marco (2017). Activation of planarian TRPA1 by reactive oxygen species reveals a conserved mechanism for animal nociception. *Nature Neuroscience.* 20(12): 1686-1693.

Ashley, Paul J.; Sneddon, Lynne U.; and McCrohan, Catherine R. (2007). Nociception in fish: Stimulus-response properties of receptors on the head of trout Oncorhynchus mykiss. *Brain Research*. 1166: 47-54.

Bacqué-Cazenave, Julien; Cattaert, Daniel; Delbecque, Jean-Paul; and Fossat, Pascal (2017). Social harassment induces anxiety-like behaviour in crayfish. *Scientific Reports.* 7(1): 1-7.

Barr, Stuart; and Elwood, Robert W. (2011). No evidence of morphine analgesia to noxious shock in the shore crab, Carcinus maenas. *Behavioural Processes*. 86(3): 340-344.

Barr, Stuart; Laming, Peter R.; Dick, Jaimie T. A.; and Elwood, Robert W. (2008). Nociception or pain in a decapod crustacean? *Animal Behaviour*. 75(3): 745- 751.

Bateson, Patrick (1991). Assessment of pain in animals. *Animal Behaviour*. 42(5): 827-839.

Ben-Haim, Moshe Shay; Dal Monte, Olga; Fagan, Nicholas A.; Dunham, Yarrow; Hassin, Ran R.; Chang, Steve W. C.; and Santos, Laurie R. (2021). Disentangling perceptual awareness from nonconscious processing in rhesus monkeys (Macaca mulatta). *Proceedings of the National Academy of Sciences.* 118(15): e2017543118.

Bhimani, Rohan; and Huber, Robert (2016). Operant avoidance learning in crayfish, Orconectes rusticus: Computational ethology and the development of an automated learning paradigm. *Learning & Behavior*. 44(3): 239-249.

Birch, Jonathan (2017). Animal sentience and the precautionary principle. *Animal Sentience*. 2(16): 1.

Birch, Jonathan (2020). The search for invertebrate consciousness. *Noûs*. 56(1): 133-153.

Birch, Jonathan, Broom, Donald M.; Browning, Heather; Crump, Andrew; Ginsburg, Simona; Halina, Marta; Harrison, David et al. (2022). How should we study animal consciousness scientifically? *Journal of Consciousness Studies*. 29(3-4): 8-28.

Birch, Jonathan; Burn, Charlotte; Schnell, Alexandra, K.; Browning, Heather; and Crump, Andrew (2021). *Review of the Evidence of Sentience in Cephalopod Molluscs and Decapod Crustaceans*. Department for Environment, Food & Rural Affairs (Defra).

Birch, Jonathan; Ginsburg, Simona; and Jablonka, Eva (2020a). Unlimited Associative Learning and the origins of consciousness: A primer and some predictions. *Biology and Philosophy*. 35(6): 56.

Birch, Jonathan; Schnell, Alexandra K.; and Clayton, Nicola S. (2020b). Dimensions of animal consciousness. *Trends in Cognitive Sciences*. 24(10): 789-801.

Boissy, Alain; Manteuffel, Gerhard; Jensen, Margit Bak; Moe, Randi Oppermann; Spruijt, Berry; Keeling, Linda J.; Winckler, Christoph et al. (2007). Assessment of positive

emotions in animals to improve their welfare. *Physiology & Behavior*. 92(3): 375-397.

Bradshaw, R. Harry (1998). Consciousness in nonhuman animals: adopting the precautionary principle. *Journal of Consciousness Studies*. 5(1): 108-114.

Broom, Donald M. (2014). *Sentience and animal welfare*. CABI.

Brown, Sheena; and Wolff, Gabriella (2012). Fine structural organization of the hemiellipsoid body of the land hermit crab, Coenobita clypeatus. *Journal of Comparative Neurology*. 520(13): 2847-2863.

Burrell, Brian D. (2017). Comparative biology of pain: what invertebrates can tell us about how nociception works. *Journal of Neurophysiology*. 117(4): 1461-1473.

Cabanac, Michel (1992). Pleasure: the common currency. *Journal of Theoretical Biology*. 155(2), 173-200.

Campbell, I. G.; Carstens, E.; and Watkins, L. R. (1991). Comparison of human pain sensation and flexion withdrawal evoked by noxious radiant heat. *Pain*. 45(3): 259-268.

Clark, Robert E.; Manns, Joseph R.; and Squire, Larry R. (2002). Classical conditioning, awareness, and brain systems. *Trends in Cognitive Sciences*. 6(12): 524-531.

Crook, Robyn J. (2021). Behavioural and neurophysiological evidence suggests affective pain experience in octopus. *iScience*. 24(3): 102229.

Crump, Andrew; and Birch, Jonathan (2022). Animal consciousness: The interplay of neural and behavioural evidence. *Journal of Consciousness Studies*. 29(3-4): 104-128.

Datta, Udita; Van Staaden, Moira; and Huber, Robert (2018). Crayfish self-administer amphetamine in a spatially contingent task. *Frontiers in Physiology*. 9: 433.

Dawkins, Marian S. (2001). Who needs consciousness? *Animal Welfare*. 10, S19-S29.

De Grave, Sammy; Pentcheff, N. Dean; Ahyong, Shane T.; Chan, Tin-Yam; Crandall, Keith A.; Dworschak, Peter C.; Felder, Darryl L. et al. (2009). A classification of living and fossil genera of decapod crustaceans. *Raffles Bulletin of Zoology*. 21(Supplement): 1-109.

De Waal, Frans B.; and Ferrari, Pier F. (2010). Towards a bottom-up perspective on animal and human cognition. *Trends in Cognitive Sciences*. 14(5): 201-207.

Mellon Jr, DeForest (2003). Dendritic initiation and propagation of spikes and spike bursts in a multimodal sensory interneuron: The crustacean parasol cell. *Journal of Neurophysiology*. 90(4): 2465-2477.

Denti, Alicia; Dimant, Beatriz; and Maldonado, Hector (1988). Passive avoidance learning in the crab Chasmagnathus granulatus. *Physiology & Behavior*. 43(3): 317-320.

Diarte-Plata, Genaro; Sainz-Hernández, Juan C.; Aguiñaga-Cruz, Jazmín A.; Fierro-Coronado, Jesús A.; Polanco-Torres, Arturo; and Puente-Palazuelos, Catalina (2012). Eyestalk ablation procedures to minimize pain in the freshwater prawn Macrobrachium americanum. *Applied Animal Behaviour Science*. 140(3-4): 172-178.

Diggles, Benjamin K. (2019). Review of some scientific issues related to crustacean welfare. *ICES Journal of Marine Science*. 76(1): 66-81.

Dimant, Beatriz; and Maldonado, Hector (1992). Habituation and associative learning during exploratory behavior of the crab Chasmagnathus. *Journal of Comparative Physiology A*. 170(6): 749-775.

Dunn, P. D. C.; and Barnes, W. J. P. (1981a). Learning of leg position in the shore crab, Carcinus maenas. *Marine & Freshwater Behaviour & Physiology*. 8(1): 67-82.

Dunn, P. D. C.; and Barnes, W. J. P. (1981b). Neural correlates of leg learning in the shore crab, Carcinus maenas. *Marine & Freshwater Behaviour & Physiology.* 8(1): 83-97.

Dyer, Adrian G.; and Neumeyer, Christa (2005). Simultaneous and successive colour discrimination in the honeybee (Apis mellifera). *Journal of Comparative Physiology A.* 191(6): 547-557.

Dyuizen, Inessa V.; Kotsyuba, Elena P.; and Lamash, Nina E. (2012). Changes in the nitric oxide system in the shore crab Hemigrapsus sanguineus (Crustacea, Decapoda) CNS induced by a nociceptive stimulus. *Journal of Experimental Biology.* 215(15): 2668-2676.

Edelman, David B.; and Seth, Anil K. (2009). Animal consciousness: a synthetic approach. *Trends in Neurosciences.* 32(9): 476-484.

Edelman, David B.; Baars, Bernard J.; and Seth, Anil K. (2005). Identifying hallmarks of consciousness in non-mammalian species. *Consciousness and cognition.* 14(1): 169-187.

Elwood, Robert W. (1995). Motivational change during resource assessment by hermit crabs. *Journal of Experimental Marine Biology & Ecology.* 193(1-2): 41-55.

Elwood, Robert W. (2019a). Discrimination between nociceptive reflexes and more complex responses consistent with pain in crustaceans. *Philosophical Transactions of the Royal Society of London B.* 374(1785): 20190368.

Elwood, Robert W. (2019b). Assessing the potential for pain in crustaceans and other invertebrates. In: *The Welfare of Invertebrate Animals* (Claudio Carere and Jennifer Mather (eds.)). Springer: 147- 177.

Elwood, Robert W. (2021). Potential Pain in Fish and Decapods: Similar Experimental Approaches and Similar Results. *Frontiers in Veterinary Science.* 8: 369.

Elwood, Robert W. (2022). Hermit crabs, shells, and sentience. *Animal Cognition.* 1-17.

Elwood, Robert W.; and Adams, L. (2015). Electric shock causes physiological stress responses in shore crabs, consistent with prediction of pain. *Biology Letters.* 11(11): 20150800.

Elwood, Robert W.; and Appel, Mirjam (2009). Pain experience in hermit crabs? *Animal Behaviour.* 77(5): 1243-1246.

Elwood, Robert W.; Barr, Stuart; and Patterson, Lynsey (2009). Pain and stress in crustaceans? *Applied Animal Behaviour Science.* 118(3-4): 128-136.

Elwood, Robert W.; Dalton, Natasha; and Riddell, Gillian (2017). Aversive responses by shore crabs to acetic acid but not to capsaicin. *Behavioural Processes.* 140: 1-5.

Elwood, Robert W.; McClean, Anne; and Webb, Linda (1979). The development of shell preferences by the hermit crab, Pagurus bernhardus. *Animal Behaviour.* 27(3): 940-946.

Elwood, Robert W.; and Neil, Susan J. (1992). *Assessments and Decisions: A study of information gathering by hermit crabs (1st edn.).* Chapman & Hall.

Feinberg, Todd E.; and Mallatt, Jon M. (2016). *The Ancient Origins of Consciousness: How the Brain Created Experience.* MIT Press.

Feinman, Richard D.; Llinas, Rafael H.; Abramson, Charles I.; and Forman, Robin R. (1990). Electromyographic record of classical conditioning of eye withdrawal in the crab. *Biological Bulletin.* 178(3): 187-194.

Fernandez-Duque, Eduardo; Valeggia, Claudia; and Maldonado, Hector (1992). Multitrial inhibitory avoidance learning in the crab Chasmagnathus. *Behavioral & Neural Biology.* 57(3): 189-197.

Fine-Levy, Jacqueline B.; Girardot, Marie-Nadia; Derby, Charles D.; and Daniel, Peter C. (1988). Differential associative conditioning and olfactory discrimination in the spiny lobster Panulirus argus. *Behavioral & Neural Biology*. 49(3): 315-331.

Fossat, Pascal; Bacqué-Cazenave, Julien; De Deurwaerdère, Philippe; Cattaert, Daniel; and Delbecque, Jean-Paul (2015). Serotonin, but not dopamine, controls the stress response and anxiety-like behavior in the crayfish Procambarus clarkii. *Journal of Experimental Biology*. 218(17): 2745-2752.

Fossat, Pascal; Bacqué-Cazenave, Julien; De Deurwaerdère, Philippe; Delbecque, Jean-Paul; and Cattaert, Daniel (2014). Anxiety-like behavior in crayfish is controlled by serotonin. *Science*. 344(6189): 1293-1297.

Frith, Chris D. (2021). The neural basis of consciousness. *Psychological Medicine*. 51(4): 550-562.

Gherardi, Francesca (2009). Behavioural indicators of pain in crustacean decapods. *Annali dell'Istituto Superiore di Sanità*. 45: 432-438.

Ghosh, D. Dipon; Sanders, Tom; Hong, Soonwook; McCurdy, Li Yan; Chase, Daniel L.; Cohen, Netta; Koelle, Michael R.; and Nitabach, Michael N. (2016). Neural Architecture of Hunger-Dependent Multisensory Decision Making in C. elegans. *Neuron*. 92(5): 1049-1062.

Ginsburg, Simona; and Jablonka, Eva (2019). *The Evolution of the Sensitive Soul: Learning and the Origins of Consciousness*. MIT Press.

Godoy, Adriana M.; and Maldonado, Héctor (1995). Modulation of the escape response by [DAla2]met-enkephalin in the crab Chasmagnathus. *Pharmacology Biochemistry & Behavior*. 50(3): 445-451.

Gordon, Joshua A.; and Hen, Rene (2004). The serotonergic system and anxiety. *Neuromolecular Medicine*. 5(1): 27-40.

Greenwald, Anthony G.; and De Houwer, Jan (2017). Unconscious conditioning: Demonstration and difference from conscious conditioning. *Journal of Experimental Psychology: General*. 146(12): 1705-1721.

Griffin, Donald R. (1998). From cognition to consciousness. *Animal Cognition*. 1(1): 3-16.

Haag, E.; and Dyson, K. (2014). Trade-off between safety and feeding in the sea anemone Anthopleura aureoradiata. *New Zealand Journal of Marine and Freshwater Research*. 48(4): 540-546.

Halanych, Kenneth M. (2004). The new view of animal phylogeny. *Annual Review of Ecology, Evolution, and Systematics*. 35: 229-25.

Hamilton, Trevor James; Kwan, Garfield T.; Gallup, Joshua; and Tresguerres, Martin (2016). Acute fluoxetine exposure alters crab anxiety-like behaviour, but not aggressiveness. *Scientific Reports*. 6(1): 19850.

Haralson, John V.; Groff, Charlene I.; and Haralson, Sally J. (1975). Classical conditioning in the sea anemone, Cribina xanthogrammica. *Physiology & Behavior*. 15(4): 455-460.

Harlıoğlu, Muzaffer Mustafa; Farhadi, Ardavan; and Harlıoğlu, Ayşe Gül (2020). Roles of neurotransmitters in decapod reproduction. *Thalassas*. 36(2): 633-639.

Hodgson, V. S. (1981). Conditioning as a factor in the symbiotic feeding relationship of sea anemones and anemone fishes. *Proceedings of the International Coral Reef Symposium*. 4: 553-561.

Hoyle, Graham (1976). Learning of leg position by the ghost crab Ocypode ceratophthalma. *Behavioral Biology*. 18(2): 147-163.

Im, Seol Hee, and Galko, Michael J. (2012). Pokes, sunburn, and hot sauce: Drosophila as an emerging model for the biology of nociception. *Developmental Dynamics.* 241(1): 16-26.

International Association for the Study of Pain (2017). *IASP terminology*.

Irvine, Elizabeth (2020). Developing valid behavioral indicators of animal pain. *Philosophical Topics.* 48(1): 129-153.

Kaczer, Laura, and Maldonado, Héctor (2009). Contrasting Role of Octopamine in Appetitive and Aversive Learning in the Crab Chasmagnathus. *PLoS ONE.* 4(7): e6223.

Kaczer, Laura; Klappenbach, Martín; and Maldonado, Héctor (2011). Dissecting mechanisms of reconsolidation: octopamine reveals differences between appetitive and aversive memories in the crab Chasmagnathus. *European Journal of Neuroscience.* 34(7): 1170-1178.

Kádková, A.; Synytsya, V.; Krusek, J.; Zímová, L.; and Vlachová, V. (2017). Molecular basis of TRPA1 regulation in nociceptive neurons. A review. *Physiological Research.* 66: 425-439.

Karin-D'Arcy, M. Rosalyn (2005). The modern role of Morgan's canon in comparative psychology. *International Journal of Comparative Psychology.* 18(3).

Kawai, Nobuyuki; Kono, Reiko; and Sugimoto, Sanae (2004). Avoidance learning in the crayfish (Procambarus clarkii) depends on the predatory imminence of the unconditioned stimulus: a behavior systems approach to learning in invertebrates. *Behavioural Brain Research.* 150(1-2): 229-237.

Klappenbach, Martín; Maldonado, Héctor; Locatelli, Fernando; and Kaczer, Laura (2012). Opposite actions of dopamine on aversive and appetitive memories in the crab. *Learning & Memory.* 19(2): 73-83.

Kotsyuba, E. P.; Dyuizen, I. V.; and Lamash, N. E. (2010). Stress-induced changes in the nitric oxide system of shore crabs living under different ecological conditions. *Russian Journal of Marine Biology.* 36(3): 201-208.

Kozma, Mihika T.; Ngo-Vu, Hanh; Wong, Yuen Yan; Shukla, Neal S.; Pawar, Shrikant D.; Senatore, Adriano; Schmidt, Manfred; and Derby, Charles D. (2020). Comparison of transcriptomes from two chemosensory organs in four decapod crustaceans reveals hundreds of candidate chemoreceptor proteins. *PLoS ONE.* 15(3): e0230266.

Kozma, Mihika T.; Schmidt, Manfred; Ngo-Vu, Hanh; Sparks, Shea D.; Senatore, Adriano; and Derby, Charles D. (2018). Chemoreceptor proteins in the Caribbean spiny lobster, Panulirus argus: Expression of ionotropic receptors, gustatory receptors, and TRP channels in two chemosensory organs and brain. *PLoS ONE.* 13(9): e0203935.

Krieger, Jakob; Sandeman, Renate E.; Sandeman, David C.; Hansson, Bill S.; and Harzsch, Steffen (2010). Brain architecture of the largest living land arthropod, the giant robber crab Birgus latro (Crustacea, Anomura, Coenobitidae): Evidence for a prominent central olfactory pathway? *Frontiers in Zoology.* 7(1): 25.

LeDoux, Joseph (2020). *The Deep History of Ourselves: The Four-Billion-Year Story of How We Got Conscious Brains.* Penguin Books.

Lindahl, B. I. B. (1997). Consciousness and Biological Evolution. *Journal of Theoretical Biology.* 187: 613-629.

Low, P.; Panksepp, J.; Reiss, D.; Edelman, D.; Van Swinderen, B.; and Koch, C. (2012). *The Cambridge declaration on consciousness.* 375-397.

Lozada, Mariana; Romano, Arturo; and Maldonado, Hector (1988). Effect of morphine and naloxone on a defensive response of the crab Chasmagnathus granulatus. *Pharmacology Biochemistry & Behavior*. 30(3): 635-640.

Machon, Julia; Krieger, Jakob; Meth, Rebecca; Zbinden, Magali; Ravaux, Juliette; Montagne, Nicolas; Chertemps, Thomas; and Harzsch, Steffen (2019). Neuroanatomy of a hydrothermal vent shrimp provides insights into the evolution of crustacean integrative brain centers. *eLife*. 8: e47550.

Magee, Barry; and Elwood, Robert W. (2013). Shock avoidance by discrimination learning in the shore crab (Carcinus maenas) is consistent with a key criterion for pain. *Journal of Experimental Biology*. 216(3): 353-358.

Magee, Barry; and Elwood, Robert W. (2016a). Trade-offs between predator avoidance and electric shock avoidance in hermit crabs demonstrate a non-reflexive response to noxious stimuli consistent with prediction of pain. *Behavioural Processes*. 130: 31-35.

Magee, Barry; and Elwood, Robert W. (2016b). No discrimination shock avoidance with sequential presentation of stimuli but shore crabs still reduce shock exposure. *Biology Open*. 5(7): 883-888.

Maldonado, Hector; Romano, Arturo; and Lozada, Mariana (1989). Opioid action on response level to a danger stimulus in the crab (Chasmagnathus granulatus). *Behavioral Neuroscience*. 103(5): 1139.

Mallatt, Jon; and Feinberg, Todd E. (2021). Multiple Routes to Animal Consciousness: Constrained Multiple Realizability Rather Than Modest Identity Theory. *Frontiers in Psychology*. 3895.

Maza, Francisco Javier; Sztarker, Julieta; Shkedy, Avishag; Peszano, Valeria Natacha; Locatelli, Fernando Federico; and Delorenzi, Alejandro (2016). Context-dependent memory traces in the crab's mushroom bodies: Functional support for a common origin of high-order memory centers. *Proceedings of the National Academy of Sciences*. 113(49): E7957-E7965.

McCambridge, Claire; Dick, Jaimie T. A.; and Elwood, Robert W. (2016). Effects of autotomy compared to manual declawing on contests between males for females in the edible crab cancer pagurus: implications for fishery practice and animal welfare. *Journal of Shellfish Research*. 35(4): 1037-1044.

Mikhalevich, Irina; and Powell, Russell (2020). Minds without spines: Evolutionarily inclusive animal ethics. *Animal Sentience*. 29(1).

Navratilova, Edita; Xie, Jennifer Yanhua; King, Tamara; and Porreca, Frank (2013). Evaluation of reward from pain relief. *Annals of the New York Academy of Sciences*. 1282(1): 1-11.

Orlosk, Jaimie L.; Walker, Jenna M.; Morrison, Ariel L.; and Atema, Jelle (2011). Conditioning the crab Carcinus maenas against instinctive light avoidance. *Marine & Freshwater Behaviour & Physiology*. 44(6): 375-381.

Panksepp, Jaak (2005). Affective consciousness: Core emotional feelings in animals and humans. *Consciousness and Cognition*. 14(1): 30-80.

Passantino, Annamaria; Elwood, Robert W.; and Coluccio, Paolo (2021). Why protect decapod crustaceans used as models in biomedical research and in ecotoxicology? Ethical and legislative considerations. *Animals*. 11(1): 73.

Paul, Elizabeth S.; Sher, Shlomi; Tamietto, Marco; Winkielman, Piotr; and Mendl, Michael T. (2020). Towards a comparative science of emotion: affect and consciousness in humans and animals. *Neuroscience & Biobehavioral Reviews*. 108, 749-770.

Perrot-Minnot, Marie-Jeanne; Banchetry, Loan; and Cézilly, Frank (2017). Anxiety-like behaviour increases safety from fish predation in an amphipod crustacea. *Royal Society Open Science*. 4(12): 171558.

Punzo, Fred (1983). Localization of brain function and neurochemical correlates of learning in the mud crab, Eurypanopeus depressus (Decapoda). *Comparative Biochemistry & Physiology Part A: Physiology*. 75(2): 299-305.

Puri, Sakshi; and Faulkes, Zen (2010). Do decapod crustaceans have nociceptors for extreme pH? *PLoS ONE*. 5(4): e10244. 4

Puri, Sakshi; and Faulkes, Zen (2015). Can crayfish take the heat? Procambarus clarkii show nociceptive behaviour to high temperature stimuli, but not low temperature or chemical stimuli. *Biology Open*. 4(4): 441-448.

Putnam, Hilary (1967). Psychological predicates. *Art Mind Religion*. 1: 37–48.

Rial, R. V.; Nicolau, M. C.; Gamundí, A.; Akaârir, M.; Garau, C.; and Esteban, S. (2007). The Evolution of Consciousness in Animals. In: *Consciousness Transitions* (Liljenström, H. & Århem, P. (Eds)), Amsterdam: 45-76.

Riemensperger, Thomas; Völler, Thomas; Stock, Patrick; Buchner, Erich; and Fiala, André (2005). Punishment prediction by dopaminergic neurons in Drosophila. *Current Biology*. 15(21): 1953-1960.

Romano, Arturo; Lozada, Mariana; and Maldonado, Hector (1990). Effect of naloxone pretreatment on habituation in the crab Chasmagnathus granulatus. *Behavioral & Neural Biology*. 53(1): 113-122.

Romano, Arturo; Lozada, Mariana; and Maldonado, Hector (1991). Nonhabituation processes affect stimulus specificity of response habituation in the crab Chasmagnathus granulatus. *Behavioral Neuroscience*. 105(4): 542-552.

Rose, James D. (2002). The neurobehavioral nature of fishes and the question of awareness and pain. *Reviews in Fisheries Science*. 10(1): 1-38.

Ross, D. M. (1965). The behavior of sessile coelenterates in relation to some conditioning experiments. *Animal Behaviour Supplement*. 1: 43-55.

Sandeman, David C.; Kenning, Matthes; and Harzsch, Steffen (2014). Adaptive trends in malacostracan brain form and function related to behavior. In *Crustacean nervous system and their control of behaviour* (Charles Derby and Martin Thiel (Eds.)). Oxford University Press: 11-48.

Sandeman, David; Beltz, Barbara; and Sandeman, Renate (1995). Crayfish brain interneurons that converge with serotonin giant cells in accessory lobe glomeruli. *Journal of Comparative Neurology*. 352(2): 263-279.

Sayre, Marcel E.; and Strausfeld, Nicholas J. (2019). Mushroom bodies in crustaceans: Insect-like organization in the caridid shrimp Lebbeus groenlandicus. *Journal of Comparative Neurology*. 527(14): 2371-2387.

Scott, Kevin; Harsanyi, Petra; and Lyndon, Alastair R. (2018). Understanding the effects of electromagnetic field emissions from Marine Renewable Energy Devices (MREDs) on the commercially important edible crab, Cancer pagurus (L.). *Marine Pollution Bulletin*. 131: 580-588.

Seth, Anil (2022). *Being You*. Faber & Faber, London, UK.

Sherwin, Christopher M. (2001). Can invertebrates suffer? Or, how robust is argument-by-analogy? *Animal Welfare*. 10(1): S103-S118.

Skora, Lina I.; Yeomans, M. R.; Crombag, Hans S.; and Scott, Ryan B. (2021). Evidence that instrumental conditioning requires conscious awareness in humans. *Cognition*. 208: 104546.

Skoulakis, Efthimios M. C.; Kalderon, Daniel; and Davis, Ronald L. (1993). Preferential expression in mushroom bodies of the catalytic subunit of protein kinase A and its role in learning and memory. *Neuron*. 11(2): 197-208.

Smith, Ewan S. J.; and Lewin, Gary R. (2009). Nociceptors: A phylogenetic view. *Journal of Comparative Physiology A*. 195(12): 1089-1106.

Smith, Jane A.; and Boyd, Kenneth M. (Eds.) (1991). *Lives in the balance: The ethics of using animals in biomedical research*. Oxford University Press.

Sneddon, Lynne U. (2015). Pain in aquatic animals. *Journal of Experimental Biology*. 218(7): 967-976.

Sneddon, Lynne U.; Braithwaite, Victoria A.; and Gentle, Michael J. (2003). Do fishes have nociceptors? Evidence for the evolution of a vertebrate sensory system. *Proceedings of the Royal Society of London B: Biological Sciences*. 270(1520): 1115-1121.

Sneddon, Lynne U.; Elwood, Robert W.; Adamo, Shelley A.; and Leach, Matthew C. (2014). Defining and assessing animal pain. *Animal Behaviour*. 97: 201-212.

Solms, Mark (2021). *The Hidden Spring: A Journey to the Source of Consciousness*. WW Norton & Company.

Stevens, E. D.; Arlinghaus, R.; Browman, H. I.; Cooke, S. J.; Cowx, I. G.; Diggles, B. K. et al. (2016). Stress is not pain. Comment on Elwood and Adams (2015) 'Electric shock causes physiological stress responses in shore crabs, consistent with prediction of pain'. *Biology Letters*. 12(4): 20151006.

Strausfeld, Nicholas James; Wolff, Gabriella Hanna; and Sayre, Marcel Ethan (2020). Mushroom body evolution demonstrates homology and divergence across Pancrustacea. *eLife*. 9: e52411.

Taylor, J.; Vinatea, L.; Ozorio, R.; Schuweitzer, R.; and Andreatta, E. R. (2004). Minimizing the effects of stress during eyestalk ablation of Litopenaeus vannamei females with topical anesthetic and a coagulating agent. *Aquaculture*. 233(1-4): 173-179.

Tomina, Yusuke; and Takahata, Masakazu (2010). A behavioral analysis of force-controlled operant tasks in American lobster. *Physiology & Behavior*. 101(1): 106-116.

Tomsic, Daniel; and Maldonado, Hector (1990). Central effect of morphine pretreatment on short- and long-term habituation to a danger stimulus in the crab Chasmagnathus. *Pharmacology Biochemistry & Behavior*. 36(4): 787-793.

Tomsic, Daniel; Maldonado, Hector; and Rakitin, Ana (1991). Morphine and GABA: Effects on perception, escape response and long-term habituation to a danger stimulus in the crab Chasmagnathus. *Brain Research Bulletin*. 26(5): 699-706.

Tomsic, Daniel; Massoni, V.; and Maldonado, Hector (1993). Habituation to a danger stimulus in two semiterrestrial crabs: ontogenic, ecological and opioid modulation correlates. *Journal of Comparative Physiology A*. 173(5): 621-633.

Tracey Jr, W. Daniel; Wilson, Rachel I.; Laurent, Gilles; and Benzer, Seymour (2003). painless, a Drosophila gene essential for nociception. *Cell*. 113(2): 261-273.

Travers, Eoin; Frith, Chris D.; and Shea, Nicholas (2018). Learning rapidly about the relevance of visual cues requires conscious awareness. *Quarterly Journal of Experimental Psychology*. 71(8): 1698-1713.

Valeggia, Claudia; Fernandez-Duque, Eduardo; and Maldonado, Hector (1989). Danger stimulus-induced analgesia in the crab Chasmagnathus granulatus. *Brain Research*. 481(2): 304-308.

Varner, Gary E. (2012). *Personhood, ethics, and animal cognition: Situating animals in Hare's two-level utilitarianism*. Oxford University Press.

Wachowiak, M.; Diebel. C. E.; and Ache, B. W. (1996). <u>Functional organization of olfactory processing in the accessory lobe of the spiny lobster</u>. *Journal of Comparative Physiology A*. 178(2): 211-226.

Walters, Edgar T. (2018). <u>Nociceptive biology of molluscs and arthropods: Evolutionary clues about functions and mechanisms potentially related to pain</u>. *Frontiers in Physiology*. 9: 1049.

Wolfe, Joanna M.; Breinholt, Jesse W.; Crandall, Keith A.; Lemmon, Alan R.; Lemmon, Emily Moriarty; Timm, Laura E.; Siddall, Mark E.; and Bracken-Grissom, Heather D. (2019). <u>A phylogenomic framework, evolutionary timeline and genomic resources for comparative studies of decapod crustaceans</u>. *Proceedings of the Royal Society of London B: Biological Sciences*. 286(1901): 20190079.

Call for Commentary: *Animal Sentience* publishes <u>Open Peer Commentary</u> on all accepted target articles. Target articles are peer-reviewed. Commentary articles are editorially reviewed. There are submitted commentaries as well as invited commentaries. Commentary articles appear as soon as they have been reviewed, revised and accepted. Target article authors may respond to their commentaries individually or in a joint response to multiple commentaries.

-- NOTICE --

The Edge of Sentience:

Risk and Precaution in Humans, Other Animals, and AI

Jonathan Birch
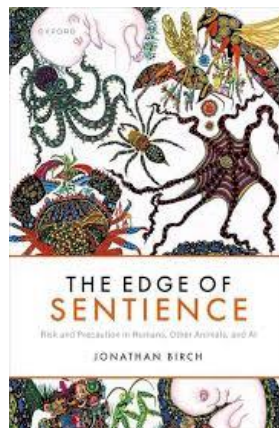
Open Access Online PDF

Abstract: Can octopuses feel pain and pleasure? What about crabs, shrimps, insects, or spiders? How do we tell whether a person unresponsive after severe brain injury might be suffering? When does a fetus in the womb start to have conscious experiences? Could there even be rudimentary feelings in miniature models of the human brain, grown from human stem cells? And what about AI? These are questions about the edge of sentience, and they are subject to enormous, disorienting uncertainty. The stakes are immense, and neglecting the risks can have terrible costs. We need to err on the side of caution, yet it's often far from clear what 'erring on the side of caution' should mean in practice. When are we going too far? When are we not doing enough? *The Edge of Sentience* presents a comprehensive precautionary framework designed to help us reach ethically sound, evidence-based decisions despite our uncertainty.

Collection: Oxford Scholarship Online