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The Experience of Pain in Decapod Crustaceans from a Neurobehavioral Perspective: A Challenge for the Invertebrate Welfare Theory

Ощущение боли у десятиногих ракообразных с нейроповеденческой точки зрения
Вызов для теории благополучия беспозвоночных

Абстракт

Лишь немногие потребители осознают, что так называемые морепродукты, употребляемые человеком в пищу, поступают из коммерческой аквакультуры, где омары, крабы и креветки содержатся в жестоких условиях промышленного разведения. В то же время чувствительность и нейроповедение ракообразных продолжают представлять вызов для нейробиологии, сравнительной когнитивной науки, а также этической рефлексии. Знания о чувствительности десятиногих, эксплуатируемых в пищевой и развлекательной индустриях (зоомагазины, рыболовные магазины, аквакультуры) особенно важны для современной этики животных и биополитики в контексте осуждения жестоких практик разведения, выработки рекомендаций по правовой защите десятиногих и обеспечения стандартов их благополучия. В связи с этим в статье рассматриваются основы феноме-

The Experience of Pain in Decapod Crustaceans from a Neurobehavioral Perspective: A Challenge for the Invertebrate Welfare Theory

Abstract

Few consumers are aware that the so-called seafood comes from commercial aquaculture, where lobsters, crabs or shrimps and prawns are kept in cruel conditions of crustaceans factory farming. At the same time, the sentience and neurobehaviour of crustaceans continue to pose challenges for neurobiology, comparative cognition, and ethical reflection. Knowledge about the sentience of decapods, exploited in the food and entertainment industries (pet shops, fishkeeping hobbies, aquafarming), is particularly important for contemporary animal ethics and biopolitics in the context of condemning cruel breeding practices, proposing legal protection of decapods and enforcing welfare standards. For this reason, the article presents the foundation of the sentience phenomenon, which is the ability to experience pain in selected species of crabs, crayfish and prawns. The discussed cases of pain perception seem to be representative of на чувствительности, а именно способность к ощущению боли у отдельных видов крабов, раков и креветок. Обсуждаемые случаи восприятия боли представляются репрезентативными для всей группы разводимых десятиногих. Выводы, основанные на результатах экспериментов, указывают на необходимость включения всех десятиногих в международные правовые акты, ограничивающие жестокие формы их разведения, транспортировки и убоя.

Ключевые слова: ноцицепция, восприятие боли, чувствительность десятиногих, благополучие десятиногих, чувствительность ракообразных, благополучие ракообразных, промышленное разведение ракообразных

the entire group of farmed decapods. The conclusions resulting from the experiments indicate all decapods should be included as soon as possible in international legal acts to limit brutal forms of breeding, transporting, and slaughtering them.

Keywords: nociception, pain perception, decapoda sentience, decapoda welfare, crustaceans sentience, crustaceans welfare, crustaceans factory farming

Introduction

Plans to further develop industrial farming of insects, crustaceans or cephalopods are promoted in the media as allegedly cost-effective, sustainable, and ethical forms of obtaining meat protein which are not associated with suffering of mammals or birds and are environmentally friendly. Unfortunately, as the researchers write, "The farming of decapod crustaceans is a key economic driver in many countries, with production reaching around 9.4 million tonnes (USD 69.3 billion) in 2018. These efforts are currently dominated by the farming of Pacific whiteleg shrimp, *Penaeus vannamei*, which translates into approximately 167 billion farmed *P. vannamei* being harvested annually. Further production growth is expected in the future and hence the need for more research into its health and welfare is required."[1] Documents are published that either suggest a pressing need for modification of the international law, such as the New York Declaration on Animal Consciousness of April 2024, or ready-made proposals for the legal protection of invertebrates, addressed to a parliament in a relevant country, such as the *Review of the Evidence of Sentience in Cephalopod Molluscs and Decapod Crustaceans*.[2] Unfor-

[1] Amaya Albalat et al., "Welfare in Farmed Decapod Crustaceans, with Particular Reference to Penaeus vannamei," *Frontiers in Marine Science* 9 (2022): 886024, https://doi.org/10.3389/fmars.2022.886024.

[2] Jonathan Birch et al., *Review of the Evidence of Sentience in Cephalopod Molluscs and Decapod Crustaceans* (London: London School of Economics, 2021).

tunately, the real legal protection of the welfare of at least cephalopods and selected decapods still remains a concept that has not been implemented on the international level. The only sign of changes is the amendment of the UK Animal Welfare (Sentience) Act 2022, following the intensive research work of Jonathan Birch and his team, which resulted in a clear recommendation: all cephalopods and decapods should be covered by welfare legislation.[3] The UK government accepted this recommendation from the Birch's team and began the amendment procedure of a new bill. Due to the extraordinarily slow progress in implementation of legal changes limiting cruel forms of animal exploitation even on a scale of a given country, we should continue to emphasize that crustaceans are also capable of suffering, to stimulate the initiation of at least local work on welfare criteria for these animals. While the perception and sentience of cephalopods are the subjects of an increasing number of scientific papers, decapods still remain on the margin of cognitive and ethical reflection. For this reason, an attempt was made in this text to bring together a selection of representative experiments and findings from successive studies on pain in crabs, crayfish, and prawns. Their ability to generate pain experiences can be reliably identified by recording the apparent effect of a noxious stimulus on their neurological or endocrine system, or on their motivation to change their behavioural pattern. This article is divided into four parts, according to types of evidence, and focusing on neurological and behavioural arguments in crabs, crayfish, and prawns, successively, with endocrine evidence of pain omitted. Since pain responses in vertebrates are an argument proving that treatment of, for example, mammals, compromises their welfare, it seems that the argument of analogy in the pain perception in crustaceans should be used to inspire thinking about the welfare of, at least, decapods.

Nociception and Nociceptors

When reviewing specialized literature on the subject, one can distinguish six criteria that indicate the possibility of experiencing pain in non-human animal species:

1. At the neurological level, this criterion is a centralized or centralizing nervous system (not peripheral processing of nervous signals) and the presence of specialized receptors and nociceptive pathways.[4]

[3] Jonathan Birch, *The Edge of Sentience* (Oxford: Oxford University Press, 2024), 240–242.

[4] Barbara S. Beltz and David C. Sandeman, "Regulation of Life-Long Neurogenesis in the Decapod Crustacean Brain," *Arthropod Structure & Development* 32, no. 1 (2003): 39–60.

2. The presence of opioid receptors and a reduction in the aversive reaction to noxious stimuli after the use of anaesthetics – methods to induce analgesia and anaesthesia have been used in over 70 species of crustaceans.[5]

3. Physiological and endocrine changes under the influence of harmful stimuli, for instance, electric shock or being chased by a predator, caused in crabs a higher level of lactate in the hemolymph (a biochemical indicator of stress) compared to crabs not subjected to stressors. In Atlantic ghost crabs (*Ocypode quadrata*), glucose and lactate increase when the animals are exposed to several types of stress, including alterations in temperature, salinity, or being chased by humans. As the effect of chasing stress, "the levels of lactate in the hemolymph of stressed crabs were six times higher than those of control crabs immediately after chasing and decreased progressively during recovery."[6] A study of stress or anxiety in crayfish showed increased levels of serotonin, an indicator of changes in threat processing, when the crayfish were about to enter a brightly lit arm of the maze (we will return to this study).[7]

4. At the cognitive level, the criterion is – among others – the ability to learn avoidance and the broader ability to generate affective-cognitive experiences, with particular emphasis on the so-called anxiety-like emotion: "Crayfish have a sense of defeat/victory and can display either an emotion homologous to anxiety or an exaggerated aggression, the latter of which has similar features as human psychological harassment."[8]

5. Having cognitive abilities, for instance, motivational trade-offs between predator avoidance and avoidance of electric shock, indicating a higher, and therefore non-reflexive, response to noxious stimuli, demonstrating the prediction of pain in crabs (flexible modulation of behaviour according to the context).[9]

[5] Guiomar Rotllant et al., "Methods to Induce Analgesia and Anesthesia in Crustaceans: A Supportive Decision Tool," *Biology* 12, no. 3 (2023): 387, https://doi.org/10.3390/biology12030387.

[6] Éverton Lopes Vogt et al., "The Impact of Chasing Stress on the Metabolism of the Atlantic Ghost Crab *Ocypode quadrata* (Fabricius, 1787)," *The Journal of Experimental Zoology A: Ecological and Integrative Physiology* 339, no. 9 (2023): 887–897; Mauricio Díaz-Jaramillo et al., "Biochemical Responses and Physiological Status in the Crab *Hemigrapsus crenulatus* (Crustacea, Varunidae) from High Anthropogenically-Impacted Estuary (Lenga, South-Central Chile)," *Marine Environmental Research* 83 (2013): 73–81.

[7] Pascal Fossat et al., "Anxiety-Like Behavior in Crayfish is Controlled by Serotonin," *Science* 344 (2014): 1293–1297, 6189, https://doi.org/10.1126/science.1248811.

[8] Julien Bacqué-Cazenave et al. "Social Harassment Induces Anxiety-Like Behaviour in Crayfish," *Scientific Reports* 7 (2017): 4, 39935, https://doi.org/10.1038/srep3993; Pascal Fossat et al., "Measuring Anxiety-like Behavior in Crayfish by Using a Sub Aquatic Dark-light Plus Maze," *Bio-protocol* 5, no. 3 (2015): 1–9, https://doi.org/10.21769/BioProtoc.1396.

[9] Barry Magee and Robert W. Elwood, "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 (2016): 31–35.

6. At the behavioural level, the criteria are motor and locomotion reactions such as grooming (limping, rubbing, holding a painful part of the body), protective (defence against stimulation, autotomy) or escape behaviours.[10]

Some, perhaps even all, of the criteria listed above arise when examining pain in decapods. The subphylum Crustacea is a highly diverse group of arthropods, characterized by a variety of lifestyles, for example, pelagic, benthic, terrestrial, parasitic, or sedentary, which implies a multitude of distinct behavioural patterns. These behaviours, in turn, represent a variety of adaptations, specific for particular taxa, but controlled by cognitive (high-order memory centres[11]), sensory (photoreceptors; mechanosensory, chemosensory, and olfactory receptors; statocysts and proprioceptors[12]) and the central nervous system, the basic organization of which remains the same within Crustacea.[13] Scientific evidence from the last two decades indicates that decapod crustaceans (crabs, lobsters, crayfish, shrimp, and prawns) can experience pain, defined as a "complex constellation of unpleasant sensory, emotional and cognitive experiences provoked by real or perceived tissue damage and manifested by certain autonomic, psychological, and behavioural reactions."[14] It should be emphasized here that pain is understood as a perception unit, generated by specialized neurosensory pathways. This unit is not a simple nociceptive sensation, triggering an equally simple nocifensive reflex, but a complex experience resulting in an aversive cognitive-affective state and a longer sequence of animal movements. A lower nociceptive ability is "the ability to perceive a noxious stimulus and react in a reflexive manner and occurs across a wide range of taxa in nonvertebrates,"[15]

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[10] Robert W. Elwood et al., "Pain and Stress in Crustaceans?," *Applied Animal Behaviour Science* 118, nos. 3–4 (2009): 128–136.

[11] Francisco J. Maza et al., "A Crabs' High-Order Brain Center Resolved as a Mushroom Body-Like Structure," *The Journal of Comparative Neurology* 529, no. 3 (2021): 501–523; Francisco J. Maza et al., "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, no. 49 (2016): e7957–e7965, https://doi.org/10.1073/pnas.1612418113.

[12] María G. Lepore et al., "Neural Organization of First Optic Neuropils in the Littoral Crab Hemigrapsus oregonensis and the Semiterrestrial Species Chasmagnathus granulatus," *The Journal of Comparative Neurology* 513, no. 2 (2022): 129–150.

[13] Jeremy M. Sullivan and Jens Herberholz, "Structure of the Nervous System," in *Functional Morphology and Diversity*, eds. Les Watling and Martin Thiel (Oxford: Oxford University Press, 2013), 451.

[14] John D. Loeser et al. (eds.), *Management of Pain*, 3rd ed. (Philadelphia: Lippincott Williams and Wilkins, 2003), 73. Earlier definitions of pain omitted the affective aspect, for example, according to Zimmermann, pain is "an aversive sensory experience caused by actual or potential injury that elicits protective motor and vegetative reactions, results in learned avoidance and may modify species specific behaviours, including social behaviour" – Manfred Zimmermann, "Physiological Mechanisms of Pain and Its Treatment," *Klinische Anästhesiologie und Intensivtherapie* 32 (1986): 1.

[15] Stuart Barr et al., "Nociception or Pain in a Decapod Crustacean?," *Animal Behaviour* 75, no. 3 (2008): 745, https://doi.org/10.1016/j.anbehav.2007.07.004.

and it was repeatedly observed in selected molluscs and annelids.[16] Higher pain perception is the ability to associate aversive sensations and feelings, being a sensory and mental experience of evaluating and interpreting pain, together with perceptually conscious learning to avoid it and long-term storage of this experience as a memory trace.[17] The experience of pain understood as a complex, polymodal percept or association of an affective-cognitive nature is a concept popularized, for example, by Donald Broom: "[Pain is] an aversive sensation and feeling associated with actual or potential tissue damage."[18] The ability of an animal's cognitive system to experience pain can be determined by recording the effects of a noxious stimulus at three levels: (1) neurobiological, as the presence and activity of cells called nociceptors; (2) endocrine, or physiological, by determining, for example, the secretion of stress hormones into the bloodstream; and (3) behavioural, at which the animal's behaviours are interpreted.

Information on the presence of nociceptors (receptors that preferentially identify and inform about the effects of noxious stimuli[19]) in different groups of crustaceans is still relatively scarce. Although the presence of nociceptors alone does not mean that decapods experience pain, nociceptive fields are a prerequisite for the activation of a mechanism called nociception. The process of nociception consists of "the neural processes of encoding and processing noxious stimuli"[20] and refers to the mechanism of recording stimuli that are potentially harmful to the animal "or that may compromise their integrity."[21] When a stimulus excites the action potential of the nociceptors, the processed neural signal – at the level of the spinal cord – activates the protective nocifensive reflex, while further processing of the impulse in the decapod's central nervous system forms the full experience

[16] Riley T. Paulsen and Brian D. Burrell, "Comparative Studies of Endocannabinoid Modulation of Pain," *Philosophical Transactions of the Royal Society B* 374 (2019): 20190279, https://doi.org/10.1098/rstb.2019.0279.

[17] Donald M. Broom, "Welfare, Stress and the Evolution of Feelings," *Advances in the Study of Behavior* 27 (1998): 371–403.

[18] Donald M. Broom, "Evolution of Pain," *Royal Society of Medicine International Congress and Symposium Series* 246 (2001): 17–25.

[19] Nociceptors are "specialized peripheral sensory neurons" whose function is to warn the animal about "potentially damaging stimuli by detecting extremes in temperature and pressure and injury-related chemicals, and transducing these stimuli into long-ranging electrical signals that are relayed to higher brain centers. The activation of functionally distinct cutaneous nociceptor populations and the processing of information they convey provide a rich diversity of pain qualities" – Adrienne E. Dubin and Ardem Patapoutian, "Nociceptors: The Sensors of the Pain Pathway," *Journal of Clinical Investigation* 120, no. 11 (2010): 3760.

[20] John D. Loeser and Rolf-Detlef Treede, "The Kyoto Protocol of IASP Basic Pain Terminology," *Pain* 137 (2008): 473.

[21] Jean-Marie Besson and Athmane Chaouch, "Peripheral and Spinal Mechanisms of Nociception," *Physiological Reviews* 67, no. 1 (1987): 67.

of pain. "Thus, nociception provides immediate action whereas [experience of] pain enables long-term protection."[22] Nociceptive pathways are connected to areas of procedural learning to avoid potentially harmful stimuli, and this protects a crab, crayfish or prawn against further possible injuries in the future. The adaptive significance of nociception is clear and relies on effective avoidance of physical injury to increase the crustacean's chances of survival.

A minimum and necessary, though probably insufficient, condition for pain perception (the ability to process stimuli into experiences, assessing the harmfulness of these stimuli, resulting in the observed behavioural pattern, for instance, grooming, defence, or escape) is the presence of nociceptors.[23] These receptors are responsible for detecting changes or stimulation that can be harmful to the decapod. When identifying mechanical, chemical or thermal changes in the environment (or animal's own body), nociceptive cells change their potential from resting to functional and trigger afferent impulsation to the central nervous system. The signal processed in subsequent areas of the nociceptive pathway – at the level of the centralized nervous system – informs the crustacean of the injury characteristics (mechanical, chemical) and evaluates the injury severity in the form of a pain experience. Nociceptors are present in all vertebrates, but the problem is that studies on a nociceptive ability and nociceptors themselves have previously focused primarily on mammals, less frequently on other vertebrates, and definitely too rarely on invertebrates. Below I will only outline a few selected representative experiments that should be widely used when discussing the issue of welfare, suffering, and pain in decapods.

Crabs and Electrophysiological Evidence of Nociceptors

To resolve doubts as to whether a given animal species experiences pain, it must be demonstrated that the said species meets the aforementioned minimum criterion for generating such an experience, namely, that it has nociceptors. Only then can it be credibly argued that a particular type of stimulus has (for a certain group of animals) a negative, harmful value and further, ethical and political consequences must be drawn from this knowledge. The first step, therefore, involves finding a method for obtaining reliable evidence that animals have specialized nociceptive receptors.

[22] Robert W. Elwood, "Evidence for Pain in Decapod Crustaceans," *Animal Welfare* 21, no. 1 (2012): 24, https://doi.org/10.7120/096272812X13353700593365.

[23] Ewan S. J. Smith and Gary R. Lewin, "Nociceptors: A Phylogenetic View," *Journal of Comparative Physiology A* 195 (2009): 1089–1106.

One of the effective methods for identifying these receptors is to study the electrophysiological activity of the brain under potentially noxious external stimulation. In this case, the assumption is the neuroanatomical condition of having a centralized nervous centre, which is fulfilled by decapods, and crabs in particular.

To be more precise, "the crustacean brain consists of three main regions, the protocerebrum, deutocerebrum, and tritocerebrum, each associated with a specific sensory structure of the head," and with the circumesophageal, abdominal, and thoracic ganglia that "innervate the chelae, walking legs, thoracic musculature, and heart."[24] Given the centralization and functional complexity of the crab nervous system, the hypothesis that crabs experience pain becomes highly plausible. Furthermore, as decapods are used in laboratory research and aquaculture farming for consumption, the high likelihood of crabs experiencing pain has far-reaching ethical implications for the exploitation and welfare of these crustaceans. This hypothesis was verified by, among others, Eleftherios Kasiouras and his team – due to its well-studied physiology, a shore crab species (*Carcinus maenas*) was chosen as a decapod model for *in vivo* analyses. Kasiouras's team formulated two hypotheses. Firstly, if nociceptors are present in selected areas of the shore crab's body, stimulation of these areas with unpleasant mechanical and chemical stimuli would reveal visible, measurable nociceptive pathway activity, electrophysiological activity in the central nervous system, and characteristic behavioural responses. Secondly, if the electrophysiological recordings from the brain and periaqueductal ganglion under mechanical and chemical stimuli differ, this would be evidence that the nociceptor fields in the irritated body parts are specialized to detect different types of injury, that is, have different modalities

During empirical *in vivo* experiments, the team subjected selected 32 body parts of crabs to stimulation with so-called von Frey hairs (mechanical stimuli, tactile measurement of mechanosensitivity[25]) and with acetic acid at different concentrations (chemical stimuli – standard vertebrate pain test[26]). During the mechanical and chemical stimulations performed, the animals' behaviour was recorded as behavioural expression and, at the same time, the electrophysiological activity of the brain ganglion and circumesophageal connective ganglion of the crabs was measured with electrodes. Stimulated body parts included "the eyes, the anten-

[24] Sullivan and Herberholz, "Structure of the Nervous System," 457, 462; Michael S. Laverack, "The Numbers of Neurones in Decapod Crustacea," *Journal of Crustacean Biology* 8, no. 1 (1988): 1–11.

[25] Matt Carter and Jennifer Shieh, "Animal Behavior," in *Guide to Research Techniques in Neuroscience*, 2nd ed. (Academic Press, 2015): 39–71.

[26] Lynne U. Sneddon, "Evolution of Nociception in Vertebrates: Comparative Analysis of Lower Vertebrates," *Brain Res. Rev*. 46, no. 2, (2004): 123–130; Craig W. Stevens, "Alternatives to the Use of Mammals for Pain Research," *Life Sciences* 50, no. 13, (1999): 901–912; Michael J. Gentle, "Pain in Birds," *Animal Welfare* 1, no. 4, (1992): 235–247.

nae, antennules, soft tissue between the claws, and the soft tissues at the joints of the pereiopods."[27]

The conclusions of the measurements confirmed the assumed hypotheses. It was found that stimulation of the eye and feelers with acetic acid triggered a strong neurological response, recorded by electrodes in the brain ganglion. Additionally, chemical and mechanical stimulation of soft tissues in the legs and between the pincers induced a neurological response in the circumesophageal ganglion. At the behavioural level, the crabs responded with protective and grooming behaviours, that is, reflexes of rubbing body parts irritated by mechanical and chemical stimuli. As has been demonstrated in other studies, conducted by Robert Elwood, under the influence of irritant chemical stimuli crabs also undertook escape behaviour from the site of painful stimulation.[28] In a subsequent experiment, Elwood's team tested the behavioural patterns of shore crabs as a result of exposure to irritant chemical stimuli – acetic acid and capsaicin – on crab eyes and mouthparts.[29] In subsequent experiments performed by Kasiouras's team, when acetic acid was applied on the mouthparts of shore crabs, similar or the same behavioural pattern of cleaning and rubbing of this body part by the animals was induced. The crabs reacted in the same way when acetic acid was injected into their limbs and when acid was applied in the antennae and antennule area. There was no significant ganglionic activity in response to mechanical (tactile) stimulus in the antennae and antennule areas, although there was intense ganglionic activity to chemical stimulation of the antennae, supporting the second hypothesis that crabs (and perhaps all decapods) have specialized nociceptor fields, or actually, complete specialized nociceptive mechanisms for recording and processing different types of noxious stimuli. Interestingly, the responses of neurological pathways to mechanical stimuli were shorter and more intense (higher amplitude), while chemical stimuli elicited a neuronal response of longer duration but lower amplitude of intensity when the acid concentration was equally low (1% acetic acid compared to 5%).[30] This seems to prove that different mechanical and chemical stimuli are encoded in a different way

[27] Eleftherios Kasiouras et al., "Putative Nociceptive Responses in a Decapod Crustacean: The Shore Crab (*Carcinus maenas*)." *Biology (Basel)* 13, no. 11 (2024): 851, https://doi.org/10.3390/biology13110851.

[28] Robert W. Elwood during his own experiments also observed protective motor reactions, which was presented in: Elwood, "Evidence for Pain," 23–27.

[29] Elwood observed the following crabs' behaviour under the influence of irritating substances: "Application of acetic acid had a marked effect on behaviour that included vigorous movement of mouth parts, scratching at the mouth with the claws and attempts to escape from the enclosure. Acetic acid also caused holding down of the acid-treated eye in the socket." Robert W. Elwood et al., "Aversive Responses by Shore Crabs to Acetic Acid but Not to Capsaicin," *Behavioural Processes* 140 (2017): 1, https://doi.org/10.1016/j.beproc.2017.03.022.

[30] Kasiouras et al., "Putative Nociceptive Responses in a Decapod Crustacean," 9.

in the central nervous system. Thus, pain perception (from nociceptive receptors, through nociceptive pathways up to the brain) of vertebrates and crabs is characterized by polymodality, similar to exteroceptive sensory perception.[31]

Escaping, grooming, cleaning, or protecting body parts are complex behavioural patterns that appear to be characteristic for the perception and experiencing of pain, just as the rapid withdrawal reflex, called the nocifensive reflex, characterizes simple nociception. The evaluation of the behavioural responses of shore crabs reinforces the neurological or electrophysiological argument that these animals generate pain sensations, and therefore experience pain. The observed behaviours and measured electrophysiological activity of the crabs' central nervous system clearly indicates the presence of nociceptors in crab's soft tissues and the experience of pain, as lower nociceptive ability would not motivate such complex neurobehavioural responses.

Additional arguments for crabs experiencing pain were provided by the following two highly ethically questionable experiments:

(a) Mariana Lozada and her team induced defensive behaviours in crabs of the species *Chasmagnathus granulatus* with electric shocks, indicating a pain experience.[32] The researchers then administered morphine to the crabs, which, in the right dose, presumably suppressed the pain, as the crabs – despite further electric shocks – stopped reacting with defensive behaviours.

(b) Mirjam Appel and Robert Elwood proved that *Pagurus bernhardus* crabs exhibit behavioural trade-offs and abandon more comfortable snail shells, choosing less comfortable shelters just to avoid painful stimuli.[33] The researchers applied electric shocks to the crab abdomen, and this resulted in grooming behaviours focused on the sore abdomen and a change in crab's preference – the animals chose the absence of pain while choosing shells of inferior quality, associating comfort with a painful experience.

Crayfish and Pain-Related Behaviours

The second – after the presence of nociceptors – key criteria for pain assessment are specific behavioural responses and sequences. It is assumed that the complex result from of avoidance reflex and then escape and defensive behaviours painful experi-

[31] Lynne U. Sneddon, "Comparative Physiology of Nociception and Pain," *Physiology* 33 (2018): 63–73.

[32] Mariana Lozada et al., "Effect of Morphine and Naloxone on a Defensive Response of the Crab *Chasmagnathus granulatus*," *Pharmacology Biochemistry and Behavior* 30, no. 3 (1988): 635–640.

[33] Mirjam Appel and Robert W. Elwood, "Motivational Trade-Offs and Potential Pain Experience in Hermit Crabs," *Applied Animal Behaviour Science* 119, nos. 1–2, (2009): 120–124.

ences, and thus prove that the taxon in question is capable of advanced pain perception. As cruel practices of cooking live lobsters, crabs, or crayfish are used in various parts of the world, successive teams of researchers have analyzed the potential presence of thermal nociceptors in the crayfish of the species *Procambarus clarkii*.

Sakshi Puri and Zen Faulkes exposed the animals to high and low temperature stimuli. As in the case of crabs, also in this case two soft tissue areas on the animal body, regions of crayfish pincers and antennae, were selected. During the experiment, they confirmed the hypothesis that crayfish – and perhaps also all decapods – have thermal nociceptors. Arguments that proved the forwarded hypothesis were the unambiguous behavioural patterns of the animals and the neurophysiological responses of the nervous system to spot exposure to high temperatures. *Procambarus clarkii* crayfish, when exposed to hot temperatures, immediately exhibited whole sequences of escape or defence behaviours, while the nocifensive reflex alone never appeared. More specifically, the researchers touched spots on soft tissues between the pincers and the antennae with a soldering iron heated to approximately 54 degrees Celsius. The behavioural response of the animals was immediate: "The behaviours of the crayfish when touched with high temperatures often included repeated tailflipping (an escape response) walking rapidly away from the soldering iron, grabbing the soldering iron with the non-touched claw. […] All crayfish responded to high temperature touches on the antenna by moving the touched antenna away from the soldering iron."[34] The neurophysiological response also leaves no doubts as to whether pain sensations were processed: "Neural activity to high temperature stimuli was significantly higher than control stimuli in both the low-baseline and the high baseline branches of the nerve."[35]

The experiment conducted by Puri and Faulkes was not the first to test the response of crayfish to the heat stimulus. Tests from previous decades had already clearly showed that crayfish strongly avoid high temperatures, while they do not avoid low temperatures.[36] In 2003, Aaron L. Payette and Iain J. McGaw confirmed the hypothesis that high water and air temperatures have a very detrimental effect on the crayfish physiological processes, causing severe heat stress and death of the animals.[37] In contrast, the results of a study by a team led by Sonia Espina

[34] Sakshi Puri and Zen Faulkes, "Can Crayfish Take the Heat? *Procambarus clarkii* Show Nociceptive Behaviour to High Temperature Stimuli," *Biology Open* 4, no. 4, (2015): 445, https://doi.org/10.1242/bio.20149654.

[35] Puri and Faulkes, "Can Crayfish Take the Heat?," 446.

[36] Lenwood W. Hall Jr. et al., "Temperature Preference of the Crayfish *Orconectes obscurus*," *Archives of Environmental Contamination and Toxicology* 7, no. 3 (1978): 379–383, https://doi.org/10.1007/BF02332065.

[37] Aaron L. Payette and Iain J. McGaw, "Thermoregulatory Behavior of the Crayfish *Procambarus clarki* in a Burrow Environment," *Comparative Biochemistry and Physiology part A* 136, no. 3, (2003): 539–556.

identified the optimum temperature preferendum for *Procambarus clarkii*, which was 23.4°C.[38] In the context of all presented analyses, it should be strongly emphasized: the rapid and complex behaviours of crayfish when exposed to high temperatures indicate (as it has been repeatedly demonstrated over several decades) that hot stimulation, for example, boiling water, is undoubtedly an extremely harmful and intensely painful impact not only for crayfish, but possibly also for all decapods exploited in the food industry.

Prawns and Behavioural Evidence of Pain

One of accepted criteria for the potential experiencing of pain by selected animal species is observation of grooming behaviours, focusing on that part of the body which was exposed to the noxious stimulus. The argument reinforcing this criterion is the situation when (in the next stage of the experiment) anaesthetics administered to that body part minimize grooming behaviours, despite the continued application of the noxious stimulus.

Stuart Barr and Robert Elwood met those scientific challenges and subjected a group of 18 prawns of the species *Palaemon elegans* to a noxious chemical stimulus being sodium hydroxide and acetic acid, with which the prawn eyestalks were brushed, and the animal's behavioural responses were then observed and assessed. The chemical substance applied to the eye immediately triggered in the prawns not a single nocifensive reflex, but a whole process consisting of, as the authors write, successive sequences of: "Brushing of caustic soda or acetic acid on one antenna caused immediate tail-flicking escape responses, […]. Further, there was a marked increase in grooming of the specific antenna and rubbing that antenna against the side of the tank. […] Grooming of the eyestalks consisted of the animal remaining stationary and using its chelipeds to nip and pick at its eyestalks."[39] It should be emphasized that grooming and rubbing of the antennae was directed at a specific, non-accidental part of the animal's body. At the further stage of the study, the effect of the anaesthetic on the presence of behavioural activity of grooming and escape was verified. Barr and Elwood applied topically (on the eyestalks) benzocaine, where the act of applying the substance (brushing) itself triggered the escape

[38] Sonia Espina et al., "Preferred and Avoided Temperatures in the Crawfish *Procambarus clarkii*," *Journal of Thermal Biology* 18, no. 1, (1993): 35–39.

[39] Stuart Barr and Robert W. Elwood, "The Effects of Caustic Soda and Benzocaine on Directed Grooming to the Eyestalk in the Glass Prawn, Palaemon elegans, Are Consistent with the Idea of Pain in Decapods," *Animals* (*Basel*) 14, no. 3, (2024): 2–3, 364, https://doi.org/10.3390/ani14030364.

response in the prawns. This is due to the fact that the chemical composition of benzocaine is itself an irritant to skin receptors, as was proven when the agent was applied onto human skin – it causes burning sensations in humans.[40] Despite the initial, highly probable experience of pain under the influence of the applied benzocaine, once the agent began to locally anaesthetize the body region, further application of the irritant sodium hydroxide onto the anaesthetized area induced an inhibition of nociceptive reactions: a decrease in grooming behaviours and no rubbing of the irritated areas. As the authors wrote: "There was some amelioration of the response to sodium hydroxide by pretreatment with benzocaine."[41] The inhibition of escape and grooming behaviours following the application of local anaesthesia is a phenomenon regularly observed in vertebrates (from fish to mammals) and provides further evidence that prawns experience pain.

All findings presented above – the awareness of the location of irritant stimuli, complex pain behaviours, and a lack of response after anaesthetics were applied – imply the advanced perception of pain in prawns, where the generation of pain experience must involve higher levels of pain stimulus processing in the central nervous system. We should also mention another interesting observation, concerning results of mechanical stimulation of prawn antennae in another study. As we have already seen, although these animals responded to noxious chemical stimuli, tactile (mechanical) stimulation of their antennae did not trigger grooming behaviour. With a probability bordering on certainty it can be stated that in prawns antennae have a higher threshold of sensitivity to mechanical than to chemical stimuli. Another possible explanation is that prawn antennae do not contain mechanoreceptors, but only chemical nociceptors (analogous to thermal nociceptors in crayfish) or chemonociceptors.[42]

Discussion

The above argumentation based on neuroanatomical, physiological, and behavioural analogies indicates that certain crustacean species experience pain similarly to

[40] Sharad Mutalik, "How to Make Local Anesthesia Less Painful," *Journal of Cutaneous and Aesthetic Surgery* 1, no. 1 (2008): 37–38, https://doi.org/10.4103/0974-2077.41161.

[41] Barr and Elwood, "The Effects of Caustic Soda and Benzocaine," 6.

[42] Girolamo Di Maio et al., "Mechanisms of Transmission and Processing of Pain: A Narrative Review," *International Journal of Environmental Research and Public Health* 20, no. 4 (2023): 3064, https://doi.org/10.3390/ijerph20043064.

vertebrates, including mammals.[43] Particularly convincing evidence is provided by long-term experiments conducted by the teams of Robert Elwood and, separately, by Lynne Sneddon. This evidence has important implications for increasingly bold plans concerning exploitation of arthropods as a food source in the worrying absence of opposition from the scientific or social communities[44] and the lack of official welfare practices blocking the unethical treatment of crustaceans. As the Eurogroup for Animals report (September 2024), *Insect Farming: A Six-Legged Problem*, states, no comprehensive and species-specific model to ensure welfare of insects or other arthropods in the context of their exploitation as food is currently being implemented.[45] Therefore, it is necessary to politically and legally enact, even locally, a theory of welfare of industrially exploited groups of crustaceans. The research results outlined above concerning studies on stimulus processing and experiencing pain perhaps not only in decapods, but across the entire crustacean taxon make us realize the urgency of changing the awareness of consumers and decision-makers on the international level. Currently continued experiments add to the existing body of knowledge on perception of pain in representatives of selected decapod taxa, and more of the brutal testing of each successive species within these taxa seems to be a pointless, unnecessary tormenting of animals. I would like to recall briefly, why the premise that an organism is capable of experiencing pain leads us to the conclusion that we should offer moral consideration to it. As evidenced by the ethics of animal welfare (founded on the theory of ethical utilitarianism and consequentialism), causing suffering in animals is always morally unacceptable when this suffering prevents the animal from pursuing individual goals or meeting its species needs or interests.[46] Hence the need for urgent changes in the legal limitation or abolition of cruel procedures for handling crustaceans, the consequence of which is a lot of unnecessary suffering.

An example of such a procedure is a crude method of hormonal manipulation known as the practice of eyestalk ablation in freshwater and saltwater shrimps and prawns. It involves cutting, crushing or cauterizing one or both of the animal's eyestalks, most often without anesthesia. This has been a practice used in female shrimp in commercial farming since the 1970s, for instance, in tiger shrimp

[43] Edgar T. Walters and Amanda C. de C Williams, "Evolution of Mechanisms and Behaviour Important for Pain," *Philosophical Transactions of the Royal Society B: Biological Sciences* 374, no. 1785 (2019): 20190275.

[44] Robert W. Elwood, "Discrimination between Nociceptive Reflexes and More Complex Responses Consistent with Pain in Crustaceans," *Philosophical Transactions of the Royal Society B* 374 (2019): 20190368.

[45] Eurogroup for Animals, *Insect Farming: A Six-Legged Problem*, Brussels 2024.

[46] David DeGrazia and Andrew Rowan, "Pain, Suffering, and Anxiety in Animals and Humans," *Theoretical Medicine and Bioethics* 12, no. 3 (1991): 193–211.

(*Penaeus monodon*), to minimize the perception of light stimuli and stimulate ovarian development and gamete production, as captive conditions induce high concentrations of hormones that inhibit reproduction.[47] Hormones that inhibit reproductive readiness are produced in the eyestalk, so ablation significantly reduces their concentration, initiating the reproductive season. As research by Hoang's team has shown, there is a high sensitivity of the shrimp breeding stock to light, where high intensity of light stimuli, that is, high brightness, inhibits the maturation of the ovaries in the so-called banana shrimp *Penaeus merguiensis*, and limited light intensity induces readiness to spawn.[48] The fact that the practice of ablation is painful and highly traumatizing results from an experiment where ablation performed without anesthesia on the prawns *Macrobrachium americanum* induced a nocifensive reflex, escape behaviour and rubbing of the injured area, while ablation performed under anesthesia significantly reduced these reactions.[49] The cruelty of ablation is even greater when the tiger shrimp's eyestalks regenerate within several months and the entire procedure must be repeated many times. Further restrictions on cruel practices towards decapods, which should be immediately implemented on an international scale, have been suggested by the European Food Safety Authority and mainly concern extremely painful methods of killing: splitting lobsters or crabs in half with a blade, along the midline of the whole body or placing freshwater crustaceans in water with high salt concentrations to induce osmotic shock and eventual death. The most outrageous procedure seems to be "[t]he most commonly practiced slaughter method [of] placing live, fully conscious crustaceans into boiling water" though.[50] Live cooking of decapods without prior stunning is currently illegal in Switzerland (under the Tierseuchenverordnung – Animal Protection Order) and New Zealand (under the Animal Welfare Regulations 2018), but such a ban should apply wherever the seafood industry operates. Without strengthening and enforcing animal welfare laws and policies, all appeals for the humane treatment of decapod crustaceans will remain ineffective.

Decapods have complex pain experiences, comparable to pain perception in vertebrates – at the neurological and behavioural level, they respond with varying intensity to noxious chemical, thermal, and mechanical stimulation. At the neurological

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47 Umaporn Uawisetwathana et al., "Insights into Eyestalk Ablation Mechanism to Induce Ovarian Maturation in the Black Tiger Shrimp," *PLoS One* 6, no. 9 (2011): e24427, https://doi.org/10.1371/journal.pone.0024427.

48 Tung Hoang et al., "Ovarian Maturation of the Banana Prawn, *Penaeus merguiensis* De Man under Different Light Intensities," *Aquaculture* 208, nos. 1–2 (2002): 159–168.

49 Genaro Diarte-Plata et al., "Eyestalk Ablation Procedures to Minimize Pain in the Freshwater Prawn Macrobrachium americanum," *Applied Animal Behaviour Science* 140, nos. 3–4 (2012): 172–178.

50 Stephanie Yue, "The Welfare of Crustaceans at Slaughter," *WellBeing International. WBI Studies Repository* (2008): 3.

level, nociceptive pathways generate impulses from different parts of the body to the decapod's central ganglia, while at the behavioural level, these animals show movement patterns characteristic for pain that are not simple reflexes. These neurobehavioural processes and phenomena should form the basis for including at least selected species in the list of animals protected by legislation prohibiting cruel practices of catching, transporting, holding, and extremely brutal killing of decapods.[51] A separate, but equally important problem is the trade in crustaceans in the aquarium industry, where Decapoda are treated as animated decorations or an aesthetic attraction. However, as we know, crabs (and probably also shrimps and crayfish) "are stressed by minimum human contact"[52] and keeping crustaceans in home or public aquariums should not be promoted and it ought to even be prohibited by law. Unfortunately, fads and fashions often point in directions opposite to legal regulations. When we look at the situation of exploited mammals and birds, their neurobehavioural responses to pain and stress are perceived as serious indicators of a lack of welfare in the chosen area of exploitation. In light of the research to date, the argument of an analogy between the suffering of higher vertebrates and the suffering of decapods proves to be sensible and verifiable and should be used for considering the concept of crustacean welfare. Reasons why it is avoided by the scientific community and opposed by policy makers are a topic for further consideration, which should definitely be pursued.

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[51] For documented details of the cruel treatment of crustaceans from different regions of the world in the food industry, see the Crustacean Compassion website. Accessed November 16, 2024, https://www.crustaceancompassion.org/.

[52] Éverton Lopes Vogt et al., "The Impact of Chasing Stress," 897.

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