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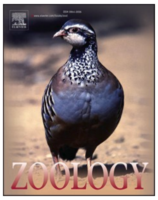

The Neurobiology of Ocean Change – insights from decapod crustaceans

Wolfgang Stein [a,*,1], Steffen Harzsch [b,2]

[a] Illinois State University, School of Biological Sciences, Normal, IL 61790, USA
[b] University of Greifswald, Zoological Institute and Museum, Department of Cytology and Evolutionary Biology, D-17498 Greifswald, Germany

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A B S T R A C T

The unprecedented rate of carbon dioxide accumulation in the atmosphere has led to increased warming, acidification and oxygen depletion in the world's oceans, with projected impacts also on ocean salinity. In this perspective article, we highlight potential impacts of these factors on neuronal responses in decapod crustaceans. Decapod crustaceans comprise more than 8,800 marine species which have colonized a wide range of habitats that are particularly affected by global ocean change, including estuarine, intertidal, and coastal areas. Many decapod species have large economic value and high ecological importance because of their global invasive potential and impact on local ecosystems. Global warming has already led to considerable changes in decapod species' behavior and habitat range. Relatively little is known about how the decapod nervous system, which is the ultimate driver of all behaviors, copes with environmental stressors. We use select examples to summarize current findings and evaluate the impact of current and expected environmental changes. While data indicate a surprising robustness against stressors like temperature and pH, we find that only a handful of species have been studied and long-term effects on neuronal activity remain mostly unknown. A further conclusion is that the combined effects of multiple stressors are understudied. We call for greater research efforts towards long-term effects on neuronal physiology and expansion of cross-species comparisons to address these issues.

1. Global ocean change, crustaceans, and their nervous systems: why does it matter?

The last decades have seen a rapid accumulation of CO_2 in the atmosphere and a concomitant rise in atmospheric temperature (Fig. 1A) (Reid et al., 2009). As a consequence, survival and demographics of many animal and plant species are threatened. Marine ecosystems have been particularly affected by these changes (Doney et al., 2012; Poloczanska et al., 2013; Molinos et al., 2016), because the oceans not only cover 71 percent of the Earth's surface and contain 97 percent of the world's water, they also absorb ~90 percent of the energy produced by global warming. Accordingly, many ocean water parameters track atmospheric changes (Figs. 1A-C) and models predict continuous and more dramatic changes for the next few centuries (Fig. 1D) (Wiltshire et al., 2010). Most alarming, water parameters in some regions change at a rapid pace (Reid et al., 2009; Burrows et al., 2011; Boersma et al., 2016), and long term data series indicate that global ocean change already has a major impact on marine ecosystems (Beaugrand et al., 2009; Burrows et al., 2011; Poloczanska et al., 2013; Molinos et al., 2016; Boyd et al., 2018).

Arthropods contribute about half of the animal biomass on Earth, and crustaceans account for 80% of this arthropod biomass (Bar-On et al., 2018). For example, the Antarctic krill species *Euphausia superba* contributes ≈0.05 Gt Carbon to the global biomass (Atkinson et al., 2009). Crustaceans also represent one of the most species-rich taxa in our oceans and display a large diversity of sizes, morphologies, life styles, and life histories (Watling and Thiel, 2012; Schram, 2013). Members of the malacostracan crustaceans have been particularly successful in colonizing a wide range of habitats. The decapods, an order within the malacostracans, comprise an estimated 15,000 species of marine, freshwater, semiterrestrial and terrestrial crustaceans (De Grave et al., 2009), including well-known representatives such as crayfish, clawed and spiny lobsters, hermit crabs, and true crabs. Their range extends from the deepest ocean trenches and hydrothermal vents of the Midatlantic Ridge, through equatorial intertidal mud flats and freshwater ecosystems to the mountainous plateaus of Christmas Island

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* Corresponding author.
E-mail addresses: wstein@neurobiologie.de (W. Stein), steffen.harzsch@uni-greifswald.de (S. Harzsch).

[1] www.neurobiologie.de.

[2] https://zoologie.uni-greifswald.de/struktur/abteilungen/cytologie-und-evolutionsbiologie/personal/steffen-harzsch-ag-leiter/.

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(Greenaway, 2003; Watling and Thiel, 2012). Many decapod species have high global invasive potential, signifying their ability to adapt to new and changing environments and their ecological importance (Hänfling et al., 2011; Epifanio, 2013; Leignel et al., 2014; Gallardo et al., 2016; Young and Elliott, 2020). More than 8,800 decapod species live in marine environments (Ocean Biogeographic Information System). Many of them represent key species in estuarine, intertidal, and coastal areas where they can occur in such high abundance that changes

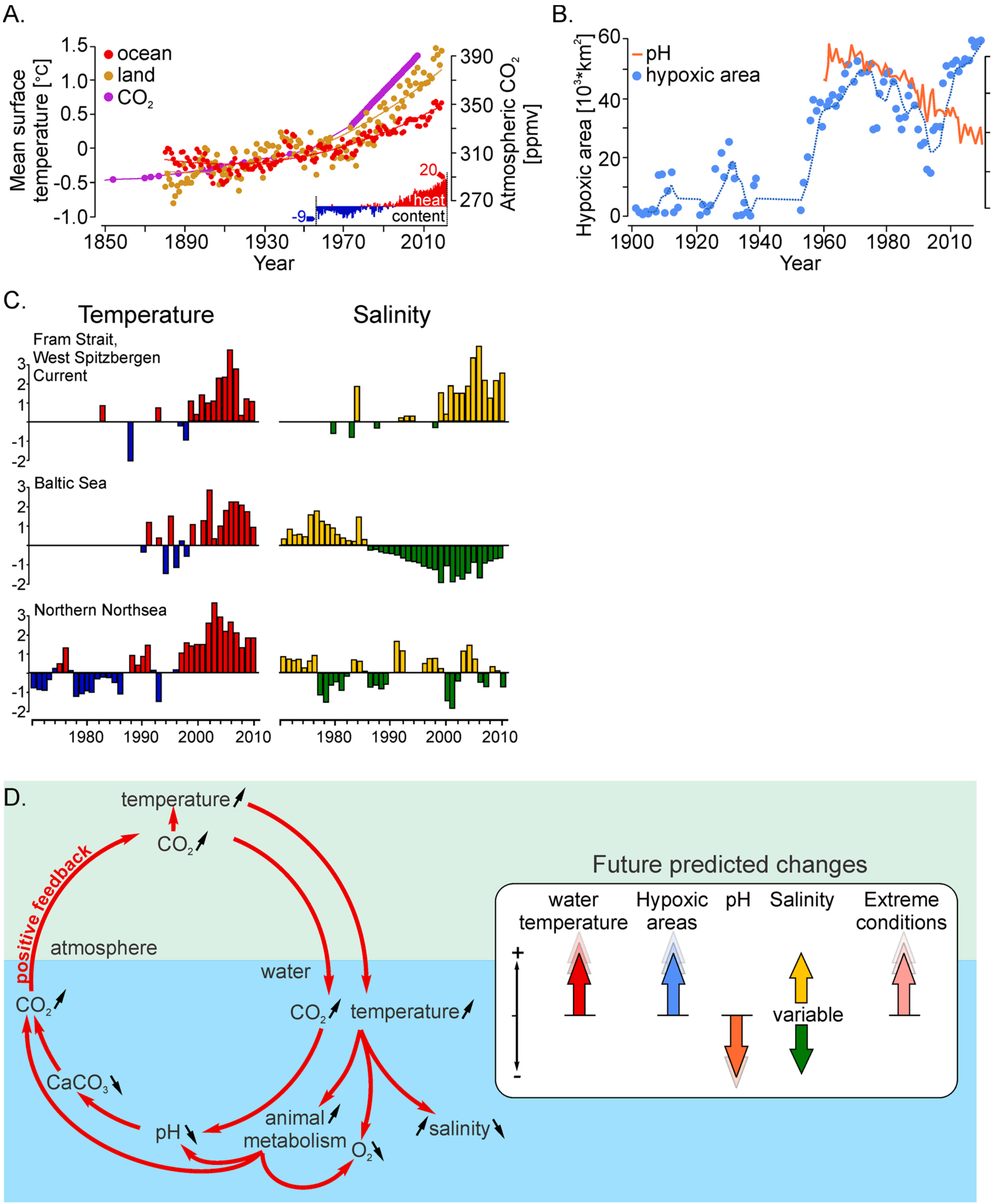

Fig. 1. Current and future environmental changes in marine habitats. A. Annual mean atmospheric CO_2 over the last 250 years (Pawlak, 2013) and annual mean land and sea surface bottom temperatures (data from https://data.giss.nasa.gov/gistemp/graphs_v4; accessed 2020/06/30). Inset: Mean ocean heat index of ocean surface water (https://www.climate.gov/news-features/understanding-climate/climate-change-ocean-heat-content; accessed 2020/06/30). B. Annual hypoxic area (oxygen concentrations <2 mg/L) in the Baltic Proper (Carstensen et al., 2014; Laffoley and Baxter, 2019) and annual average surface water pH in the Eastern Gotland Basin of the Baltic Sea (Omstedt et al., 2012). C. Salinity changes diversely in different ocean regions (right), even if they possess similar temperature profiles (left), making it difficult to predict future salinity changes. Comparison of temperature and salinity anomalies in different seas (Hughes et al., 2011). Anomalies are normalized to the standard deviation and calculated relative to a long-term mean (e.g. a value of +2 indicates 2 standard deviations above normal). D. Left: Different abiotic factors interact with each other, with increasing atmospheric CO_2 initiating a positive feedback loop with predicted increases in atmospheric and ocean temperature, decreases in ocean oxygen and pH levels, and diverse effects on salinity. Right: Direction of predicted ocean water changes in the next century. Besides the predicted average changes in abiotic factors, it is expected that extreme conditions such as heat waves will occur more often.

in their population structure may directly influence the whole ecosystem (Young and Elliott, 2020). Assessing how environmental factors affect decapod crustaceans is thus imperative to our understanding of how global climate change impacts marine ecosystems.

Water parameters affected by global change, such as oxygen availability, salinity, pH, and temperature (Fig. 1), are known to affect many physiological processes and natural behaviors in decapod crustaceans (Pörtner, 2010; Somero, 2010, 2012; Clements and Hunt, 2015; Whiteley and Taylor, 2015). While many studies have addressed the ecology and population dynamics that result from environmental changes, it is the nervous system that controls all animal behavior (Fig. 2). Yet, surprisingly little is known about how decapod crustacean nervous systems respond to environmental stressors, how well they are adapted to changes in habitat conditions, and what impact global change may have on the functioning of their nervous system. This is despite a long history of studies that investigated how the nervous system of decapod crustaceans controls natural behaviors - a research field called 'neuroethology'. In this manuscript, we discuss known responses of the decapod nervous system to environmental stressors (Fig. 2). We outline challenges for future studies, but also opportunities that these studies may offer to understand the effects of climate change and other anthropogenic changes in the oceans. It is not the intention of this manuscript to provide an exhaustive overview of all studied cases. Instead, we highlight examples that demonstrate general problems and advancements when studying environmental influences on the nervous system.

2. Anthropogenic changes to crustacean habitats

To understand the effects of global change on nervous system function and physiology, one first needs to consider which environmental challenges and stresses nervous systems are typically exposed to and then what further changes are expected to occur. Many decapod species inhabit waters that show distinct daily, monthly, or seasonal cycles in physical parameters. Such natural fluctuations can be caused by seasons, tides, rainfall, or metabolic activities of algae and microbionts. They are thus highly site-dependent, with areas close to the shore typically experiencing larger fluctuations (Hofmann et al., 2011; Duarte et al., 2013). For example, estuarine organisms experience diel pH changes that are greater than the predicted *average* pH decrease in the open ocean within the next 100 years (Hofmann et al., 2011). Similarly, physico-chemical parameters of intertidal rockpools at the coast of Brittany (France) exhibit strong diurnal and seasonal fluctuations that exceed the predicted average change for many decades of further global warming. For example, in summer, temperature varies between 13 °C at night and 21 °C in the middle of the day (Legrand et al., 2018) and oxygen and pH exhibit strong daily fluctuations related to the photosynthetic activity of the algae. Rocky intertidal ecosystems are also known to have complex mosaics of abiotic conditions within just a few meters (Helmuth et al., 2006a, b; Somero, 2012). Another iconic example for coastal habitats with extreme environmental fluctuations are temperate tidal salt marshes at the US east coast and the Gulf of Mexico. Tidal salt marshes provide highly valuable ecosystem services and are characterized by an extraordinary productivity. They also show dramatic fluctuations in temperature, pH, and oxygen levels on diel and seasonal scales (Figs. 3A-D). Nevertheless, decapod crustaceans have invaded even these extreme habitats. In the Flax Pond saltmarsh, for instance, at least four species of brachyuran crustaceans were found (Baumann et al., 2015).

At first glance, this appears to suggest that species that already tolerate large environmental fluctuations may be largely insensitive to further anthropogenic changes. Alternatively, these species may live

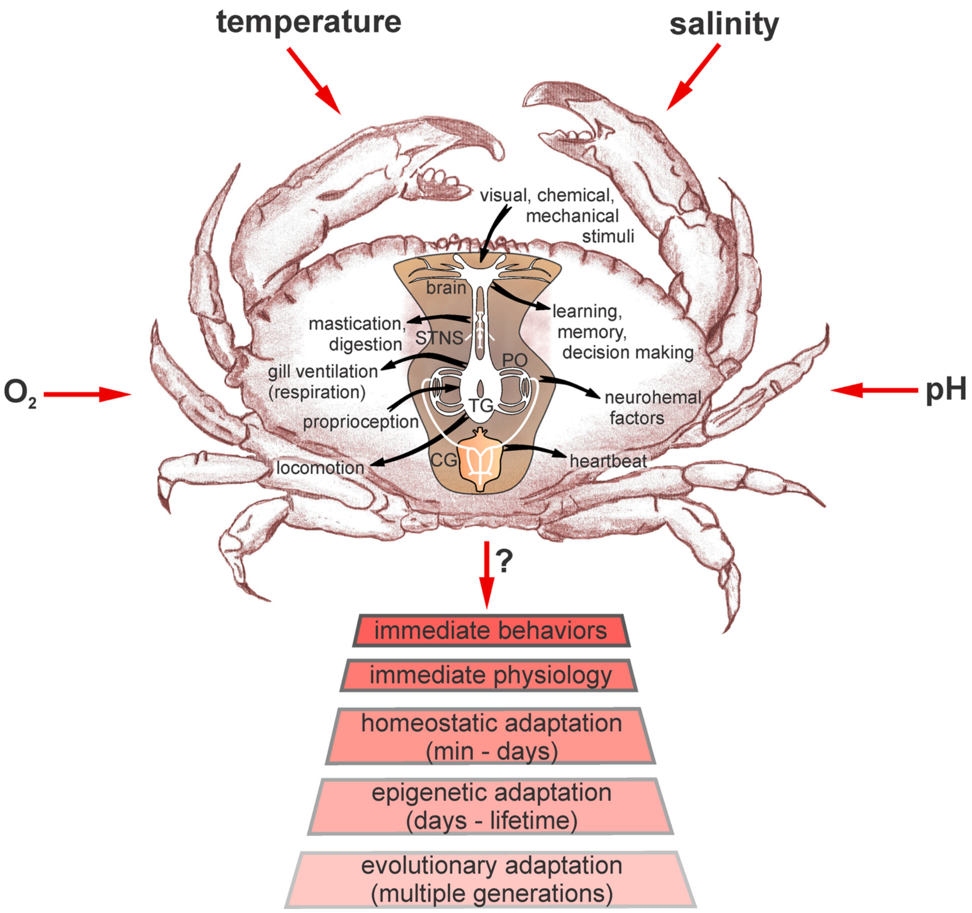

Fig. 2. Schematic of the decapod crustacean nervous system, using the example of a brachyuran crab. This manuscript highlights the effects of abiotic factors on neurons and neuronal circuits in the decapod nervous system, and their potential effects on behavior and physiology on different timescales. The schematic shows the function and approximate location for the main nervous system component. Brain: supraesophageal ganglion; STNS: stomatogastric nervous system; TG: thoracic ganglion, PO: pericardial organ; CG: cardiac ganglion.

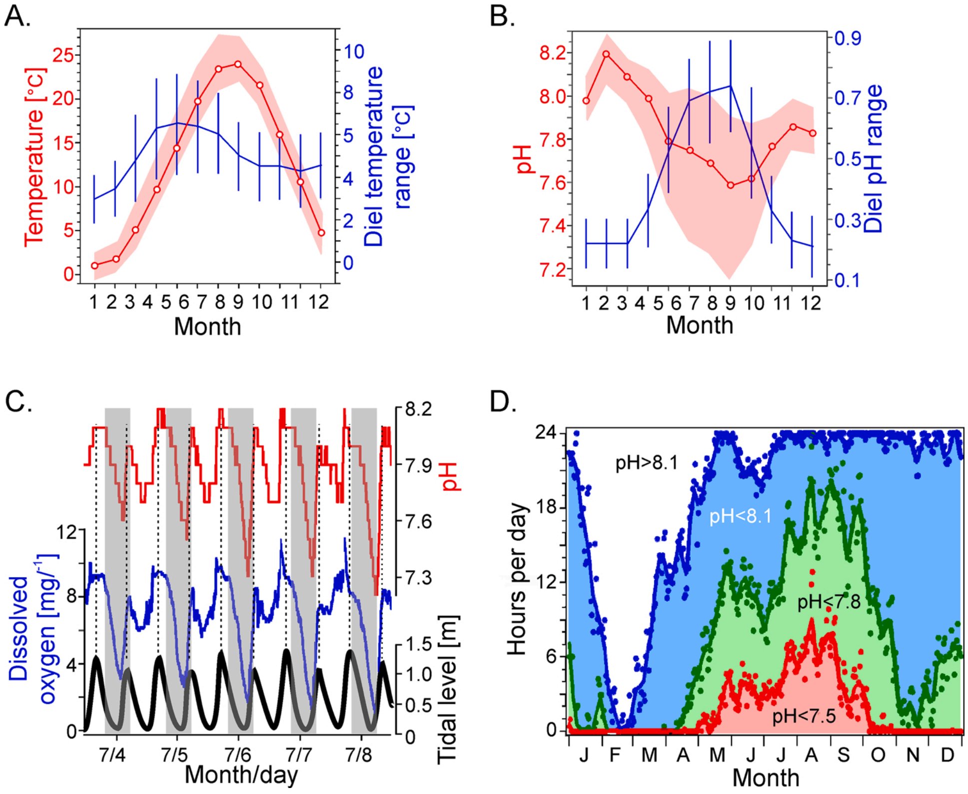

Fig. 3. Diel, seasonal and annual changes in abiotic factors. A. Average seasonal temperature and diel temperature ranges can be quite different. Example from a temperate tidal salt marsh (Baumann et al., 2015). Monthly means and averages of daily minima and maxima in red (left ordinate). Monthly average of diel amplitudes±1 SD in blue (right ordinate). B. Average pH and diel pH range from the same salt marsh. Colors as in A. C. Water oxygen content and pH vary dramatically with time of the day and tidal level (Baumann et al., 2015). Flax Pond salt marsh dissolved oxygen (blue, left ordinate) and pH (red, right top ordinate) at selected days in June 2010. Shaded areas: times between sunset and sunrise. Tidal elevations are shown in black (right bottom ordinate). D. Seasonal changes in pH in Flax Pond saltmarsh. The observed diel changes are larger the predicted average changes caused by anthropogenic influences. Dots represent the average hours per day for the indicated pH conditions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

close to their physiological limits and thus suffer from additional environmental extremes in their habitat (Hofmann et al., 2011; Baumann et al., 2015). This may be especially the case when changes of multiple environmental drivers coincide to provide additive or synergistic effects (Boyd et al., 2018). A recent study comparing differently temperature-adapted species of crabs shows that warm-adapted crab species have a lower survival rate to additional increases in habitat temperature than cold-adapted ones (Faria et al., 2020). This fact was also highlighted previously by a comparison of 20 congeneric species of porcelain crabs *Petrolisthes* from the eastern Pacific. These animals live in different vertical zones in intertidal and subtidal habitats, with accordingly different habitat temperatures (Stillman and Somero, 2000). The study suggests that, compared to subtidal species, intertidal species may live closer to their thermal maxima and may be less apt to increase their upper thermal tolerance limits in response to anthropogenic climate change. Further confirmation comes from a subsequent study, in which Somero (2010) concluded that marine species that live in temperature extremes (both cold and warm) show a high vulnerability to additional temperature changes.

These studies demonstrate that physiological adaptations that help crustacean species survive in extreme environments and invade new habitats may limit them in their ability to cope with additional environmental changes. What anthropogenic environmental changes should we expect? The answer to this question is far from clear. Future fluctuations in environmental factors are expected to be heterogeneous and highly site-dependent as they will differ between open ocean, estuarine, and near-shore sites. Semi-enclosed seas such as the Baltic Sea and North Sea are particularly susceptible to the effects of global change and are expected to increasingly affected by rising surface temperatures and water freshening by increased river runoff (Meier, 2006; Gräwe et al., 2013; Hiddink et al., 2015; Robins et al., 2016). In contrast, the predictions for pH changes in enclosed seas are less universal because of the manifold natural and man-made influences on water pH in these areas. This has led some authors to consider acidification due to anthropogenic CO_2 emissions an “open ocean syndrome” (Duarte et al., 2013). Nevertheless, intertidal ecosystems have already shown particularly pronounced and rapid biogeographic changes in response to anthropogenic influences, much more so than open oceans, where comparably slow and small changes occur. It seems clear that slow ’average’ changes pose less of a threat than the increasing fluctuations of environmental factors. With this in mind, it is particularly important to study intertidal species to evaluate physiological effects of global ocean change (Somero, 2002; Stillman, 2002; Helmuth et al., 2006b; Somero, 2010, 2012).

The nervous system of decapod crustaceans must continue to function across a wide range of environmental conditions, at least for species that experience large fluctuations in abiotic drivers. A good example is neuronal activity in the cardiac ganglion. Cardiac thermal sensitivity is seen as an essential factor for survival in warming waters (Somero, 2002, 2010; Somero, 2012). Unlike in vertebrates, heartbeat in crustaceans is driven by neuronal tissue, namely the cardiac ganglion (Fig. 2) (Tazaki and Cooke, 1979). Consequently, to enable survival, cardiac neuronal activity must be tolerant to temperature changes. Data from the Jonah crab, *Caner borealis,* indicate that this is indeed the case (Kushinsky et al., 2019). Importantly, neuronal activity must be maintained across many timescales, from acute and sudden temperature changes to longer-lasting daily and seasonal changes. Maintained neuronal activity is thus seen as a prerequisite to enable behavioral and neuroendocrine responses that mitigate the effects of environmental changes.

Numerous elements of the decapod nervous system have been under scrutiny for many decades, and have served as proxies for studying many basic nervous system functions (Edwards et al., 1999; Nusbaum and Beenhakker, 2002; Marder et al., 2005; Harris-Warrick, 2011; Marder, 2012). This scrutiny has led to the discovery of several ground-breaking mechanisms that underlie neuronal function in animals and humans (Wiese, 2002), owing to the easy access to identified neurons that can be tracked across individuals and species, as well as throughout evolution (Stein et al., 2016; Stein, 2017). Early studies identified the neurons and neuronal circuits that underlie many natural behaviors, including crayfish locomotion and posture control (Clarac et al., 1992; Mulloney and Smarandache, 2010), crayfish escape tail flip (Edwards et al., 1999), swimming (Mulloney and Smarandache-Wellmann, 2012), and statocyst control of equilibrium (Fujisawa and Takahata, 2007). Studies on centrally generated rhythmic activities have also shed light on modulation-induced neuronal plasticity (Stein, 2009; Nusbaum and Blitz, 2012) and mechanisms that stabilize neuronal patterns against environmental perturbations (Marder et al., 2015; Städele et al., 2015; Haley et al., 2018). Most recently, research on the stomatogastic and cardiac ganglia have provided insight into the mechanisms of homeostatic plasticity and the molecular determinants of neuronal identity (Schulz and Lane, 2017; Northcutt et al., 2019). The combination of traditional recording techniques with cutting-edge molecular measurements thus makes the decapod nervous system ideal for studying how environmental stressor impact neuronal activity.

2.1. Oxygen

There is currently a rapid expansion of benthic oxygen minimum zones at intermediate ocean depths due to increasing water temperature and eutrophication (Vaquer-Sunyer and Duarte, 2008; Laffoley and Baxter, 2019; Limburg et al., 2020). Oxygen deprivation is a classic example for a positive feedback loop. Increased ocean temperatures lead to lower oxygen solubility and concentration but also higher plant and animal metabolic activity and growth. This further decreases oxygen availability and increases the production of CO_2. CO_2 emissions into the atmosphere further increase atmospheric temperatures, which feeds forward to the heating of the oceans (Fig. 1D). The number of benthic oxygen minimum zones has increased steadily from ~45 in 1960 to over 700 today. Most oxygen minimum zones are found near coastal lines with high human impact (Limburg et al., 2020). In contrast, pelagic open waters are usually well-aerated through wind and breaking waves, for example (Laffoley and Baxter, 2019). The most dramatic effects are seen where large freshwater influx leads to water stratification that reduces the mixing of bottom and surface waters, such as in polar regions and semi-enclosed oceans like the Black and the Baltic seas (Figs. 1 B,C) (Meier, 2006; Gräwe et al., 2013; Hiddink et al., 2015; Robins et al., 2016; Limburg et al., 2020). These seas have been designated some of the largest dead zones (Humborg et al., 2019). Here, eutrophication and increases in hypoxia have had a severe impact on species variety and ecological health (Wulff et al., 2007).

Marine decapods show a wide range of behavioral, physiological and metabolic responses to mitigate reduced environmental oxygen levels (summarized in (Whiteley and Taylor, 2015)). Behavioral responses usually involve movement away from hypoxic conditions. This can lead to a number of atypical behaviors such as, for example, animals leaving their shelters and exposing themselves to a higher risk of predation (Haselmair et al., 2010), the active search for more oxygen-rich or colder waters (Whiteley and Taylor, 2015) or even moving into air (Taylor and Wheatly, 1979). Decapods also show a range of physiological adaptations. Some species are able to maintain a substantial venous reservoir of O_2 due to the high O_2 affinity of their hemocyanin. Responses to mild hypoxia typically include changes in gill ventilation, heart rate, and respiratory pigments (Whiteley and Taylor, 2015). During severe hypoxia, most species become immobile and moribund, and switch to anaerobic metabolism, with death rates rising during prolonged phases of anoxia.

Nervous system activity must be maintained at least at minimum levels to enable behavioral responses and survival. For example, heartbeat and gill ventilation are essential to providing oxygen uptake and distribution, and both are controlled by neurons in the suboesophageal and cardiac ganglia (Simmers, 1979; Taylor, 1982; McMahon and Wilkens, 1983; Dicaprio, 1989; McMahon, 1995). There are several lines of evidence that the central pattern generators in both ganglia are modulated by oxygen and its partial pressure in the surrounding water. As the partial pressure of oxygen drops towards a critical threshold, ventilation rates and cardiac stroke volume increase, but heartbeat rate decreases. This ’hyperventilation’ continues until a critical level is reached below which heartbeat and ventilation stop. Experiments on *Carcinus maenas*, *Cancer productus,* and *Cancer magister* show that ventilation and heartbeat rates are controlled by the same set of command-like neurons (Mendelson, 1971; Wilkens et al., 1974) and that the pattern generators receive sensory input from oxygen-sensitive fibers at the scaphognathites (Larimer, 1964; McMahon and Wilkens, 1977) - an appendage of the second maxilla that serves as a pumping organ to move water towards the gills. There is also evidence that the pattern generators in the central nervous system are directly modulated by oxygen: For example, when normoxic solution is applied to an isolated *Carcinus maenas* cardiac ganglion after prolonged periods of hypoxia, transient compensatory increases in heartrate occur that exceed the control levels before hypoxia (Wilkens et al., 1989).

The high metabolic requirements of decapod crustaceans are reflected in the finding that crustaceans show critical minimum O_2 thresholds that are significantly higher than for other taxa. They also die the fastest in severe hypoxic conditions. This holds true across ontogenetic stages as well. In an exhaustive comparison across taxa, Vaquer--Sunyer and Duarte (2008) found, for example, that the first larval zoea stage of *Cancer irroratus* was the most sensitive species tested. Their critical oxygen threshold was more than 5 times higher than the median of all tested organisms. The critical level at which heart rate and ventilation cease, however, varies with aquatic habitat. Generally speaking, species that encounter hypoxic conditions more frequently have lower critical levels. For example, the vent crab, *Bythograea thermydron*, has a critical partial pressure of 1.7 kPa (Mickel and Childress, 1982), while that of *Carcinus maenas* is several times higher ($>$ 5 kPa; (Whiteley and Taylor, 2015)). Critical levels also vary with temperature, presumably because of changing metabolic demands and oxygen solubility of the water. For *Carcinus maenas*, the critical level increases from ~5 kPa at 10 °C to ~8 kPa at 20 °C.

The reasons why neuronal activity fails at or around these critical levels are not clear. One hypothesis suggests that there is a relation to energy expenditure. The nervous system of resting *Carcinus maenas* crabs, for example, appears to consume at least twice as much oxygen as all other tissues combined (Treherne:, 1966; Forgue et al., 1992). Massabuau and Meyrand (1996) therefore proposed that the shutdown of neuronal activity during severe hypoxia is a way to reduce energy expenditure when high levels of neuronal activity are not required. In their experiments with the pyloric central pattern generator of the lobster, *Homarus gammarus*, reducing oxygen partial pressure from normoxic 20 kPa to hypoxic 1 kPa disrupted the pyloric activity pattern. Membrane potentials of the pyloric network neurons depolarized, and the rhythm slowed down in a dose-dependent fashion. In support of their hypothesis, the effects on circuit activity were mediated through a single neuron, while all other neurons remained unaffected by hypoxia. This suggests that blood oxygen, in addition to its classical role in satisfying tissue energy demands, modulates neuronal activity and may play a physiologically important role in reducing neuronal activity and energy expenditure to support the animal’s tolerance of low oxygen levels. A finding consistent with this role is that the transient drop in blood oxygen levels during ecdysis appears to be responsible for short-term changes in pyloric neuron activity associated with exuviation (Clemens et al., 1999).

Further support for the idea that oxygen continuously modulates neuronal activity comes from *in vivo* recordings in the same neuronal system, showing that variations in oxygen levels enable long-lasting interactions between two stomatogastric circuits (Clemens et al., 1998). Specifically, within one hour after feeding, the arterial partial pressure of oxygen doubles from 1 - 2 kPa to ~ 4 kPa and remains high for up to 24 hours (Fig. 4A). Concurrently, the pyloric rhythm speeds up and long-lasting gastric mill rhythms are elicited (Yarger and Stein, 2015). Importantly, these two rhythms usually influence each other in that the timing of one determines that of the other (so called gastropyloric interactions, Fig. 4B). These interactions vanished after feeding,

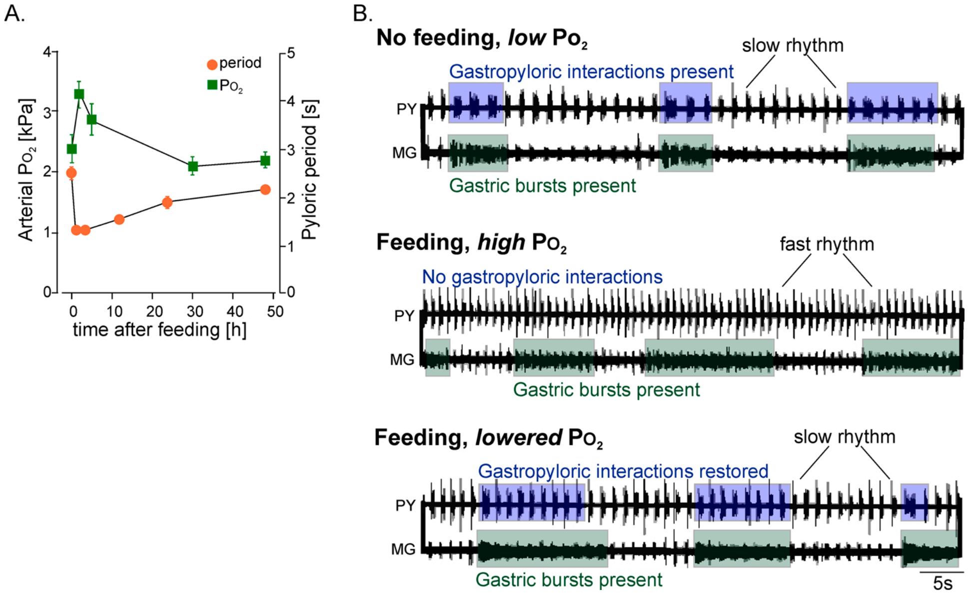

Fig. 4. Oxygen modulates neuronal activity. A. Changes in arterial oxygen content and in the cycle period of the pyloric rhythm in the stomatogastric nervous system of the lobster, *Homarus gammarus* (Clemens et al., 1998). Feeding increases oxygen content and decreases cycle period (speeds up the neuronal rhythm). B. Original recordings of two stomatogastric nerves from the same study. The top recording shows the activity of a pyloric neuron ('PY'). The bottom recording depicts the bursts of the gastric mill neuron ('MG', highlighted in green). Prior to feeding (top panel), oxygen content is low, the pyloric rhythm is slow and gastropyloric interactions are present (highlighted in blue). When gastropyloric interactions are present, the pyloric rhythm slows down whenever the gastric mill neuron bursts. Feeding (middle panel) heightens arterial oxygen, speeds up the pyloric rhythm and abolishes the gastropyloric interactions. Gastric mill bursts no longer influence the pyloric rhythm. When arterial oxygen was artificially lowered after feeding (bottom panel), the pyloric rhythm slowed down again, and gastropyloric interactions returned. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

but only when oxygen levels were allowed to increase (Clemens et al., 1998). *In vitro* experiments with isolated ganglia supported these conclusions, suggesting that coordinated operation of multiple neural networks may be modulated by local changes in oxygenation. So far, however, relatively little is known about the cellular actions of oxygen in crustacean neurons.

Only a few studies have explored homeostatic responses to oxygen in neurons. A family of highly conserved transcription factors, the hypoxia-inducible factors, appear to play a role in homeostatic neuronal plasticity. For example, continued hypoxia increases the number of hypoxia-inducible factor-expressing cells in the central nervous system of mitten crabs, suggesting that these transcription factors may mediate protective processes and increase the adaptive potential to hypoxic stress in neurons (Chertok and Kotsyuba, 2016).

In conclusion, whether and how decapod crustacean nervous systems are affected by changes in ocean oxygen levels may be contingent on their capacity to regulate oxygen uptake, oxygen's ability to modulate neuronal circuits, and the ability of neuronal circuits to adapt to long-term changes. However, only a few species have been studied. An obvious research question for future studies would be to evaluate whether low oxygen availability limits neuronal function or if it instead modulates neuronal activity to meet energetic demands.

2.2. pH

Currently, the *average* acidification of the open ocean is mild and within the range of pH changes usually experienced by decapod crustaceans in their natural habitats - a change of 0.1 pH units in the last 50 years, mostly limited to the topmost water layers (Raven et al., 2005; Doney et al., 2009; Reid et al., 2009). This is especially the case in coastal and estuarine ecosystems, where large pH changes are observed. The mild average ocean acidification, while significant, is well within the ability of homeostatic ion regulation in decapods (Whiteley and Taylor, 2015). In fact, most behavioral studies in marine animals suggest that behavioral effects only occur when pH changes more than a unit (a factor of 10 for the H^+ ions) (Appelhans et al., 2012; De la Haye et al., 2012; Leduc et al., 2013). Models predict a continuous decrease in ocean pH over the next centuries, peaking at ~0.8 units in surface layers and ~0.4 units in deeper waters through vertical exchange (Doney et al., 2009; Duarte et al., 2013). There are very few studies that have systematically analyzed the effects of such pH changes on the decapod nervous system. The few available studies report that even large pH changes appear to have little influence on neuronal activity. A recent study (Haley et al., 2018) exemplifies this aspect by probing spontaneous bursting activity in the stomatogastric ganglion at different pH levels. Bursting here results from the intricate interactions of many intrinsic and synaptic ion channels (Stein, 2017). Even though the pH regulatory organs had been removed and the nervous system was directly exposed to pH changes in these *in vitro* experiments, changes of less than 1 pH unit showed little to no effect on spontaneous neuronal activity. These data are surprising since the species studied (*Cancer borealis*) lives in somewhat deeper waters with relatively small changes in pH. The data corroborate earlier measurements of pH effects on the same neuronal circuit in a related species, *Cancer pagurus* (Golowasch and Deitmer, 1993), and thus indicate the large capacity of crab neurons to compensate for extracellular pH changes. Taken together with the fact that climate change-induced alterations in pH in the open ocean are comparatively small and occur over decades to centuries, it appears that the pH changes predicted for the open ocean may not have strong effects on the decapod nervous system.

In some coastal ecosystems pH fluctuations can be much larger and can reach up to 1 pH unit during diel, seasonal and decadal oscillations, or as a result of eutrophication via anthropogenic interactions (e.g. (Borgesa and Gypensb, 2010; Hofmann et al., 2011; Melzner et al., 2013), review: (Duarte et al., 2013)). However, due to the heterogeneity of coastal ecosystems and the many types of anthropogenic influences they are exposed to (e.g. (Salisbury et al., 2008)), identifying a common prediction for the future pH trajectories of coastal ecosystems is unlikely. Coastal areas in arid regions or regions without major human settlements will likely experience small pH changes that align with the anthropogenic CO_2. In contrast, pH changes will be exaggerated and larger than expected from CO_2 emission alone in coastal regions with high-level watershed influences or human urbanization. Here, pH changes could range from steep acidification to basification (Duarte et al., 2013), both of which will challenge the pH buffering abilities of decapod crustaceans.

In marine fish, water acidification appears to reduce olfactory performance and predator recognition (Leduc et al., 2013), and to increase anxiety (Hamilton et al., 2014), although these ideas have recently been challenged (Raby et al., 2018; Clark et al., 2020). The suggested mechanism involves increased excitatory neuronal responses when enhanced and sustained osmoregulation is required. Specifically, the reversal potential of $GABA_A$ receptors, through which bicarbonate and chloride are transported, is hypothesized to shift during high osmoregulatory demand such that instead of being inhibitory, these channels become excitatory (Tresguerres and Hamilton, 2017). Direct physiological measurements supporting this phenomenon are lacking, as well as the exact pH ranges in which this may occur. A handful of studies have indicated that similar effects could occur in decapods. For example, bicarbonate accumulation was observed in the green crab, *Carcinus maenas*, after a 10 week-long exposure to pH levels predicted for the year 2100 and after (pH 7.38). Concurrently, feeding rates were reduced, indicative of a potential impairment of olfactory processing (Appelhans et al., 2012). Similarly, in hermit crabs (*Pagurus bernhardus*) feeding-related behaviors and antennal flicking were reduced, and crabs were less successful in locating food odor sources and optimal shells for shelter (De la Haye et al., 2011, 2012). However, crabs also showed an overall reduction of locomotion, the tested pH levels were acidic (pH 6.8), and no clear distinction to concurrently induced CO_2 changes were assessed. Roggatz et al. (2016) have shown that even smaller pH changes (0.4 pH units) impair peptide-induced egg ventilation behaviors in *Carcinus maenas*. However, this effect was not mediated through effects on the nervous system directly, but *via* protonation of the signaling peptides and a subsequent reduction in affinity to the receptors. The question thus remains whether pH changes affected the nervous system and contributed to the observed behavioral changes. Data from crayfish suggest that there are interactions between GABA receptors and bicarbonate (Voipio et al., 1991), and it is established that bicarbonate and chloride are involved in pH regulation in decapods (Moody, 1981; Boron, 1987; Whiteley and Taylor, 2015). It is thus at least conceivable that pH changes can affect GABA signaling, which should, in principle, be straight forward to test through measurements of $GABA_A$ receptors currents using traditional electrophysiology.

2.3. Salinity

Warming of the atmosphere and the ocean waters is expected to increase surface water evaporation and air humidity. Each degree of warming of the lower troposphere is expected to add around 7% atmospheric moisture (Held and Soden, 2006). Along with an intensification of water redistribution by the heated air, this is expected to increase precipitation and thus surface water flux (~8% per degree surface warming, (Durack et al., 2012)). Consequently, surface water salinity will trend toward more extremes: already low salinity areas will become less salty and high salinity areas will increase in salinity due to the temperature-driven increase in the ocean water cycle (Durack et al., 2012). Salinity changes will likely be dramatic in polar areas due to melting ice, and in semi-enclosed oceans or areas with little convection such as the Black and Baltic seas (Fig. 1C) (Durack et al., 2012). Here, heavy rainfalls will increase river run-off and act in addition to quick and large local temperature changes. This could severely alter the microenvironment of decapods.

Decapods appear to possess a variety of behavioral and physiological responses that allow them to cope with salinity changes, including highly active osmoregulatory tissues (Charmantier, 1998; Whiteley and Taylor, 2015; Whiteley et al., 2018). In contrast, we know very little about the responses of the nervous systems to salinity changes, but there are likely important differences between osmoregulating and osmoconforming species (Taylor and Taylor, 1992; McMahon, 1995; Pequeux, 1995; Wirkner and Richter, 2013). In osmoregulating species, the nervous system is likely shielded from salinity changes through a set of osmoregulatory processes that maintain internal osmotic conditions, at least within the range of the naturally experienced water salinities. This should be less the case in osmoconforming species. Indeed, hemolymph studies indicate that the shore crab, *Carcinus maenas*, was able to osmoregulate (Winkler et al., 1988) in largely different salinities (although maybe not for extended periods of time (Siebers et al., 1972)). This was not the case in *Cancer pagurus*, a known osmoconformer (Whiteley et al., 2018). We are not aware of any studies testing neuronal responses in osmoconformers, but investigations in a variety of osmoregulating decapods, including freshwater and marine species, have demonstrated a clear connection between the neuroendocrine system and changes in salinity (McNamara et al., 1991). Specifically, osmoregulation depends on the secretion of neuroendocrine factors from the eyestalk X-organ/sinus glands complex. A variety of environmental stressors, including temperature and salinity changes, modulate immune functions through this complex (Manfrin et al., 2016) and enable efficient osmoregulation (Engel et al., 1974; Freire and McNamara, 1992; Henry and Campoverde, 2006; Mitchell and Henry, 2014; Zhao et al., 2016). Very little is known about how these neuroendocrine factors facilitate osmoregulation and whether they affect neuronal activity. It is known, however, that neuroendocrine factors, including a variety of neuropeptides, exhibit changes in their relative abundances in response to environmental changes (Zhang et al., 2015), and that they accumulate in different nervous system tissues (Freire and McNamara, 1992). At least one study has suggested neuro-behavioral consequences from salinity stress. Here, salinity changes altered long-term memory in *Neohelice* crabs (Delorenzi et al., 2000). Thus, it is at least feasible that salinity changes alter neuronal activity, but further research is necessary to determine the mechanisms and extent to which these changes act.

For more peripheral neuronal structures, such as sensory and motor axons, salinity stress may come with more immediate challenges. Peripheral areas are less perfused with osmocontrolled hemolymph and more exposed to environmental factors. Leg nerve axons indeed appear to be sensitive to salinity changes: The membrane potential and volume of peripheral leg nerve axons of the osmoconforming European spider crab, *Maja squinado*, for example, show clear dependencies on salinity (Pichon and Treherne, 1976). Behavioral experiments in another osmoconforming species, *Cancer magister*, indicate that the sensory system in these crabs detects salinity changes of 3.5‰, and elicits behavioral changes in response (Curtis et al., 2010). In contrast, in osmoregulating species, specific adaptations may protect the peripheral nervous system from direct influences of salinity. In the blue crab, *Callinectes sapidus*, for example, paracellular ion movement to the antennae appears to sustain olfaction even when salinity fluctuates (Gleeson et al., 2000). Yet, the considerable morphological heterogeneity between crustacean taxa and the wide range of physical challenges their different habitats provide pose a significant challenge for the study of crustacean sensory responses (Hallberg and Skog, 2011).

2.4. Temperature

The effects of climate change on temperature in marine environments are highly heterogenous. Globally, surface temperatures have continuously risen for over a century now (Fig. 1A). Superimposed on these average changes are local seasonal and decadal variabilities, and some markedly rapid and larger temperature changes in specific areas (Reid et al., 2009). For example, until recently, a cooling was observed in the Northwest Atlantic, while warming was prevalent in the Northeast. In the Baltic Sea, the annual mean temperature of the surface water has increased by ~0.1 °C/decade since 1861, but this warming has accelerated to 1 °C/decade between 1990 and 2008 (Pawlak, 2013). In 2018, the highest bottom coastal water temperatures since the beginning of the recordings were measured (Humborg et al., 2019). Models predict a further acceleration of the temperature increase (Meier et al., 2012) and more frequent warming periods (Mann et al., 2018).

There is no organ for temperature regulation in marine invertebrates. Consequently, their body temperature tracks the ambient temperature with relatively small time delays (on the order of minutes, (Soofi et al., 2014)). As a result, all physiological processes are exposed to temperature changes, and the survival of the animal depends on either behavioral responses to avoid temperature changes, or on physiological adaptations that allow them to continue to function despite them. Quick evasion to less temperature-fluctuating microhabitats, for example, supports survival during transient temperature changes, while slower homeostatic responses are required to adjust to persistent temperature changes. For instance, in coastal habitats, the vertical zonation of the subtidal to intertidal gradient creates different thermal niches. Animals living higher on the shore, especially those exposed to the air at low tide, experience large daily and seasonal fluctuations in their microhabitat (Somero, 2002; Stillman, 2002). The porcelain crab, *Petrolisthes cintipes,* spends low tides hidden underneath rocks of the upper intertidal. On days with high sun exposure the temperature can rise to almost 31 °C under the rocks, more than 15 °C higher than the air temperature (Stillman and Somero, 1996). The neuronal mechanism underlying this behavioral response remains unknown but could provide insight into immediate responses to transient temperature changes. During high tide, the temperature drops rapidly to 8 - 9 °C with the incoming seawater, which highlights the selective importance of a high thermal tolerance for crustaceans inhabiting the higher intertidal. The same authors later compared the thermal tolerance of 20 species of porcelain crabs from the eastern Pacific (Stillman and Somero, 2000), showing a strong correlation between maximal habitat temperature and upper lethal temperature. This suggests that compared to subtidal species, intertidal species may be living nearer to their thermal maxima. Thus, they may be less able to increase their upper thermal tolerance limits in response to slow and longer-lasting temperature changes. An exhaustive review of the physiological consequences and responses can be found in Hofmann and Todgham (2010).

With respect to the nervous system, it appears that the upper thermal limits for survival correlate with compromised nervous function. In excised leg motor neuron bundles of *Astacus astacus*, for example, action potential propagation was lost before the upper critical temperature for cardiovascular function (Ern et al., 2015). However, decapod crustaceans also appear to possess compensation mechanisms to keep detrimental temperature effects in the nervous system to a minimum. An example comes from crabs of the genus *Cancer*, where temperature robustness of pattern generating neurons has been tested *in vitro* and *in*

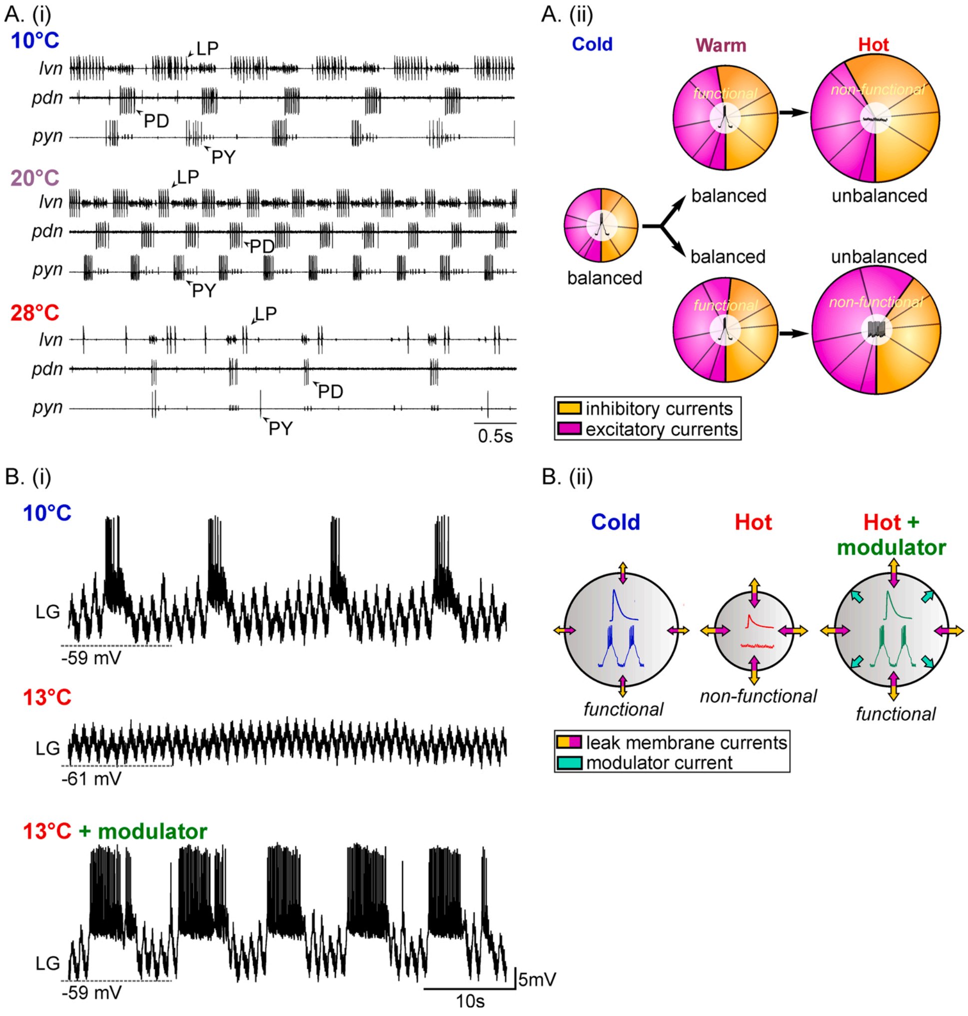

Fig. 5. Temperature effects on stomatogastric neurons and circuits. A. (i) The pyloric rhythm of *Cancer magister* continues to function over a wide range of temperatures. Recording of three neuron types ('LP', 'PD', 'PY') on their respective nerves ('*lvn*', '*pdn*', '*pyn*') at 10 °C, 20 °C and 28 °C. At 28 °C rhythmicity ceases and only sporadic neuronal activity remains. Courtesy of Liisi Vink-Lainas (Illinois State University). (ii) Temperature increases all ionic membrane conductances. The plot represents the relative contribution of excitatory and inhibitory conductances at increasing temperatures. Only when the temperature sensitivities of the ion channels are coordinated, a balanced set of ionic conductances can be achieved and neuronal activity remains functional. Excessive temperature increase leads to an imbalance between excitatory and inhibitory ionic conductances, either favoring inhibition (top, leading to inhibited neuronal activity) or excitation (bottom, leading to overexcitation). B. (i) Excessive leakage in neurons prevents action potential generation. Even small increases from 10 °C to 13 °C lead to a crash of the gastric mill rhythm in *Cancer borealis* by shunting action potential generation (Städele et al., 2015). The recordings show the intracellular membrane potential of the lateral gastric (LG) neuron at different temperatures. Extrinsic neuromodulation with a neuropeptide restores the neuron's ability to fire and allows the rhythm to continue even at elevated temperature. (ii) Leak currents increase dramatically with temperature and render a neuron non-functional due to a shunt of electrical events across the membrane. Circle size represents neuron excitability, inside traces show neuronal membrane potential (bottom) and synaptic input (top). Left: At cold temperatures, synaptic inputs are large, and the neuron is bursting. Middle: Increased shunt reduces excitability and diminishes the amplitude of synaptic events. This silences the neuron. Right: Peptide neuromodulation increases neuron excitability through an 'anti-leak' current, which increases synaptic events and restores functional neuronal activity.

vivo (Tang et al., 2010; Soofi et al., 2014; Städele et al., 2015; Kushinsky et al., 2019). These crabs can live at rather cold ocean temperatures (http://www.cfrfoundation.org/jonah-crab-lobster-research-fleet; accessed 2020/06/30) and experience fluctuations between 3 °C and 18 °C during the year. Nevertheless, the rhythmic activities of neurons in the stomatogastric nervous system (see Fig. 2 for location and function) remain stable up to 28 °C (Fig. 5A, i). High temperature alters the balance of ion flow across the neuronal membrane. It is this balance that allows neurons to produce their activity patters and responses, and changes to this balance can severely impair neuronal activity. In the stomatogastric nervous system, the temperature responses of ion channels in neurons controlling the pyloric filtering of food in the stomach appear to be matched (Tang et al., 2010; Soofi et al., 2014; Kushinsky et al., 2019) such that an appropriate balance of ion flow is maintained when temperature changes (Fig. 5A, ii). The temperature responses of ion channels are due to their inherent biophysical properties, allowing stomatogastric neurons to continue to function even when temperature changes rapidly. More recent experiments show that the axons of these motor neurons also continue to function at such high temperatures (DeMaegd and Stein, 2020). There is additional evidence that homeostatic responses change the temperature range in which robust neuronal activity is generated (Tang et al., 2012). In crabs acclimated for several weeks to high temperatures, neuronal activity at these high temperatures was more stable than in cold-acclimated animals, suggesting long-term homeostatic plasticity of the biophysical properties within stomatogastric neurons. However, no data is available on whether this was the result of an extension of the temperature-robust range, a shift towards higher temperatures, or the result of temperature-induced neuromodulation.

Neurons in the same system also exploit an additional mechanism to avoid detrimental temperature effects on neuronal activity. A major problem for neurons is the exorbitant increase in membrane leakage due to the increasing ion flow through ion channels when temperature rises. The leakage shunts neuronal responses, leading to crashes of neuronal activity. Städele et al. (2015) demonstrated that extrinsic neuromodulatory inputs counterbalance the leakage (Fig. 5B, i, ii) and stabilize neuronal activity beyond the temperatures that the intrinsic biophysical properties of the neurons by themselves allow. It thus appears that even for benthic species that live in mostly temperature-stable cold waters, the climate change-induced average temperature changes in the open ocean are small and without major implications on the functioning of neurons and circuits beyond a generally higher activity. This corroborates data from shrimp and hermit crabs, which attest them a temperature tolerance large enough to survive the temperature increase projected for nearly two centuries (Madeira et al., 2018). It remains to be seen, however, whether the observed temperature-compensation mechanisms are shared with deep ocean and coastal species that experience vastly different temperature challenges. With respect to climate change, *Carcinus maenas*, one of the most successful decapod invaders, may serve as a good study organism due to its extensively described responses to abiotic influences (Leignel et al., 2014), including temperature effects on food processing (McGaw and Whiteley, 2012). Future studies should also address if homeostatic plasticity or evolutionary adaptations to higher temperatures introduce an increased sensitivity to additional changes as predicted by population survival data (Faria et al., 2020). Studies should also determine the cellular responses of neurons to elevated temperatures (such as heat shock protein expression (Jost et al., 2012)), and how multiple interacting environmental factors influence neuronal activity (Harrington et al., 2020).

3. Development

Many marine decapod crustaceans develop through a complex biphasic life cycle. Their larval phase occurs in pelagic environments, followed by juvenile and adult phases mostly at the benthos (Anger, 2001, 2006; Martin et al., 2014; Anger et al., 2015; Torres et al., 2019; Møller et al., 2020). Larvae grow by successive moults in a species-dependent sequence of larval instars (Zeng et al., 2020) and go through a more or less pronounced metamorphosis towards the end of their larval life to settle as a benthic juvenile. Metamorphosis involves major transitions in habitat, behaviour, locomotion, feeding, morphology, and ecology (Gebauer et al., 2020; Haug, 2020). Decapod larvae display a rich behavioral repertoire that allows for responses to fluctuations in environmental factors such as light, hydrostatic pressure, tidal currents, and temperature (Forward, 2009; Epifanio and Cohen, 2016; Cohen and Epifanio, 2020). These behaviors are controlled by highly developed larval sensory systems, including compound eyes and abundant chemo- and mechanosensory sensilla (Spitzner et al., 2018).

Decapod larvae often represent the most sensitive stage of the crustacean life cycle and therefore are strongly affected by fluctuations in the animal's environment. Temperature, for example, determines the length of the larvae's dispersal phase (longer at lower temperatures) and affects larval growth and survival (Anger, 2006; Epifanio, 2013; Anger et al., 2015; Torres et al., 2019; Giménez, 2020). Crab larvae show a suite of responses to environmental drivers, including changes in their acclimation state, timing of moulting, growth rate, chemical composition, body size, and switches from short to long developmental pathways that include additional larval stages (summarised in Giménez (2020)). Information on reaction norms of brachyuran larvae were also used to predict future range expansion or range shifts of crab species in the future ocean (Sanford et al., 2006; deRivera et al., 2007).

In parallel with the availability of new neuroanatomical techniques, our understanding of the processes that guide the ontogeny of the crustacean central nervous system (e.g. (Scholtz and Gerberding, 2002; Sandeman and Sandeman, 2003; Whitington, 2004; Harzsch and Hafner, 2006; Harzsch et al., 2015; Harzsch and Viertel, 2020; Jirikowski et al., 2020), including chemosensory (Sandeman and Sandeman, 2003) and visual systems (Harzsch and Hafner, 2006), has persistently grown. Neuroblasts - embryonic neuronal stem cells - generate ganglion mother cells which later divide to give birth to ganglion cells (neurons). This process continues after hatching into larval life (Harzsch and Dawirs, 1994, 1996c; Harzsch et al., 1998). At hatching, decapod larvae already possess a functional central nervous system that drives their behavioral responses to environmental stimuli (Harzsch and Dawirs, 1993, 1996a). For example, hatching lobster larvae are equipped with the neuronal networks that constitute the circadian clock (Harzsch et al., 2009). However, the nervous system continues to grow (Spitzner et al., 2018) and neurons continue to mature in the larval stage (Harzsch and Dawirs, 1995, 1996b; Chung and Webster, 2004). For example, there are obvious ontogenetic changes with respect to neuromodulation as neurons continue to associate with neuroendocrine centers (Webster and Dircksen, 1991; Rotllant et al., 1994, 1995).

Recently, the impact of future ocean conditions on the development of decapod crustacea has moved into focus. Sustained exposure to low pH levels, for example, appears to be detrimental to larval metabolism and developmental performance (Carter et al., 2013; Ceballos-Osuna et al., 2013; Rato et al., 2017). CO_2-induced pH reduction also affects geotactic behavior (vertical migration) and may thus influence tidal transport and dispersal of the larvae (Gravinese et al., 2019). Some studies have also addressed the effects of multiple drivers. For instance, temperature and salinity lead to multiple stressor effects on larval development (e.g. (Gonzalez-Ortegon et al., 2013; Spitzner et al., 2019)). Exposure of spider crab larvae (*Hyas araneus*) to the combined effects of elevated CO_2 and heat alters heat shock protein expression, resulting in a decrease of the animal's thermal limits (Schiffer et al., 2014).

To our knowledge there is not a single study that has assessed how environmental drivers alter the histology or cellular organization of single organ systems. It is sensible to assume that environmental stress has an impact on the development and function of the central nervous system, with corresponding consequences for essential behaviors such as vertical migration or predator avoidance. Whether the acute and homoeostatic mechanisms that protect the adult nervous system against environmental fluctuations are similarly efficient in the various ontogenetic stages is unknown. Future studies may thus focus on rates of mitosis, levels transmitter expression, growth of neurites and synaptogenesis, and how they are affected by environmental stressors.

4. Conclusions

At first glance, the current changes of ocean waters appear to have only mild to immediate effects on nervous system function. However, it is also obvious that we lack the breadth as well as the depth in the data to make convincing arguments that this conclusion is pertinent to more than a handful of species or to future changes in oxygen, pH, salinity, and temperature.

Environmental changes and their effects are highly heterogenous. This challenges the approach taken in most neuroscientific studies, i.e. to select a few well-characterized species to extrapolate and generalize neuronal mechanisms from them. This approach attracts much attention when it comes to understanding the basic functioning of the nervous system and is helpful for improving human health. However, it is inherently inadequate to address the issue of how changing environments affect neuronal function and behavior. The recent focus of neurobiological research on a handful of well-characterized systems has severely limited our understanding of how environmental factors alter neuronal responses in species that possess largely different physiologies. It has also left us struggling to understand how idiosyncrasies between species impact neuronal responses. The demise of decapod crustaceans for studying nervous system function in recent decades is a good example for this. The consequence is that we know much about their behavioral and populations responses to climate change, but relatively little about how their nervous systems copes with changes in the environment.

There is a clear contradiction between the observed effects of climate change on species migration and survival and neuronal studies that indicate that the current ocean changes have little effect on neurophysiology. One reason may be that the nervous system is protected by several layers of physiological barriers, and that neurons, as the ultimate drivers of behavior, are particularly adapted to extreme conditions to ensure survival. It may also be the case that synergies between different stressors are simply unexplored. Data from other tissues and physiological processes suggest that synergistic effects are rather common (Boyd et al., 2018; Klymasz-Swartz et al., 2019). The effects of combined stressors on the nervous system are beginning to be explored more rigorously. For example, recent data from Australian crab species indicate that even small temperature changes combined with mild acidification lead to changes in range extension and a shift in hierarchy between invasive and native decapod species (Lauchlan et al., 2019). This emphasizes the need for studying the *combined* effects of environmental stressors as none of them act in isolation. The combined effects are likely nonlinear and likely differ between species, developmental stages, and environments. Addressing this issue requires an interdisciplinary effort that includes geneticists, molecular biologists, neurophysiologists, behavioral biologists, ecologists and, importantly, modelers and data analysts to interpret the data. A challenge for these efforts will be to bring the important factors from the field into the laboratory and to create appropriate experimental designs. We already know that for some physiological processes the dynamics rather than the average of environmental change is critical. For temperature-dependent sex determination in turtles, for example, it is not the average temperature, but the way temperature fluctuates that is critical for the sex ratio of the offspring (Bowden and Paitz, 2018). It would not be surprising if similar mechanisms existed for neuronal physiology (Boersma et al., 2016).

An additional caveat of our current knowledge is that it stems mostly from studies of immediate neuronal responses, ignoring long-term plastic responses that are clearly happening. Almost all examples we discussed here are about immediate or short-term neuronal responses. There are very few studies that address longer-term effects, although phenotypic plasticity and evolutionary adaptation are currently discussed as essential mechanisms to adapt to environmental changes in marine ecosystems (Reusch, 2014; Boyd et al., 2018). A first step would surely be experiments involving gene expression changes through homeostatic mechanisms. Such experiments might be within reach in the next few years, given the recent surge in less-expensive molecular and transcriptomic approaches even in genetically less-well studied species. Studies on prolonged effects that may involve maternal effects, and ontogenetic and epigenetic influences will require many years unless species with rapid generation times are used. Funding agencies are usually not prepared for such long-term approaches, in particular if the research investigates so called non-model organisms with limited economic impact or implications for human health. Typical funding cycles range between 3 and 5 years, tending towards shorter ones, and thus may not be sufficiently long to draw meaningful conclusions from long-term studies. One of the challenges will be that the early live stages of many marine decapod crustaceans live in vastly different waters and, during ontogeny, move from pelagic to benthic areas (Torres et al., 2019). Providing appropriate environmental conditions in laboratory conditions will not be easy, but it can be expected that the different live stages show distinct sensitivities to environmental stressors.

5. Perspectives

Decapod crustaceans offer many opportunities to address the challenges mentioned above. More and more genomes and transcriptomes now become available (e.g. (Gutekunst et al., 2018; Zhang et al., 2019)). This makes it possible to ask epigenetic and genomic questions even in these non-genetic model systems. Together with the fact that there is significant knowledge of (neuro-)physiological processes, this now opens the opportunity to investigate neuronal responses from the genetic to physiology levels.

One strong advantage of decapods is that we can carry out comparative approaches between many different species, in many different habitats. We call for greater research efforts towards cross-species comparisons of neuronal anatomy, modulation and physiology to enable a broader understanding of the processes involved in dealing with changing environmental influences. Even more, there are around 3,000 species of decapods that live in freshwater or semi-terrestrial that can be used for further comparative approaches. Despite this diversity, the general bauplan of the nervous system is conserved, and individually identifiable neurons and circuits can be traced across evolutionary distances. Some decapod species, such as *Carcinus maenas*, have invaded many different habitats and live in various distinct environmental conditions. This makes them ideal organisms to study the influence of environmental changes on the nervous system (Leignel et al., 2014; Rodrigues and Pardal, 2014). Common garden experiments, where the *same* species can be collected from distinct environments and then tested together in a controlled lab environment may complement or even replace long-term transgenerational lab experiments. New sensors may even allow measurements of the individual animal's microenvironment and make *in vivo* physiology for longer-term experiments possible. This eco-physiology approach would combine laboratory and field studies, and ultimately strengthen our understanding of how climate change affects the development, physiology, and evolution of the decapod nervous system.

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Declaration of Competing Interest

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