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**Impact of
anthropogenic ocean
acidification**

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Impact of anthropogenic ocean acidification on thermal tolerance of the spider crab *Hyas araneus*

K. Walther, F. J. Sartoris, C. Bock, and H. O. Pörtner

Alfred-Wegener-Institute for Polar and Marine Research, Department Integrative Ecophysiology, Am Handelshafen 12, 27570 Bremerhaven, Germany

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Correspondence to: K. Walther (kathleen.walther@awi.de)

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Abstract

Future scenarios project combined developments of elevated CO₂ concentrations and global warming and their impact on marine ecosystems. The synergistic impact of both factors was addressed by studying the effect of CO₂ accumulation on thermal tolerance of the cold-eurythermal spider crab *Hyas araneus*. Animals were exposed to present day normocapnia (380 ppm CO₂), CO₂ levels expected towards 2100 (710 ppm) and beyond (3000 ppm). Heart rate and haemolymph PO₂ (P_eO₂) were measured during progressive short term cooling from 10 to 0°C and during warming from 10 to 25°C. An increase of P_eO₂ occurred during cooling with highest values reached at 0°C under all three CO₂ levels. Heart rate increased during warming until a critical temperature (T_c) was reached. The putative T_c under normocapnia was presumably >25°C, from where it fell to 23.5°C under 710 ppm and then 21.1°C under 3000 ppm. At the same time, thermal sensitivity, as seen in the Q_{10} values of heart rate, rose with increasing CO₂ concentration in the warmth. Our results suggest a narrowing of the thermal window of *Hyas araneus* under moderate increases in CO₂ levels by exacerbation of the heat or cold induced oxygen and capacity limitation of thermal tolerance.

1 Introduction

The ongoing increase of CO₂ in the atmosphere is a key driver of global warming (IPCC, 2001, 2007) and causes an increase in accumulation of CO₂ in the oceans leading to an acidification. Caldeira and Wickett (2005) modelled different future scenarios for CO₂ concentrations in the atmosphere and ocean. By 2100 they projected atmospheric and surface ocean levels of 710 ppm CO₂ and for the year 2300 much beyond depending on the use of fossil fuel resources. Values reached may potentially comprise 3000 ppm CO₂. This leads to questions about the potential impact of ocean acidification on marine ecosystems in times of ocean warming (cf. Pörtner et al., 2005, 2008). Physiological mechanisms affected by CO₂ have been identified, however, past stud-

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ies on the influence of CO₂ on crustaceans were conducted with a different focus and used concentrations of about 10 000 ppm CO₂ (Cameron, 1978, 1985; Cameron and Iwama, 1987; Metzger et al., 2007; Pane and Barry, 2007; Wickins, 1984) or realistic scenarios (Spicer et al., 2007). For reliable conclusions concerning the impact of CO₂ on the physiology and fitness of crustaceans in the near future, it is necessary to include realistic CO₂ concentrations in those studies, as postulated for 2100 (710 ppm) or beyond (3000 ppm).

The present study investigates the impacts of CO₂ and temperature on the physiology of *Hyas araneus* in the context of the thermal tolerance concept originally developed by Frederich and Pörtner (2000) for *Maja squinado*. The thermal tolerance window as characterized by temperature dependent haemolymph oxygen partial pressure (P_eO₂), heart and ventilation rates comprises the temperature range of aerobic performance (or scope). The thermal optimum is the temperature where performance is maximal, supported by high haemolymph oxygen tension, and maximum scope (i.e. increase above maintenance) for heart and ventilation rates. The earliest limits of the thermal tolerance range with ecological effect (Pörtner and Knust, 2007) are set by high and low pejus temperatures (T_p). An increased temperature leads to rising oxygen demand that can be met by oxygen supply through enhanced ventilation and heart rate (Zainal et al., 1992). The upper T_p indicates the point, where ventilation and heart rate level off to remain constant. Haemolymph oxygen partial pressure decreases within the subsequent pejus range, as a result of a mismatch developing between the rising oxygen demand for maintenance and the limited capacities of ventilation and circulation in oxygen supply. Beyond pejus range, a critical temperature defines the onset of anaerobic metabolism, where accumulation of L-lactate, succinate and inorganic phosphate sets in and aerobic scope is minimized (Zainal et al., 1992; Stillmann and Somero, 1996; Frederich and Pörtner, 2000; Melzner et al., 2006). In the following pessimum range animal life is sustained for limited time only. Such critical temperatures can be identified from patterns of P_eO₂ or heart rate. A drop in heart rate also characterizes the critical temperature as it coincides with the onset for anaerobic metabolite accu-

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mulation (Frederich and Pörtner, 2000; Melzner et al., 2006). As P_{eO_2} levels depend on oxygen consumption and are controlled by ventilation and heart rate the determination of critical temperatures in different crab species (Ahsanullah and Newell, 1971; Cuculescu et al., 1998; Stillman and Somero, 1996; Worden et al., 2006) from heart rate measurements would then match critical thermal limits according to the concept of oxygen and capacity limited thermal tolerance.

The impact of moderate elevations in CO_2 on thermal window may be small in the thermal optimum but may exert stronger effects on thermal limits as hypothesized earlier (Pörtner et al., 2005; Pörtner and Farrell, 2008). The reduction in aerobic scope towards thermal extremes will decrease functional capacity and fitness and may minimize survival in the field once animals are exposed to thermal extremes (Pörtner and Knust, 2007).

Little is known about the interaction of CO_2 and temperature tolerance of cold-eurythermal invertebrates. For an analysis of the impact of CO_2 on crustaceans, the spider crab *Hyas araneus* (L.) was chosen as a model. *Hyas araneus* is distributed in the North Atlantic from the North Sea, near Helgoland, Germany, to the Arctic around Svalbard, Norway (Christiansen, 1969). The mean ambient temperature of the North Sea ranges from 3°C to 18°C throughout the year (Wiltshire and Manly, 2004), whereas in Svalbard waters *Hyas araneus* is exposed to temperatures between 0°C and 6°C (Svendsen et al., 2002). The present study investigates the thermal window of the *Hyas araneus* population around Helgoland in the context of the large temperature fluctuations experienced by the species in the North Sea. One further question addressed in this study is to what extent CO_2 affects the thermal tolerance range and whether this effect sets in under expected CO_2 accumulation scenarios in atmosphere and surface waters.

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2 Materials and methods

2.1 Animals

Adult *Hyas araneus* (L.) were caught between August and October 2007 around Helgoland, Germany. The animals (carapace length: 68.8 ± 2.8 mm) were held in tanks with aerated re-circulating natural seawater at $10 \pm 0.2^\circ\text{C}$, 32–33‰ salinity, pH 8.0 and a 12 h light cycle at the Alfred Wegener Institute in Bremerhaven, Germany, for at least 4 weeks before the beginning of the experiments. The animals were fed twice a week with pieces of mussels (*Mytilus edulis*). A thermostat (Lauda, T1200) ensured tight temperature control in the experimental setup tank. The temperature ramp starting from a control temperature of 10°C was coded using the wintherm plus program (Version 2.2) of the thermostat. The water was cooled from 10°C to 0°C and warmed continuously from 10°C to 25°C at a rate of 1°C per h. The accuracy of the temperature ramp was $1 \pm 0.2^\circ\text{C/h}$ for cooling and $1 \pm 0.1^\circ\text{C/h}$ for warming protocols.

2.2 Surgical procedures

Prior to experimentation animals were prepared for continuous simultaneous measurements of haemolymph oxygen partial pressure (P_{eO_2}) and heart rate. Briefly, two holes were drilled through the carapace, one directly over the heart, avoiding injury to the hypodermis. This hole was covered with latex dam to prevent haemolymph loss. The sleeve of an inflexible venipuncture needle (after Strauss, BRAUN, Germany) was used as an adapter for fixation of the oxygen optode. This adapter was fixed with dental wax over the drilled hole. A second hole was drilled behind the optode preparation for fixation of the Doppler probe used for heart rate measurements.

2.3 Oxygen measurements

Measurements of P_{eO_2} were carried out with microoptodes (NTH-PSt1-L5ITF-PC3,1-NS 35x1,20-YOP, PreSens GmbH, 93053 Regensburg, Germany). Data were recorded

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on-line by use of temperature compensation via TX2-A oxygen monitors and software (Oxy View TX2 C 4.02) (PreSens Regensburg, Germany). Optodes were calibrated in air-saturated millipore water (100%) and in oxygen-free seawater, using sodium disulfide (0%). The tip of the optode was inserted through the adapter and latex dam into the pericardial sinus and fixed with parafilm. Oxygen values were recorded as % air saturation and converted to P_eO_2 .

2.4 Heart rate measurements

Measurements of heart rate were carried out with a non-invasive laser Doppler perfusion monitor (LDPM PeriFlux System 5000, Perimed AB, Järfälla, Sweden) similar to Lannig et al. (2008). Prior to the experiments, the probe was two-point calibrated. The laser Doppler signal was monitored by chart 5 (AD instruments). Heart rates (beats/min) were derived from regular changes in the laser Doppler signal caused by fluctuating haemolymph flow. Laser Doppler values were averaged for individual temperature steps (0.1°C for the warming ramp, 0.2°C for the cooling ramp).

2.5 CO₂ incubations

After the implantation of the sensors, animals were allowed to recover for 24 h in 75-liter seawater tanks at 10°C. During the experiments animals were exposed to different CO₂ concentration (normocapnia, 710 ppm, 3000 ppm) in the seawater. For normocapnic conditions (380 ppm CO₂) seawater was bubbled with air. For exposure to different CO₂ concentrations Wösthoff gas mixing pumps (Typ 2M303/a-F-T, 5kM303/a-F, 5kM402-F) were used to mix CO₂-free air with CO₂. During exposure to 3000 ppm CO₂ water, water pH dropped from 8.0 to 7.3 (expected pH value calculated as 7.29). Equilibration with 710 ppm CO₂ concentration caused a pH decrease from 8.0 to 7.8 (expected value calculated as pH 7.80). Prior to exposure to the temperature ramp animals were exposed for 24 h to 10°C at each particular CO₂ concentration. New acid-base equilibria were reached in body fluids of the crabs within 24 h (Truchot, 1984). All animals

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survived experimentation.

2.6 Data analysis

Data are presented as means±SE. Statistical significance was tested using one-way ANOVA and post hoc Tukey tests (GraphPad Software, Prism 4). Discontinuities in the slopes of heart rate changes vs. temperature were calculated from intersections of fitted two-phase regressions according to the minimum sum of squares and were presented as breakpoints and critical temperatures (T_c). Linear regression lines were calculated with Prism 4 (GraphPad Software). Nonlinear regression curves were fitted using Boltzmann sigmoidal equation at Prism 4 (GraphPad Software). Q_{10} values were calculated from heart rates after De Wachter and Wilkens (1996): $Q_{10}=(f_{H2}/f_{H1}) \exp [10/(t_2-t_1)]$ with t =temperature and f_H =heart rate.

3 Results

Acute cooling from 10°C to 0°C resulted in a slight increase of P_eO_2 under all three conditions, i.e. normocapnia, 710 ppm, as well as 3000 ppm CO_2 , starting from values of P_eO_2 which fell with rising CO_2 levels (Fig. 1a). Under normocapnia mean P_eO_2 ranged from 9.49 kPa at 10°C to 13.24 kPa at 0°C, under 710 ppm values ranged from 8.72 kPa to 13.56 kPa and, under 3000 ppm, from 6.05 kPa to 10.65 kPa. The P_eO_2 values of crabs incubated under 3000 ppm were significantly lower than in animals under both normocapnia and 710 ppm (ANOVA, $p<0.001$).

Heart rate decreased between 10°C and 6°C with different slopes depending on CO_2 concentration (Fig. 1b). The heart rate of crabs incubated under 3000 ppm CO_2 fell more strongly than in animals incubated under 710 ppm and normocapnia. The statistical comparison of the three data sets obtained between 10°C and 0°C revealed a significant difference between animals under normocapnia and 3000 ppm as well as between those under 710 ppm and 3000 ppm (ANOVA, $p<0.001$). *Hyas araneus*

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specimens incubated under 3000 ppm displayed a lower heart rate than those under 710 ppm or normocapnia. Heart rate remained more or less constant between 6 and 0°C under all conditions, at a rate of 37.2 ± 1.2 beats/min under 3000 ppm, 39.64 ± 1.4 beats/min under 710 ppm and 40.27 ± 1.4 beats/min under normocapnia.

Upon acute warming from 10°C to 25°C haemolymph P_eO_2 values of *Hyas araneus* decreased (Fig. 2a), from a maximum of about 8.5 kPa at 10°C under normocapnia to a minimum of about 2.5 kPa at 25°C. Under the same warming protocol mean P_eO_2 in crabs under 710 ppm fell from 6.3 kPa to 0.8 kPa, and in specimens under 3000 ppm from 6.9 kPa to 1.37 kPa. Differences were statistically significant between data obtained under normocapnia and 710 ppm (ANOVA, $p < 0.001$) as well as between those under 3000 ppm and normocapnia or 710 ppm (ANOVA, $p < 0.01$).

Depending on CO₂ treatment heart rate of *Hyas araneus* displayed different patterns upon acute warming between 10°C and 25°C (Fig. 2b). Lowest rates were seen under normocapnia with relatively stable mean values between 43.7 and 55.0 beats/min. In contrast, heart rate increased under 710 ppm from 48.9 beats/min at 10°C to a maximum of 63.17 beats/min at 22.4°C leveling off towards 61.67 beats/min at 23.5°C and decreasing rapidly thereafter to 48.44 beats/min at 24.8°C. Crabs under 3000 ppm displayed an increase in heart rate from 52.49 beats/min at 10°C to 65.6 beats/min at 18.4°C leveling off to 62.52 beats/min at 21.1°C and decreasing thereafter to 50.05 beats/min at 24°C. Data under 3000 ppm were significantly different from those obtained under normocapnia or 710 ppm (ANOVA, $p < 0.001$).

Figure 3 depicts the heart rates measured between 10 and 25°C for an identification of calculated breakpoints defining upper critical temperatures (T_c). The upper T_c under 710 ppm was 23.5°C (Fig. 3b) and under 3000 ppm 21.1°C (Fig. 3c). Under normocapnic conditions no breakpoint could be identified in the observed temperature range between 10 and 25°C (Fig. 3a).

Figure 4 presents the comparison of P_eO_2 values and heart rates within the whole temperature range of all three incubations (normocapnia – Fig. 4a, 710 ppm – Fig. 4b and 3000 ppm – Fig. 4c). Contrasting trends result for P_eO_2 and heart rate. Clear

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changes in the development of heart rate upon warming under 710 ppm and 3000 ppm define the critical temperatures, confirming that the T_c is found beyond 25°C under normocapnia ($T_c > 25^\circ\text{C}$).

Accordingly, Q_{10} values of *Hyas araneus* heart rates (Table 1) increased from 1.26 under normocapnia to 1.35 under 710 ppm CO₂ and 1.32 under 3000 ppm CO₂ between 0 and 10°C. The gradients of heart rate changes were different from 0 to 6°C and 6 to 10°C. Therefore Q_{10} decreased from 1.30 to 0.96 with increasing CO₂ levels between 0°C and 6°C. Between 6 and 10°C the Q_{10} increased from 1.21 under normocapnia to 2.14 under 3000 ppm. Q_{10} calculations for the temperature ranges from 0, 6 or 10°C to the critical temperature assumed a T_c of 25°C under normocapnia, shown in Table 2. When heart rate remained nearly constant beyond critical temperature, as seen between 10 to 25°C, normocapnic Q_{10} values decreased further (Table 1). The Q_{10} increment with rising CO₂ levels was seen when calculated for the temperature range between 10°C and the respective critical temperature (T_c), as well as for between 0°C and the T_c or between 6°C and the T_c . These data demonstrate a stronger response to temperature under increasing CO₂ levels.

4 Discussion

4.1 Thermal tolerance window of *Hyas araneus*

The aim of the present study was to illustrate the impact of anthropogenic CO₂ accumulation in the oceans on the thermal tolerance window of the cold-eurythermal spider crab *Hyas araneus*. For an examination of the thermal tolerance window haemolymph oxygen partial pressure ($P_e\text{O}_2$) and heart rate were measured during warming and cooling protocols.

Hyas araneus exposed to the cooling protocol from 10°C to 0°C (Fig. 1a) displayed a moderate exponential increase in haemolymph oxygen partial pressure while heart rate decreased. Mean heart rate for *Hyas araneus* at 0°C under normocapnia was about

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37.2 beats/min and mean P_{eO_2} at 0°C was 13.6 kPa. Specimens exposed to warming from 10°C to 25°C (Fig. 2a) experienced a decrease in mean P_{eO_2} value to 2.5 kPa at 25°C while heart rate rose vaguely from 43.7 to 55.0 beats/min under normocapnic conditions. The comprehensive depiction in Fig. 4 shows that haemolymph P_{eO_2} continues to rise down to 0°C. These data contrast the first such data set elaborated in the spider crab *Maja squinado* (Frederich and Pörtner, 2000) where the temperature dependent pattern of P_{eO_2} characterized the thermal tolerance window. In *Maja squinado* P_{eO_2} fell upon cooling until a lower critical temperature was reached, subsequently anaerobic metabolism set in and indicated cold induced oxygen deficiency (Frederich and Pörtner, 2000).

The optimum temperature range of *Maja squinado* was seen between low and high pejus temperatures of 8.9 and 17.8°C, respectively (Frederich and Pörtner, 2000), with a maximum P_{eO_2} of 92.6 mmHg, equivalent to 12.3 kPa, which was more or less stable between those so-called pejus thresholds. The highest P_{eO_2} value recorded in *Hyas araneus* was 13.6 kPa at the coldest temperature of 0°C. These data indicate that the optimum performance range of *Hyas araneus* is shifted to colder temperatures when compared to *Maja squinado*. As *Hyas araneus* reached their highest P_{eO_2} values in the cold this may indicate that the species experiences no oxygen limitation at extremely cold temperatures, at least in its central organs close to the heart. Nonetheless, it may still undergo limitation in the perfusion of peripheral organs or in general, in functional capacity upon further cooling as shown in *Maja squinado* (Bock et al., 2001). All reptant decapod crustaceans were hypothesized to be excluded from permanently low temperatures of -1°C in polar oceans (Frederich et al., 2000). Data on anaerobic metabolite levels would be required to test whether loss of functional capacity rather than oxygen limitation would cause cold limitation in *Hyas araneus*.

The range of thermal tolerance of *Hyas araneus* can be derived from its range of natural distribution from the North Sea around Helgoland, Germany, northward to the Arctic around Svalbard, Norway (Christiansen, 1969). *Hyas araneus* can thus be characterized as a cold-eurythermal species with a lower thermal optimum range than in

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the warm-eurythermal *Maja squinado* (Frederich and Pörtner, 2000). Mean ambient water temperature of the North Sea at Helgoland Roads is about 3°C in winter and reaches 18°C in summer (Wiltshire and Manly, 2004). Annual temperatures in Svalbard waters fluctuate between 0 and 6°C (Svendsen et al., 2002). This wide range of habitat temperatures implies a wide thermal tolerance range of this spider crab.

The heart rate of *Hyas araneus* decreased exponentially between 10°C and 0°C under normocapnic conditions (Fig. 1b). A heart rate of 37.2 beats/min was measured at 0°C. This value appears high compared to the 20 beats/min reported for *Hyas araneus* at 0°C (Frederich et al., 2000). In *Maja squinado*, heart rate at 0°C was 10 beats/min and found below the lower critical temperature and within the pessimum range. A lower heart beat rate might not only reflect thermal limitation but also relate to the somewhat larger body size of *M. squinado* (carapace length: 142.5±30.5 mm (Bernárdez et al., 2005) compared to carapace length: 68.8±2.8 mm in *H. araneus*) (Ahsanullah and Newell, 1971; DeFur and Mangum, 1979). *Maja squinado*'s heart rates in the optimum range (9.3°C to 17.3°C) were about 40 to 60 beats/min (Frederich and Pörtner, 2000), at the low end of rates seen in *H. araneus* at 10°C and beyond. Close to 0°C, high P_{eO_2} values combined with relatively high heart rates of *Hyas araneus* reflect maintenance of performance at cold temperatures. The rise in P_{eO_2} in the cold reflects the facilitation in oxygen supply in cold waters, once tissue functional capacities are cold adapted. This facilitation is due to high oxygen solubility in cold waters and body fluids combined with a putative cold induced reduction of metabolic rates (cf. Pörtner, 2002). This conclusion is supported by the relaxed oxygen supply situation and the respective molecular to systemic adaptations of polar stenotherms (cf. Pörtner, 2006).

Under normocapnia and both elevated CO₂ tensions tested *Hyas araneus* heart rate decreased from 10 to 6°C and was nearly constant between 6 and 0°C, reflecting the lower end of an exponential decline phase which characterizes the lower end of the thermal window. This pattern is similar to the pattern of oxygen consumption within thermal tolerance windows as seen in the squat lobster *Munida rugosa* (Zainal et al., 1992) and in other marine invertebrates, e.g. the lugworm, *Arenicola marina* (Wittmann

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et al., 2008). Upon warming from 10 to 25°C the heart rate of *Hyas araneus* remained more or less constant under normocapnic conditions (Fig. 2b) with a Q_{10} close to 1 (Table 2). This indicates that the exponential phase was left and that circulatory performance reached its limit beyond 10°C, which would reflect the upper pejus temperature of the species. At higher temperatures the analysis revealed no discontinuities in the normocapnic data (Fig. 3). For comparison, heart rate data of *Maja squinado* displayed a break at 31.5°C, close to their critical temperature identified by the onset of anaerobic metabolism (Frederich and Pörtner, 2000). We conclude that the upper critical temperature of *Hyas araneus* under normocapnia is likely reached above 25°C.

The facts that the maximal P_{eO_2} of *Hyas araneus* is found close to 0°C, that the upper pejus temperature is likely close to 10°C and the critical temperature of *Hyas araneus* above 25°C indicates that the pejus range starting close to 10°C is somewhat more expanded than that of *Maja squinado* which displays a pejus range between 17.3 and 31.1°C (Frederich and Pörtner, 2000). This and the progressive rise in P_{eO_2} within the optimum range towards the more extreme cold distinguish *Hyas araneus* as a cold-eurythermal species from the warm-eurythermal *Maja squinado*.

4.2 CO₂ effects on thermal tolerance

During exposure to increased CO₂ concentrations (710 ppm and 3000 ppm) the P_{eO_2} of *Hyas araneus* displayed various decline phases between 0°C and 25°C resembling those under normocapnic conditions (Fig. 4). The same was true for heart rate. However, levels of heart rate and P_{eO_2} differed between CO₂ levels. Heart rate resulted lower between 10 and 0°C under 3000 ppm than under 710 ppm or normocapnia. This observation together with a trend for P_{eO_2} to be lower under high CO₂ levels indicate a reduction in functional capacity of oxygen supply in CO₂ exposed specimens in the cold.

Above 10°C, CO₂ concentration influenced the temperature dependent rise in heart rate, which resulted steeper with higher CO₂ levels. The increase in heart rate under 3000 ppm CO₂ (0°C to $T_c=21.1^\circ\text{C}$ from 36.73 to 62.52 beats/min) was larger than under

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710 ppm (0°C to $T_c=23.5^{\circ}\text{C}$ from 37.72 to 61.67 beats/min) or under normocapnia. The stronger thermal stimulation of heart rate under increasing CO_2 levels may reflect a response to lower oxygen tensions and/or a chemosensory response. It may also reflect a stronger increase in metabolic rate.

Starting from a putative T_c above 25°C for *Hyas araneus* under normocapnic conditions CO_2 clearly induces a shift in upper critical temperature to 23.5°C under 710 ppm and to 21.1°C at 3000 ppm (Fig. 3). These results confirm those obtained earlier in *Cancer pagurus* by Metzger et al. (2007), where measurements of PaO_2 demonstrated a downward shift of critical temperature from 20.5°C (normocapnia) to 15.5°C under 1% CO_2 (=10 000 ppm CO_2). These findings support the hypothesis that with higher CO_2 concentrations and a stronger heat induced stimulation of heart rate critical temperature falls, as a result of synergistic effects of temperature and CO_2 . In contrast to observations in the cold it may also involve a CO_2 induced stimulation of metabolic costs in the warmth.

Heart rates of *Hyas araneus* (Table 1) were similar to heart rate measurements in other marine invertebrates (Table 2). Different Q_{10} values in accordance to the heart rate between intertidal and subtidal species might reflect more or less variable ambient temperatures. Experiments on *Petrolisthes cinctipes* and *Petrolisthes eriomerus*, two species with different intertidal distributions also indicate such relationships (Stillman and Somero, 1996). Stillmann and Somero (1996) identified upper thermal limits of the high intertidal crab *Petrolisthes cinctipes* and the low intertidal crab *Petrolisthes eriomerus*, which correlated with the natural habitat temperature. Heart rate measurements of *Petrolisthes* species identified a critical temperature which in the light of our present data and those by Frederich and Pörtner (2000) may indicate a shift from aerobic to anaerobic metabolism. The low intertidal crab *Petrolisthes eriomerus* displayed a narrower thermal tolerance window and a lower T_c of 26.6°C with some accumulation of L-lactate at 25°C in comparison to the high intertidal crab *Petrolisthes cinctipes* ($T_c=31.5^{\circ}\text{C}$) (Stillmann and Somero, 1996). The example of low and high intertidal *Petrolisthes* species illustrates the ability of marine species to specialize on their ther-

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mal range and live near their thermal limits. For the eurythermal *Hyas araneus* we might suggest, that the limited thermal tolerance window underpins the large scale biogeographical distribution of the species. Under normocapnia, the response of *Hyas araneus* resembles the one of the high intertidal species *P. cinctipes*. In contrast, *Hyas araneus* under elevated CO₂ showed a response similar to *P. eriomerus*, which is a low intertidal species and does not possess such a wide thermal tolerance range. A CO₂ induced narrowing of the thermal tolerance, will therefore most likely restrict the geographical distribution of a species. *Hyas araneus* from Helgoland would already exploit its upper pejus range during present summers (temperature around 18°C, Wiltshire and Manly, 2004), however without reaching the upper T_c . The situation will change dramatically under CO₂ concentrations of 3000 ppm (scenario 2300), where the critical temperature of *Hyas araneus* was determined as 21.1°C, which would imply much higher heat stress during extreme summers and high mortality rates.

During warming protocols, *Hyas araneus* showed an increase in heart rate and a decrease in haemolymph oxygen partial pressure in all incubations (Fig. 4). To support increasing oxygen demand upon warming, oxygen uptake and distribution via ventilation and circulation have to be enhanced (Zainal et al., 1992). Within the thermal optimum range oxygen consumption of a species is positively related to not yet limited ventilation rate and heart rate (McMahon et al., 1978; Zainal et al., 1992) until capacity limits are reached at upper pejus temperature. Heart and scaphognathite rates as well as oxygen consumption level off and finally drop at a critical temperature as shown in the squat lobster, *Munida rugosa* (Zainal et al., 1992), in porcelain crabs, *Petrolisthes cinctipes* and *P. eriomerus* (Stillman and Somero, 1996) and in the spider crab, *Maja squinado* (Frederich and Pörtner, 2000).

A schematic model of heart rate changes in *Hyas araneus* illustrates how the thermal tolerance window is narrowed under the influence of CO₂ (Fig. 5). The CO₂ induced rise in Q_{10} values of heart rate may be involved in eliciting the narrowing of thermal windows similar to the Q_{10} enhancement of metabolic rate as recently seen in the lugworm *Arenicola marina* (Wittmann et al., 2008). In the lugworm model the thermal

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tolerance window is influenced by seasonal acclimation to temperature resulting in a narrower window during winter, associated with lower metabolic rates and higher Q_{10} value than in summer (Wittmann et al., 2008).

We can conclude that CO_2 induced ocean acidification has the potential to cause a narrowing of thermal windows eliciting similar phenomena as observed during seasonal acclimation to temperature. At the same time animals which are permanently exposed to acidification may lose their capability to acclimate to extreme temperatures. With an increase of ambient temperature as predicted by the IPCC (2001, 2007) increased ocean acidification (Caldeira and Wickett, 2005) will cause animals to reach their physiological limits sooner. As a consequence *Hyas araneus* will lose its southern habitats and experience a stronger northward shift of biogeographical boundaries.

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Table 1. Q_{10} and heart rate (in beats/min) of *Hyas araneus* ($T_c=x^\circ\text{C}$; $x(\text{normocapnia})>25^\circ\text{C}$, $x(710\text{ ppm})=23.5^\circ\text{C}$, $x(3000\text{ ppm})=21.1^\circ\text{C}$).

Temperature range $^\circ\text{C}$		Normocapnia	710 ppm	3000 ppm
0–10	Q_{10}	1.26	1.35	1.32
	Heart rate	37.82–47.80	37.73–50.85	36.73–48.52
0–6	Q_{10}	1.30	1.21	0.96
	Heart rate	37.82–44.26	37.73–42.27	36.73–35.79
6–10	Q_{10}	1.21	1.59	2.14
	Heart rate	44.26–47.80	42.27–50.85	35.79–48.52
10– T_c	Q_{10}	<1.05	1.19	1.17
	Heart rate	47.39– \approx 51.19	48.90–61.67	52.49–62.52
0– T_c	Q_{10}	<1.13	1.23	1.29
	Heart rate	37.82– \approx 51.19	37.73–61.67	36.73–62.52
6– T_c	Q_{10}	<1.08	1.24	1.45
	Heart rate	44.26– \approx 51.19	42.27–61.67	35.79–62.52

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Table 2. Comparison of Q_{10} values and heart rates of different crustaceans.

Species	Temperature range °C	Q_{10}	Heart rate beats/min	Reference
<i>Cancer magister</i>	4–19	2	40–120	Florey and Kriebel, 1974
<i>Cancer magister</i>	5–30	4	28–55	DeWachter and Wilkens, 1996
<i>Carcinus maenas</i>	5–15	2.19	30–70	Ahsanullah and Newell, 1971
<i>Carcinus maenas</i>	20–30	1.4	80–130	Ahsanullah and Newell, 1971
<i>Homarus americanus</i>	2–18	2–3	15–50	Worden et al., 2006
<i>Hyas araneus</i>	0–7	6	18–40	Frederich et al., 2000
<i>Hyas araneus</i>	0–10	1.26	37.82–47.80	this study
<i>Hyas araneus</i>	10–25	1.05	47.39–51.19	this study

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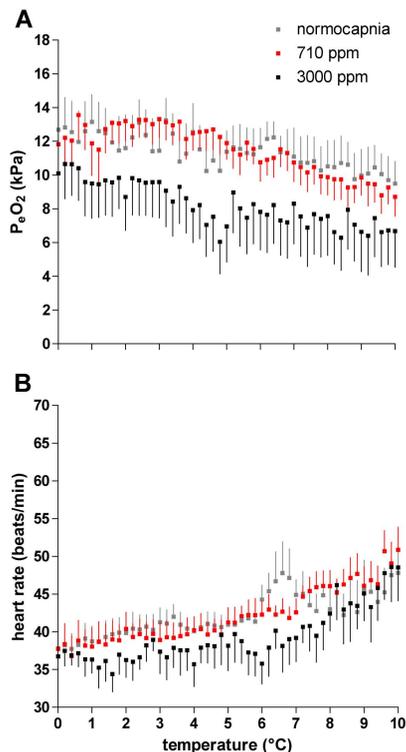


Fig. 1. Temperature dependent patterns of P_eO_2 and heart rate of *Hyas araneus* exposed to different CO_2 concentrations during acute cooling from 10 to 0°C (grey: normocapnia; red: 710 ppm; black: 3000 ppm). **(A)** P_eO_2 , values under 3000 ppm were significantly different from those under normocapnia and 710 ppm (ANOVA, $p < 0.001$). **(B)** Heart rate under 3000 ppm was significantly different from those under normocapnia and 710 ppm (ANOVA, $p < 0.001$). Data are means \pm SE, $n = 7$ (normocapnia) and 8 (710 ppm, 3000 ppm), respectively.

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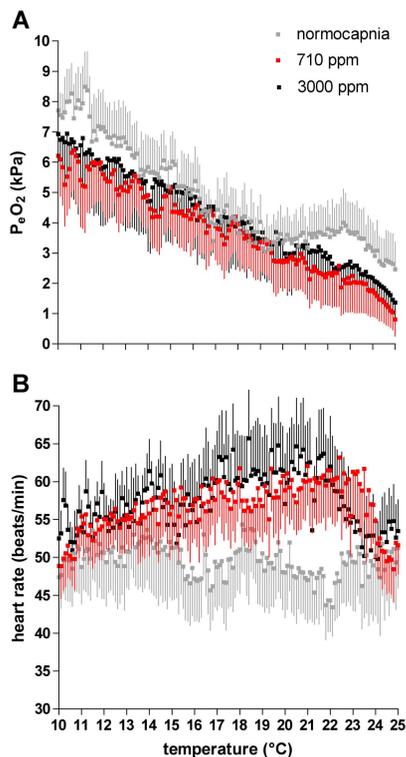


Fig. 2. Temperature dependent patterns of $P_{e}O_2$ and heart rate of *Hyas araneus* exposed to different CO_2 concentrations during acute warming from 10 to 25°C (grey: normocapnia; red: 710 ppm; black: 3000 ppm). **(A)** $P_{e}O_2$ values were significantly different between values under 3000 ppm and those under normocapnia and 710 ppm (ANOVA, $p < 0.01$) and between values under normocapnia and 710 ppm (ANOVA, $p < 0.01$). **(B)** Heart rate under normocapnia was significantly different from those under 710 ppm and 3000 ppm (ANOVA, $p < 0.001$). Data are means \pm SE, $n = 7$ (normocapnia) and 8 (710 ppm, 3000 ppm).

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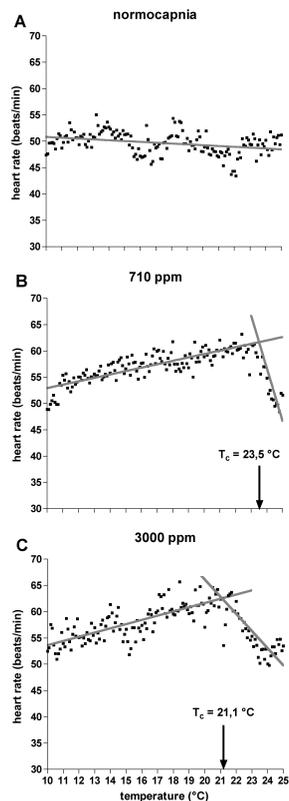


Fig. 3. Discontinuities in the temperature dependence of heart rate data (means) between 10 and 25°C under normocapnia, 710 ppm CO_2 and 3000 ppm CO_2 , analysed from linear regressions intersecting at the respective breakpoints, defined as critical temperatures (T_c). Data under normocapnia revealed no breakpoint in the tested temperature range. Under 710 ppm, the T_c was 23.5°C , under 3000 ppm, the T_c was 21.1°C . Regressions under 710 ppm are: $f(10\text{--}23.5^\circ\text{C})=46.44+(0.6482\pm 0.01816)\cdot x$, $p<0.0001$, $f(23.5\text{--}25^\circ\text{C})=296.8+(-10\pm 0.7759)\cdot x$, $p<0.0001$. Regressions under 3000 ppm are: $f(10\text{--}21.1^\circ\text{C})=45.59+(0.8025\pm 0.031)\cdot x$, $p<0.0001$, $f(21.1\text{--}25^\circ\text{C})=131.5+(-3.27\pm 0.1852)\cdot x$, $p<0.0001$.

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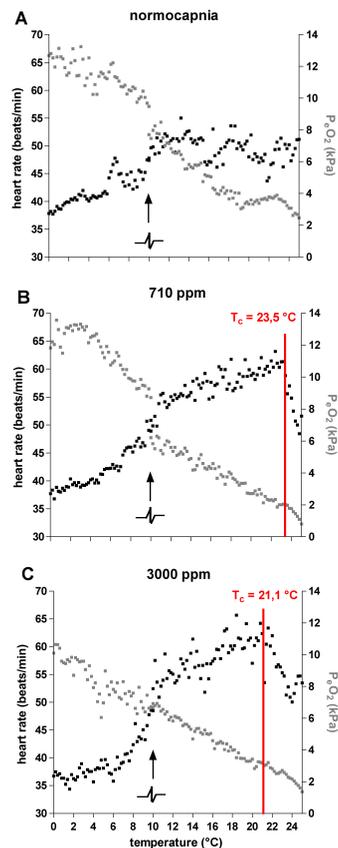


Fig. 4. Combined depiction of P_eO₂ (black) and heart rate (grey) data (means) of *Hyas araneus* between 0 and 25°C (starting point 10°C). **(A)** Normocapnia **(B)** 710 ppm **(C)** 3000 ppm. The red line indicates the shift in the upper T_c with rising CO₂ levels (n=7, normocapnia, n=8, 710 ppm and 3000 ppm).

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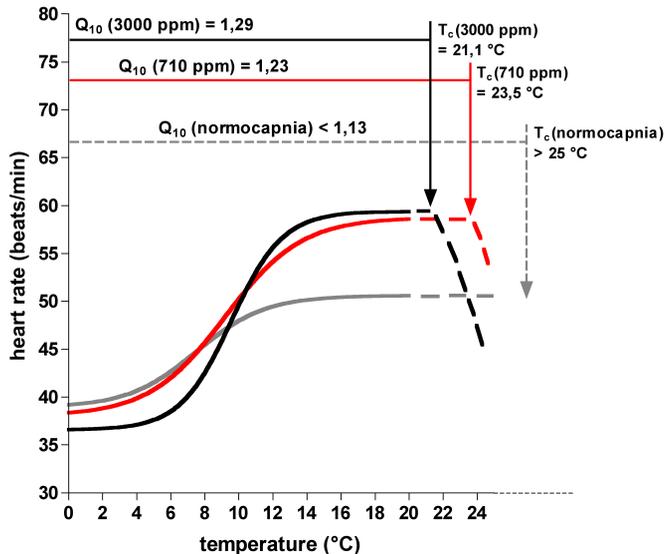


Fig. 5. Schematic model of heart rate in *Hyas araneus* under normocapnia (grey), 710 ppm (red) and 3000 ppm (black) CO₂ at temperatures between 0 and 25°C. Note the shift in heart rate thermal response, reflected in Q_{10} values, which were larger under 3000 ppm than under 710 ppm or normocapnia. As a result, onset of a drop in heart rate and upper critical temperature was seen at lower temperatures under 3000 than under 710 ppm. Heart rate under normocapnia showed no warming induced decrement. Non-linear regression fit with Boltzmann sigmoidal equation for normocapnia: $y=38.92+(50.60-38.92)/(1+\exp((7.502-x)/2.014))$; $r^2=0.8429$, for 710 ppm: $y=38.04+(58.76-38.04)/(1+\exp((9.201-x)/2.235))$; $r^2=0.9757$, for 3000 ppm: $y=36.57+(59.40-36.57)/(1+\exp((9.566-x)/1.506))$; $r^2=0.9531$.

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