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ORIGINAL PAPER

Escape performance of temperate king scallop, *Pecten maximus* under ocean warming and acidification

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Abstract Among bivalves, scallops are exceptional due to their capacity to escape from predators by swimming which is provided by rapid and strong claps that are produced by the phasic muscle interspersed with tonic muscle contractions. Based on the concept of oxygen and capacity-limited thermal tolerance, the following hypothesis was tested: ocean warming and acidification (OWA) would induce disturbances in aerobic metabolic scope and extracellular acid-case status and impair swimming performance in temperate scallops. Following long-term incubation under near-future OWA scenarios [20 vs. 10 °C (control) and 0.112 kPa CO_2 (hypercapnia) vs. 0.040 kPa CO_2 (normocapnic control)], the clapping performance and metabolic rates (MR) were measured in resting (RMR) and fatigued (maximum MR) king scallops, *Pecten maximus*, from Roscoff, France. Exposure to OA, either alone or combined with warming, left MR and swimming parameters such as the total number of claps and clapping forces virtually unchanged. Only the duration of the escape response was affected by OA which caused earlier exhaustion in hyper- than in normocapnic scallops at 10 °C. While maximum MR was unaffected, warm exposure increased RMR in both normocapnic and hypercapnic *P. maximus* resulting in similar Q_{10} values of ~2.2. The increased costs of maintenance and the observation of strongly reduced haemolymph PO_2 levels indicate that at 20 °C scallops have reached the upper thermal pejus range with unbalanced capacities for aerobic energy metabolism. As a consequence, warming to 20 °C decreased mean phasic force during escape performance until fatigue. The observed prolonged recovery time in warm incubated scallops might be a consequence of elevated metabolic costs at reduced oxygen availability in the warmth.

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Introduction

Scallops are exceptional among bivalves—when disturbed, they swim by ejecting water around the hinge. This escape response is achieved by powerful and fast shell adductions. The responsible adductor muscle consists of two functional types: the dominant phasic muscle (fast muscle) contracts rapidly and generates claps that enable scallops to swim by jet propulsion; the tonic muscle (catch muscle) contracts more slowly and operates at low energy costs; and it keeps the valves either closed for longer periods or at constant gaping for ventilation and feeding (Chantler 2006). The use of phasic and tonic contractions differs among species suggesting that lifestyle and shell morphology define muscle use during escape responses (Minchin 2003; Alejandrino et al. 2011; Tremblay et al. 2012; see also Guderley and Tremblay 2013). Furthermore, reliance on tonic contractions was higher in juvenile giant scallops, *Placopecten magellanicus* directly measured after handling stress compared with individuals given a 3-h recuperation period (Pérez et al. 2008a). Clapping via phasic contractions is fuelled by adenosine triphosphate (ATP), which is regenerated from phospho-L-arginine (PLA) followed by anaerobic and aerobic recovery after fatigue depending on closed/open status of the scallop (Grieshaber 1978). The restoration of energy balance might be supported by tonic contractions that alternate with a series of phasic contractions

allowing partial metabolic recovery of the adductor muscle (Pérez et al. 2008a, b).

In the light of the predominant use of anaerobic metabolism, the role of aerobic scope in exercise performance of scallops is thus not clear. Increasing costs for maintenance can reduce aerobic scope with trade-offs between energy-consuming processes relevant for performance/fitness such as growth, locomotion and reproduction (aerobic power budget concept by Guderley and Pörtner 2010; Guderley and Tremblay 2013). Environmental factors, in particular temperature, are known to affect the bioenergetics of marine ectotherms and thus performance and vulnerability (Pörtner et al. 2008; Guderley 2004; Somero 2011; Sokolova et al. 2012). Although physiological rates of ectotherms can acclimate/acclimatize to changing environmental conditions, aerobic metabolic rates in scallops and other bivalves remain tightly coupled to the surrounding temperature regime indicating only partial or no metabolic compensation (Aldridge et al. 1995; Pilditch and Grant 1999; Peck et al. 2002; Lannig et al. 2006). Also, thermal history more than actual habitat temperature might shape the thermal sensitivity of escape performance in scallops. Despite similar sampling temperature (~12 °C), performance of spring *P. magellanicus* was better at 6 °C than at 12 °C which contrasts to findings on *P. magellanicus* sampled in fall, which performed equally well at 6 and 12 °C (Guderley et al. 2009). However, irrespective of sampling time, an overall reduction in the effectiveness of escape response was observed at high temperatures (18–19 °C). The mean phasic force of the giant scallop, *P. magellanicus* did not change, whereas the total number of claps, the mean duration and the rate of phasic contractions (claps min^{-1}) were lowered at high temperature (18–19 vs. 6/12 °C), paralleled by an increased reliance on tonic contractions in the warmth (Guderley et al. 2009). Similarly, following cold exposure, only partial compensation of clapping performance was observed in *P. magellanicus* after approximately a week of cold acclimation. Recuperation from exhaustive exercise was significantly impaired in cold-exposed scallops compared to scallops under control conditions (8 vs. 18 °C, Lafrance et al. 2002).

The ongoing processes of ocean warming and acidification (OWA), as a consequence of anthropogenic CO_2 emissions, affect marine biota (Melzner et al. 2009; Sokolova et al. 2012; Wittmann and Pörtner 2013; IPCC 2014). According to the concept of oxygen and capacity-limited thermal tolerance (OCLTT, Pörtner 2001, 2002), synergistic effects of elevated temperature and ocean acidification will narrow the functional scope of marine ectotherms resulting in impaired performance capacities (Pörtner and Farrell 2008). Furthermore, synergistic effects of warming and acidification were suggested to cause reduced calcification rates in the blue mussel, *Mytilus galloprovincialis*, in seasonal experiments along a natural pH gradient near volcanic CO_2 vents off Ischia, Italy [pH 7.4 (May) vs. pH 8.1 (September), Rodolfo-Metalpa et al. 2011]. A combination of low pH and elevated temperatures increased lipofuscin accumulation (a marker for physiological stress) in the clam, *Arctica islandica* (7.5 vs. 16 °C, 0.039 vs. 0.136 kPa CO_2, Hiebenthal et al. 2013). Rosa and Seibel (2008) found reduced aerobic and locomotory scope for exercise in the jumbo squid, *Dosidicus gigas* under OWA conditions (10 vs. 20 °C; 0.039 vs. ~0.1 kPa CO_2) with suggested implications for predator–prey interactions. Such a synergism of OA and temperature stress was also shown for the "cold side" of the scallop's thermal tolerance range. Previous work in our laboratory revealed high mortality among the boreal king scallop, *Pecten maximus* from Norway (sampled in February at 3–5 °C), when exposed to a combination of high CO_2 levels and low winter temperature (0.11 kPa CO_2 at 4 °C, Schalkhausser et al. 2013). Mortality was negligible during simultaneous exposure to elevated CO_2 levels at higher temperature (0.11 kPa PCO_2 at 10 °C), but swimming performance was impaired in hyper- compared to normocapnic *P. maximus*.

King scallops, *P. maximus* are widely distributed, from northern Norway to West Africa (Minchin 2003) and economically important in fisheries and mariculture. They are predominantly found in the north-eastern Atlantic, and king scallops are currently the most important resource species in the Roscoff region of France where the organisms of our study have been obtained (IFREMER 2011).

The present study sets out to investigate locomotor and metabolic physiology of a temperate population of *P. maximus* to test the hypothesis of impaired performance due to lowered aerobic scope under OWA conditions according to the OCLTT concept. The International Panel for Climate Change (IPCC 2014) proposed an increase in global mean temperature by 3–5 °C, and PCO_2 might rise up to ≥1,000 ppm (≈0.10 kPa) within the year 2100 depending on the scenario. Against the background that environmental temperature of *P. maximus* from Roscoff varies from 10 to 16 °C, we assessed escape performance (rate and force of phasic and tonic contractions) and aerobic energy metabolism (routine and maximal metabolic rate, aerobic scope) in scallops exposed to control (0.040 kPa PCO_2) and elevated (0.112 kPa PCO_2) CO_2 levels at either control (10 °C) or elevated (20°C, ∼5°C above the environmental summer mean) temperature.

Materials and methods

Scallop collection and holding conditions

Wild living *P. maximus* were collected at a depth of ~20 m by SCUBA divers from Marine Station Roscoff ("Station

Table 1 Parameters of sea water during long-term incubations of *P. maximus* during normocapnia and hypercapnia at different temperatures (10 and 20 °C incubation)

	Parameter	Normocapnia	Hypercapnia
10 °C	PCO_2 (kPa)	0.037 ± 0.007	0.106 ± 0.023
	Temperature (°C)	9.70 ± 0.43	9.57 ± 0.50
	pH (NBS-scale)	8.19 ± 0.07	7.80 ± 0.10
	pH (total scale)	8.09 ± 0.10	7.70 ± 0.09
	Salinity (S_P)	32.29 ± 0.53	32.23 ± 0.62
	DIC (mM)	2.25 ± 0.04	2.36 ± 0.05
20 °C	PCO_2 (kPa)	0.045 ± 0.004	0.117 ± 0.025
	Temperature (°C)	19.49 ± 0.31	19.81 ± 0.16
	pH (NBS-scale)	8.15 ± 0.03	7.87 ± 0.07
	pH (total scale)	7.96 ± 0.04	7.66 ± 0.08
	Salinity (S_P)	33.35 ± 0.44	33.22 ± 0.39
	DIC (mM)	2.21 ± 0.04	2.29 ± 0.03

Data are mean ± SD with $N = 57$–62 (10 °C), $N = 17$–22 (20 °C); values at 10 °C contain data of incubation from 2010 to 2011

NBS, National Bureau of Standards; PCO_2, sea water partial pressure of CO_2; DIC, dissolved inorganic carbon

Biologique de Roscoff", France) at Morlaix Bay (Baie de Morlaix, Les Grandes Fourches, France; 48°42′33.6″N, 3°55′59.30″W). Environmental mean surface temperatures vary from 9.7 to 16.3 °C with pH_{NBS} values of 8.04–8.21 (pH scale of the National Bureau of Standards) in this area (monthly means February 2000–October 2012; data provided by "Service d'Observation en Milieu Littoral, INSU-CNRS, Estacade", http://somlit-db.epoc.u-bordeaux1.fr/download.php?serie=ST). Scallops were collected in two batches (first batch in July 2010, second batch in September 2011) at similar environmental temperatures around 10–12 °C (2010) and 11–14 °C (2011). Scallops were transported to the Alfred Wegener Institute (Bremerhaven, Germany) and placed in recirculating aerated aquarium systems (~10 °C and salinity of 32 S_P). After 2 weeks of recovery, the shells were carefully scrubbed to remove epibionts. Randomized groups of labelled scallops were incubated in temperature-controlled rooms in recirculation systems (one system per group, comprising header, receiver and reservoir tanks and two incubation tanks (each with ≤10 scallops) similar to the systems described by Michaelidis et al. 2005 or Findlay et al. 2010). Due to logistic constraints, scallops sampled in 2010 were incubated at 10 °C only, while scallops from 2011 were incubated at 10 and 20 °C. The systems were continuously bubbled with a specific gas mixture to reach sea water PCO_2 values of either ~0.039 kPa (390 µatm, normocapnia) or ~0.112 kPa (1,120 µatm, 0.3–0.4 units below present global average pH, projected for 2100, hypercapnia; see Schalkhausser et al. 2013). The OA incubation lasted at least 50 d. Scallops were drip-fed live phytoplankton three times per week [DT´s Premium Reef Blend (*Nannochloropsis osculata*, *Phaeodactylum* sp., *Chlorella* sp.; 25.3 µg L^{-1} phytoplankton dry weight)] for a minimum of 6 h d^{-1} at a concentration of at least 7.62×10^5 cells g^{-1} bivalve biomass h^{-1} (10 °C) or 1.07×10^6 cells g^{-1} bivalve biomass h^{-1} (20 °C), respectively (water circulation was stopped during feeding). Water was exchanged at least twice a week, and tanks were cleaned of faeces and remaining food items every day. Water parameters (Table 1) were measured twice a week as described by Schalkhausser et al. (2013). Shell dimensions of the scallops did not differ among groups (both years) prior to and after incubation resulting in overall mean ± SD of 119.6 ± 6.8 mm (height; $N = 71$), 105.7 ± 5.8 mm (length; $N = 71$) and 31.1 ± 2.0 mm (width; $N = 71$). Also tissue dry weight (DW) which was determined after drying at 75 °C for 10–16 h, when no detectable mass changes were observed, was similar among groups with an overall mean ± SD of 13.99 ± 2.67 g ($N = 67$). All measurements were carried out in Oct/Nov 2010 and Oct/Nov 2011. Condition index (CI) and the muscle index (MI) were calculated after Shriver et al. (2002) and Pazos et al. (1997) by dividing the tissue DW (total and muscle DW, respectively) with shell DW multiplied by 100.

Determination of clapping performance

Measurements of clapping performance were achieved using the same equipment and methods as described in detail in our previous study (Schalkhausser et al. 2013). In brief, after recovery from handling stress clapping was induced by injection of distilled water via a thin, gas-tight tube into the mantle cavity. Such injections, or touching the mantle with an arm of their starfish predator, stimulates scallops to exercise until they become exhausted and unresponsive to further stimulation (Bailey et al. 2003; Guderley et al. 2008). The number of claps and force strengths of adductor muscle contractions were determined until the scallop was exhausted (no response to further stimulation). Total force F_{total} (total force produced by one scallop during escape until fatigue), mean phasic force $F_{mean\ phasic}$ (mean force $clap^{-1}$) and tonic force F_{tonic} (force produced by one scallop during tonic phases [= not clapping]) were determined using the following formula (see Schalkhausser et al. 2013). F_{total} (N) was calculated by dividing the force impulse [measured force (N) multiplied by measured time (s)] by the total time, $F_{total} = \frac{\int f\,dt}{t_{total}}$, $F_{mean\ phasic}$ (N) was calculated by dividing the sum of all clap forces (F_{clap}) by the number of claps (n), $F_{mean\ phasic} = \frac{\sum_i^n F_{clap}}{n} = \frac{F_{phasic}}{n}$, and F_{tonic} (N) by subtracting F_{phasic} from F_{total}, $F_{tonic} = F_{total} - F_{phasic}$.

Determination of respiration

Measurements of routine and maximal metabolic rate after fatigue (RMR; MMR) were conducted following our previous protocol (see Schalkhausser et al. 2013). In brief, after recovery from handling stress, oxygen consumption, $\dot{M}_{O2}$ [μmol O_2 h^{-1} (g DW)$^{-1}$] (g DW = gram dry weight) was determined on non-fed scallops during rest (RMR) and after exhaustive exercise (MMR) using intermittent flow respirometry with three to five trials individual^{-1}. Intervals were chosen, so oxygen partial pressures were never <15 kPa in the chamber. Factorial aerobic scope (FAS) was calculated as the ratio of maximum to resting rate (MMR/RMR, Cutts et al. 2002) and net aerobic scope (NAS) as the difference between MMR and RMR (Fry 1947). Both FAS and NAS are often reported, and we follow Clark et al. (2013) in showing both calculations.

Recovery periods following exhaustive exercise were determined from respiration measurements and defined as the time the scallop required to return from MMR to initial RMR. The $Q_{10\ (10–20\ °C)}$ values were calculated after Precht et al. (1973).

Determination of haemolymph gas parameters

Haemolymph was sampled from the adductor muscle using a Hamilton syringe. Haemolymph P_eCO_2, P_eO_2 and pH_e were analysed using a blood gas analyser (MT 33, Eschweiler, Germany); total CO_2 (C_eCO_2) was analysed by a gas chromatograph (Agilent 6890 N GC System, Agilent Technologies, USA); the concentration of apparent bicarbonate $[HCO_3^-]_e$ was calculated using the following values of the solubility of CO_2 in sea water (αCO_2): $\alpha CO_2 = 0.465$ mmol L^{-1} kPa^{-1} at 10 °C and salinity of 32.8 S_P, $\alpha CO_2 = 0.343$ mmol L^{-1} kPa^{-1} at 20 °C and salinity of 33.3 S_P (calculated from Weiss 1974; see Schalkhausser et al. 2013). In 2010, methodological problems hampered the proper and accurate determination of P_eCO_2 during sampling of the hypercapnic group and reliable P_eCO_2 values could only be determined in two scallops.

Statistics

Data sets were analysed using SigmaPlot (Version 12.0, Systat Software, Inc.), GraphPad Prism (Version 4.0a, GraphPad Software Inc.) and R [2.15.1 GUI 1.52 Leopard build 32-bit (6188)]. A linear mixed-effects model fit by REML (package nlme) combined with an ANOVA to create a three-way repeated-measurements ANOVA was used to determine synergistic effects of CO_2 exposure, temperature and exercise level on respiration measurements (*P* value <0.05). Interactions between effects of CO_2 exposure and year or temperature on haemolymph parameters, force measurements, metabolic rates, net and FAS were considered significant if the probability of type II error was <0.05 using two-way analysis of variance in combination with a Holm–Sidak test. One-way ANOVA in combination with a Bonferroni's multiple comparison test was <0.05 to identify differences in morphological parameters [shell dimensions, tissue mass, condition and muscle indices (MI)]. Results are presented in box plots, and values are given as mean ± SD unless otherwise stated.

Table 2 Morphological indices of *P. maximus* from two different sampling years following long-term incubation under normocapnia (sea water PCO_2 ~ 0.040 kPa) and hypercapnia (sea water PCO_2 ~ 0.112 kPa) at two different temperatures (10, 20 °C)

Year/temperature	Parameter	Normocapnia	Hypercapnia
2010/10 °C	Condition index	11.9 ± 1.3 (17)	12.0 ± 1.2 (12)
	Muscle index	2.8 ± 0.5 (16)[a]	2.8 ± 0.6 (13)[a]
2011/10 °C	Condition index	13.6 ± 2.3 (9)	13.4 ± 1.5 (6)
	Muscle index	4.3 ± 0.4 (9)	4.3 ± 0.4 (5)
2011/20 °C	Condition index	13.0 ± 1.0 (9)	11.7 ± 1.5 (9)
	Muscle index	3.8 ± 0.7 (10)[#]	3.3 ± 0.2 (8)[#]

Data are mean ± SD with (*N*)

[#] Significant differences between 10 and 20 °C data at same CO_2 level

[a] Significant difference between sampling years at same CO_2 level

Results

Mortality, condition and muscle indices

Neither warming nor OA exposure nor the combination of the two affected the well-being of temperate *P. maximus* as indicated by low mortality rates of 9 % (normocapnia) and 0 % (hypercapnia) at 10 °C (combined for both sampling years) and of 20 % (normocapnia) and 9 % (hypercapnia) at 20 °C. Condition indices were similar among all groups, whereas MI was significantly affected by year of sampling (Table 2; ANOVA, $F(1, 41) = 89.459$ $P < 0.001$). Furthermore, warming from 10 to 20 °C significantly reduced MI (ANOVA, $F(1, 30) = 17.205$ $P < 0.001$), with a further reduction following additional OA exposure at 20 °C (Holm–Sidak, $t(1, 17) = 2.386$ $P = 0.024$; Table 2).

Haemolymph acid–base parameters

The data for all groups are shown in Table 3. Sampling year affected haemolymph parameters in resting scallops yielding significantly lower C_eCO_2 and $[HCO_3^-]_e$ values in scallops sampled in 2010 than in 2011, irrespective of CO_2 levels (C_eCO_2: ANOVA, $F(1, 40) = 15.494$ $P < 0.001$; $[HCO_3^-]_e$: ANOVA, $F(1, 40) = 14.549$

Table 3 Haemolymph blood gas parameters of *P. maximus* at rest from two different sampling years following long-term incubation under normocapnia (sea water PCO_2 ~ 0.040 kPa) and hypercapnia (sea water PCO_2 ~ 0.112 kPa) at two different temperatures (10, 20 °C)

Year/temperature	Parameter	Normocapnia	Hypercapnia
2010/10 °C	P_eO_2 (kPa)	10.86 ± 2.67	13.37 ± 3.99
	P_eCO_2 (kPa)	0.14 ± 0.03	0.26/0.21 (*N* = 2)
	pH_e (NBS-scale)	7.51 ± 0.07	7.34 ± 0.10*
	C_eCO_2 (mM)	1.92 ± 0.18[a]	2.22 ± 0.18[a,*]
	$[HCO_3^-]_e$ (mM)	1.85 ± 0.18[a]	2.14 ± 0.19[a,*]
	N	14–16	11–13
2011/10 °C	P_eO_2 (kPa)	9.73 ± 3.69	13.34 ± 3.17*
	P_eCO_2 (kPa)	0.13 ± 0.04	0.21 ± 0.03*
	pH_e (NBS-scale)	7.52 ± 0.09	7.31 ± 0.06*
	C_eCO_2 (mM)	2.17 ± 0.34	2.52 ± 0.07*
	$[HCO_3^-]_e$ (mM)	2.10 ± 0.32	2.41 ± 0.06*
	N	8–9	5–6
2011/20 °C	P_eO_2 (kPa)	6.24 ± 1.72[#]	6.14 ± 1.52[#]
	P_eCO_2 (kPa)	0.16 ± 0.03	0.23 ± 0.06*
	pH_e (NBS-scale)	7.49 ± 0.08	7.34 ± 0.12*
	C_eCO_2 (mM)	1.82 ± 0.23[#]	2.16 ± 0.14[#,*]
	$[HCO_3^-]_e$ (mM)	1.76 ± 0.23[#]	2.08 ± 0.14[#,*]
	N	8–10	9–10

Data are mean ± SD with *N* given for the different groups; expect for P_eCO_2 under hypercapnia in 2010 where single values are given with *N* in parentheses

P_eO_2 and P_eCO_2, extracellular partial pressure of O_2 and CO_2, respectively; pH_e, extracellular pH; NBS, National Bureau of Standards; C_eCO_2 extracellular total dissolved inorganic carbon; $[HCO_3^-]_e$, extracellular bicarbonate concentration

* Significant differences between normocapnic and hypercapnic data at same temperature

[#] Significant differences between 10 and 20 °C data at same CO_2 level

[a] Significant difference between sampling years at same CO_2 levels

$P < 0.001$). Warming significantly reduced P_eO_2 by nearly 50 % as well as C_eCO_2 and $[HCO_3^-]_e$ values in both, normocapnia- and hypercapnia-exposed scallops (P_eO_2: ANOVA, $F(1, 32) = 34.070$ $P < 0.001$; C_eCO_2: ANOVA, $F(1, 31) = 19.347$ $P < 0.001$; $[HCO_3^-]_e$: ANOVA, $F(1, 31) = 18.221$ $P < 0.001$). Following OA exposure in both years or temperatures, scallops displayed significantly elevated P_eCO_2, C_eCO_2 and $[HCO_3^-]_e$ and significantly lowered pH_e (different years P_eCO_2: ANOVA, $F(1, 26) = 18.059$ $P < 0.001$—no interaction calculable; C_eCO_2: ANOVA, $F(1, 31) = 19.347$ $P < 0.001$; $[HCO_3^-]_e$: ANOVA, $F(1, 40) = 18.796$ $P < 0.001$; pH_e: ANOVA, $F(1, 38) = 43.067$ $P < 0.001$; different temperatures P_eCO_2: ANOVA, $F(1, 30) = 20.225$ $P < 0.001$; C_eCO_2: ANOVA, $F(1, 31) = 17.606$ $P < 0.001$; $[HCO_3^-]_e$: ANOVA, $F(1, 31) = 16.208$ $P < 0.001$; pH_e: ANOVA, $F(1, 29) = 24.940$ $P < 0.001$). The hypercapnia-induced changes were similar, irrespective of incubation temperature indicating that warming and acidification had no synergistic effects.

Clapping performance and metabolic rate

The clapping performance of *P. maximus* under the various conditions was similar between sampling years in both normocapnia- and hypercapnia-exposed scallops at 10 °C (Fig. 1). The number of claps was neither affected by warming nor by OA exposure nor by the combination of both resulting in an overall mean of 69 ± 20 claps until fatigue of scallops sampled in 2011 (Fig. 1a). Warming modified clapping forces, whereas OA, solely or in combination with warming, had no effect. Exposure to 20 °C significantly increased total force F_{total} and tonic force F_{tonic} by ~80 % in the normocapnic group (F_{total}: Holm-Sidak, $t(1, 18) = 2.315$ $P = 0.028$; F_{tonic}: Holm–Sidak, $t(1, 18) = 2.331$ $P = 0.027$), and, insignificantly by ~30 % in the hypercapnic group likely due to the observed high variation in this group at 10 °C (Fig. 1b, d). The normocapnic and hypercapnic groups at 20 °C both showed significantly decreased mean phasic force $F_{mean\ phasic}$ (normocapnia 24 %, hypercapnia 31 %) compared to the respective values at 10 °C (normocapnia: Holm–Sidak, $t(1, 17) = 2.077$ $P = 0.047$; hypercapnia: Holm–Sidak, $t(1, 13) = 2.522$ $P = 0.018$; Fig. 1c).

No clear pattern was observed for the duration of the escape response (Fig. 2a). Irrespective of CO_2 level, time to fatigue of 10 °C incubated *P. maximus* was similar between sampling years. However, in 2011, but not in 2010, scallops displayed a longer-lasting escape response in the normocapnic than in the hypercapnic group (2011 10 °C: Holm–Sidak, $t(1, 14) = 2.078$ $P = 0.046$). Warming significantly reduced the duration of the escape response in normocapnia- but not in hypercapnia-exposed *P. maximus* linked to the significant interaction between temperature and OA (ANOVA, $F(1, 32) = 5.549$ $P = 0.025$). Sampling year and warming, but not OA exposure, affected the time to recover from exhaustive exercise (Fig. 2b). Irrespective of OA exposure, it was significantly less by 2 h in *P. maximus* in 2010 than in 2011 (ANOVA, $F(1, 19) = 17.776$ $P < 0.001$) and significantly extended by warming (lasting ~9 h at 20 °C compared to 6–7 h at 10 °C; ANOVA, $F(1, 22) = 21.567$ $P < 0.001$).

Sampling year altered resting but not maximal metabolic rate of *P. maximus* resulting in marginally but significantly lowered resting metabolism in 2010 than in 2011 (ANOVA,

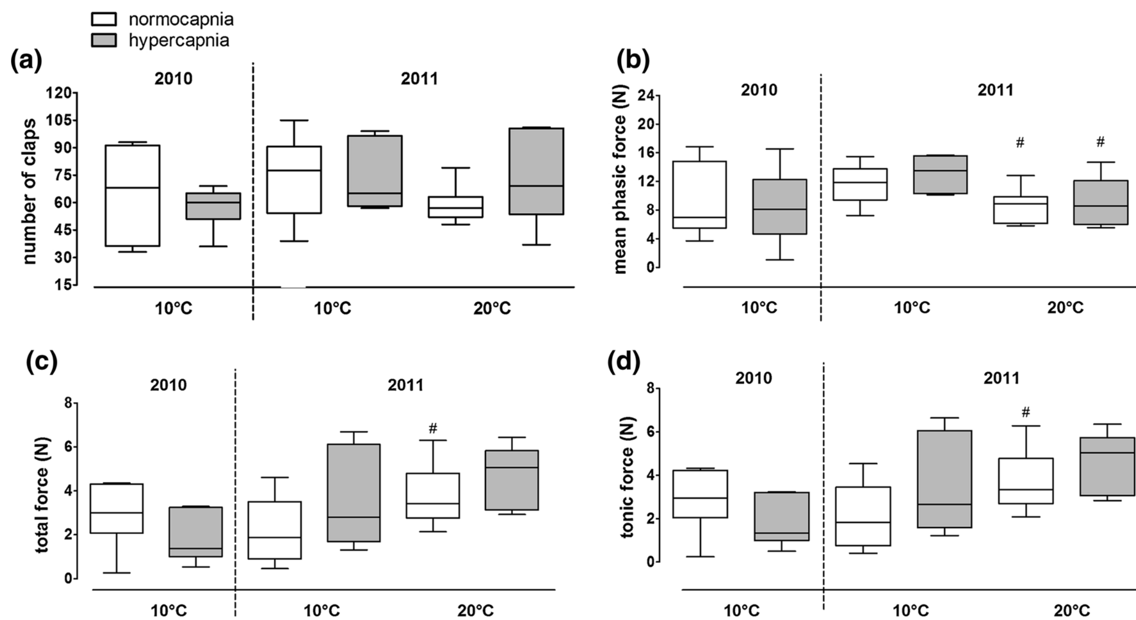

Fig. 1 Clapping performance of *P. maximus* from two different sampling years following long-term incubation under normocapnia (sea water PCO_2 ~ 0.040 kPa) and hypercapnia (sea water PCO_2 ~ 0.112 kPa) at two different temperatures (10, 20 °C). **a** Total number of claps until fatigue. **b** Total force. **c** Mean phasic force. **d** Tonic force. 2010: $N = 7$–8; 2011: $N = 8$–10 (normocapnia, 10 °C), $N = 5$ (hypercapnia, 10 °C), $N = 9$–11 (normocapnia, 20 °C), $N = 7$–9 (hypercapnia, 20 °C). Data are depicted in *boxplots*. #Significant differences between 10 and 20 °C data at same CO_2 level

$F(1, 25) = 12.427$ $P = 0.002$) without any significant effect on aerobic scopes (Fig. 3). Warming from 10 to 20 °C significantly increased resting metabolic rate (RMR) in both normocapnia- and hypercapnia-exposed groups (normocapnia: Holm–Sidak, $t(1, 11) = 6.425$ $P < 0.001$; hypercapnia: Holm–Sidak, $t(1, 13) = 7.089$ $P < 0.001$), resulting in similar Q_{10} values of 2.3 (normocapnia) and 2.2 (hypercapnia), respectively (Fig. 3a). Maximum metabolic rate (MMR) was less responsive to warming [Q_{10} values of 1.2 (normocapnia) and 1.5 (hypercapnia), respectively] (Fig. 3a). The rise in metabolic rate from RMR to MMR was 2.3 at 10 °C compared to 2.1 at 20 °C resulting in a significantly reduced FAS in the warmth (ANOVA, $F(1, 24) = 31.922$ $P < 0.001$; Fig. 3b). Warming left NAS, an indication of the absolute change in respiration rates, more or less unchanged, explicable by the quite high variation in MMR data. Irrespective of sampling year or incubation temperature, additional OA exposure had no effect on resting and on maximum metabolic rate and there was no synergistic impact of OWA on metabolic rates of *P. maximus*. Furthermore, there was no synergistic impact of OA exposure, temperature and exercise level on metabolic rates.

Discussion

Although some parameters (MI, haemolymph bicarbonate concentration and RMR) differed in temperate *P. maximus* when sampled in two consecutive years (2010 vs. 2011), the observed differences did not affect metabolic scopes or clapping performance. Only the time to recover from exhaustive exercise was reduced in *P. maximus* sampled in 2010, a potential result of seasonal variations in the thermal history (see "Introduction" and Guderley et al. 2009). Irrespective of sampling year, temperate *P. maximus* were insensitive to our chosen ocean acidification (OA) scenario of elevated PCO_2 (0.112 vs. 0.039 kPa) at 10 °C. Furthermore, following chronic exposure to warming and acidification, energy metabolism and escape performance of temperate *P. maximus* were more affected by warming than OA. In line with the OCLTT concept, the present findings revealed impaired escape performance such as decreased mean phasic force and increased recovery time after exhaustive exercise in the upper thermal pejus range. The observed changes could be linked to a progressive warming-induced mismatch between aerobic energy supply and demand, however, without a synergistic impact of exposure to ocean acidification.

Neither warm incubation nor OA exposure nor the combination of both affected the condition indices (CI), which were similar to previous studies on other scallop species (Pazos et al. 1997; Shriver et al. 2002; Schalkhausser et al. 2013). This shows that the scallops used in the experiments were in good condition. Low mortality indicated further that the chosen OWA scenario (about 5 °C above the environmental summer mean temperature) was in the

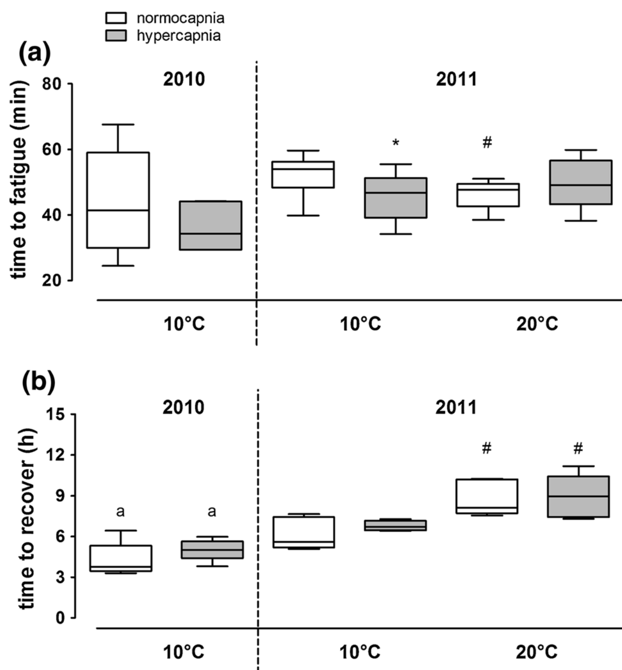

Fig. 2 Time to fatigue (**a**) and to recover from exhaustive exercise (**b**) of *P. maximus* from two different sampling years following long-term incubation under normocapnia (sea water PCO_2 ~ 0.040 kPa) and hypercapnia (sea water PCO_2 ~ 0.112 kPa) at two different temperatures (10, 20 °C). 2010: $N = 5$–8; 2011: $N = 6$–10 (normocapnia, 10 °C), $N = 4$–5 (hypercapnia, 10 °C), $N = 5$–10 (normocapnia, 20 °C), $N = 9$ (hypercapnia, 20 °C). Data are depicted in *boxplots*. [a]Significant difference between sampling years at same CO_2 level. *Significant differences between normocapnic and hypercapnic data at same temperature. [#]Significant differences between 10 and 20 °C data at same CO_2 level

range of thermal tolerance of temperate *P. maximus* and that experimental conditions did not exceed their critical temperatures. For comparison, in our previous study in boreal *P. maximus* from Norway, the observed high mortality of 90 % among scallops sampled in winter (3–5 °C) and exposed to 4 °C under hypercapnia (Schalkhausser et al. 2013) indicated that they were close to the lower limits of their thermal tolerance window.

The OA did not affect haemolymph oxygen partial pressures (P_eO_2) of *P. maximus*; values of 10–13 kPa found under resting conditions at 10 °C are close to previous data on oysters (Jones et al. 1995; Lannig et al. 2008) and a spider crab (Frederich and Pörtner 2000). A temperature increase from 10 to 20 °C, however, caused an almost twofold decline in P_eO_2 levels in both normocapnic and hypercapnic scallops. Such a decrease in haemolymph PO_2 was also found in oysters subject to an acute temperature rise (Lannig et al. 2008) and matches observations in Northern boreal scallops incubated at 10 °C (Schalkhausser et al. 2013). The lowered P_eO_2 indicates that oxygen supply via ventilation and/or circulation could not keep up with the warming-induced increase in metabolism (see below), leading to the transition to the upper pejus range according to the OCLTT concept (Pörtner 2001, 2010).

Bivalves have only limited extracellular non-bicarbonate buffering capacities (Lindinger et al. 1984; Michaelidis et al. 2005; Melzner et al. 2009). Disturbances of pH_e usually follow a non-bicarbonate buffer line similar to that of sea water: 0.3 mmol L^{-1} pH^{-1} versus 0.4 mmol L^{-1} pH^{-1} (β_{NB} of *Mytilus edulis*, Booth et al. 1984). Accordingly, in OA-exposed temperate *P. maximus,* we found a reduction in pH_e combined with elevated P_eCO_2, bicarbonate and C_eCO_2 levels in the haemolymph, independent of incubation temperature, which corresponds to previous observations in Northern boreal *P. maximus* from Stavanger, Norway (Schalkhausser et al. 2013). In both cases, the elevation in extracellular bicarbonate levels was insufficient to fully compensate for the OA-induced extracellular acidosis. Interestingly, we noticed a possible difference in OA effects on haemolymph parameters between the populations, which was more pronounced after warming to either 20 °C (temperate) or 10 °C (boreal). Temperate *P. maximus* showed an OA-induced increase in $[HCO_3^-]_e$ by ~0.32 mM (20 °C) compared to the boreal population, where $[HCO_3^-]_e$ increased by only ~0.17 mM (10 °C) at similar PCO_2s. This difference corresponds to the OA-induced drop in pH_e which was less in temperate (~0.15 pH units) than in boreal *P. maximus* (~0.25 pH units). This observation suggests that the capacity for acid–base regulation is somewhat higher in the temperate than in the boreal *P. maximus* population following OA exposure in the respective upper pejus range. In this context, it is worth noting that warm incubation did not affect pH_e in the temperate population (Table 3) but significantly increased haemolymph pH from 7.41 ± 0.23 to 7.65 ± 0.07 and decreased P_eCO_2 from 0.21 ± 0.06 to 0.13 ± 0.02 kPa in boreal normocapnic *P. maximus* (4 vs. 10 °C, B. Schalkhausser, C. Bock, H.O. Pörtner, G. Lannig, unpublished data). Understanding the underlying mechanisms will require further studies.

Ocean acidification either by itself or when combined with warming (OWA) had no impact on aerobic metabolic rates of *P. maximus* measured at rest (RMR) and after exhaustive exercise (MMR). Warming from 10 to 20 °C caused a significant rise in RMR in both normocapnic and hypercapnic scallops. The Q_{10} values of ~2.3 indicate an uncompensated temperature effect on energy demand regardless of CO_2 exposure. This lack of thermal compensation has been described previously for *P. magellanicus* (Pilditch and Grant 1999; MacDonald and Thompson 1986; Shumway et al. 1988) and for other bivalves (Peck et al. 2002; Lannig et al. 2006; Morley et al. 2012).

Due to the warming-induced rise in RMR but not in MMR, FAS of *P. maximus* was lower at 20 °C than at

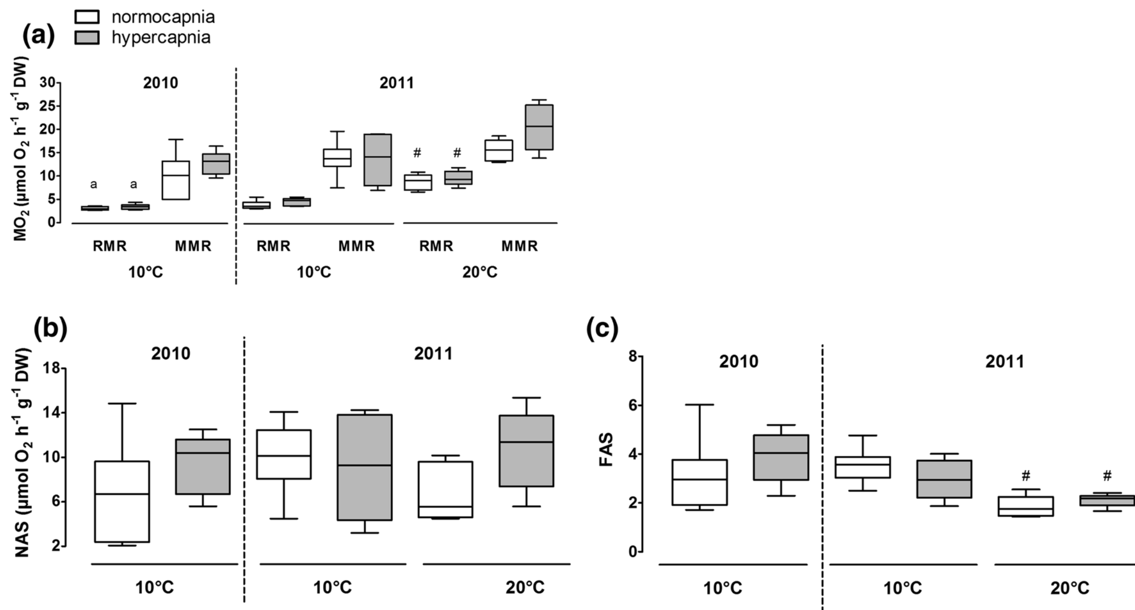

Fig. 3 Metabolic rates under resting (RMR) and fatigued (MMR) conditions (**a**), net aerobic scope (NAS, **b**) and factorial aerobic scope (FAS, **c**) of *P. maximus* from two different sampling years following long-term incubation under normocapnia (sea water PCO_2 ~ 0.040 kPa) and hypercapnia (sea water PCO_2 ~ 0.112 kPa) at two different temperatures (10, 20 °C). 2010: $N = 7$–8; 2011: $N = 7$ (normocapnia, 10 °C), $N = 5$ (hypercapnia, 10 °C), $N = 5$ (normocapnia, 20 °C), $N = 9$ (hypercapnia, 20 °C). Data are depicted in *boxplots*. [a]Significant difference between sampling years at same CO_2 level. *Significant differences between normocapnic and hypercapnic data at same temperature. [#]Significant differences between 10 and 20 °C data at same CO_2 level

10 °C; however, any effect on NAS was minimal. Interestingly, additional OA exposure had no further impact. In our previous study, we had observed an OA-induced reduction in both factorial and NAS as well as in swimming performance of boreal *P. maximus* from Norway after warming from 4 to 10 °C (Schalkhausser et al. 2013). In both studies, scallops had similarly low haemolymph PO_2 values (6.2–6.5 kPa) and displayed a reduction in aerobic scope following warm exposure (20 °C for temperate and 10 °C for boreal *P. maximus*, respectively) which indicates that both populations were in their respective upper thermal pejus range. Compared to its Norwegian conspecific, temperate *P. maximus*, however, was less sensitive to OA, possibly due to the smaller decrease in its pH_e following OA exposure and warming (see above). According to Pörtner (2008) (see also Wittmann and Pörtner 2013), OA-induced disturbances in pH_e, and thus ion exchange rates, influence cellular processes and functions. Thus, impaired performance capacities might become more prominent at larger OA-induced pH_e alterations. To what extent annual PCO_2 fluctuations in the natural habitats of the investigated populations might relate to the different OA sensitivities remains to be explored. Thermal sensitivity of escape performance in scallops may also depend on environmental history (Guderley et al. 2009). Warm incubation of winter (boreal *P. maximus*, previous study) versus warm incubation of late summer scallops (temperate *P. maximus*, present study) might also explain the differences in OA sensitivity observed in the populations. However, since both populations were in their respective upper thermal pejus range, the key reason for the lower impairment in escape performance in temperate compared to boreal OA-exposed scallops is most likely the difference in OA-induced extracellular acidosis.

In the present study, temperature more than OA exposure had a large impact on escape performance of temperate *P. maximus* indicated by the significantly decreased mean phasic force at 20 °C compared to 10 °C. Interestingly, this force reduction could not be linked to the lower MI in the warmth, because mean phasic force was similar between sampling years although the MI was significantly lower in 2010 than in 2011.

This temperature effect matches earlier findings by Guderley et al. (2009), who observed a negative warming effect (6/12–18/19 °C) on phasic contraction in the scallop, *P. magellanicus*. However, total force (present study) and force of the tonic muscle (present study and Guderley et al. 2009) increased in the warmth, indicating an augmented use of the tonic muscle. In scallops, ATP generation for swimming is firstly and mainly fuelled by phosphor-L-arginine (PLA) degradation followed by anaerobic glycolysis and octopine formation during escape response or recovery (Grieshaber 1978; de Zwaan et al. 1980; Bailey et al. 2003). Pérez et al. (2008a) suggested that the interplay

between phasic and tonic contractions allows partial recuperation of the phasic muscle during periods when the tonic muscle is used. Guderley et al. (2009) suggested further that a temperature-induced decrease in phasic performance reflects a limitation in endurance performance (i.e. overall rate of phasic contractions) rather than in the initial clapping response, due to the interplay between phasic and tonic muscle performance. These assumptions match our observations as the number of claps was not influenced by warming despite lowered metabolic scope at 20 °C compared to 10 °C. We observed a reduction in time to fatigue as well as a prolongation of the recovery period in warm-compared to control-exposed scallops under normocapnia. These findings suggest that scallops at their upper thermal limits in a warming ocean may suffer more from the same or a higher predation pressure with likely consequences at the ecosystem level. Furthermore, complete recovery from fatigue, while initially supported by anaerobic glycolysis, requires aerobic metabolism (Grieshaber 1978; Thompson et al. 1980; Bailey et al. 2003). Due to higher baseline costs at 20 °C than at 10 °C, indicated by elevated RMR and lowered haemolymph PO_2 values, the period needed to recover from exhaustive exercise was significantly extended in the warmth. Furthermore, we found the shortest recovery time in scallops from 2010, which also displayed the lowest RMR. This indicates a strong positive correlation between baseline costs and the ability to recover from exercise in line with the aerobic power budgeting concept (Guderley and Pörtner 2010).

In line with the OCLTT concept, the present findings revealed impaired performance in the upper thermal pejus range linked to a progressive warming-induced mismatch between aerobic energy supply and demand due to a warming-induced rise in maintenance costs. Performance thus does not exclusively depend on anaerobic metabolic capacity. In contrast to our initial working hypothesis and previous study (Schalkhausser et al. 2013), we observed no further impact following additional exposure to ocean acidification suggesting that the temperate scallop population is not highly affected by predicted OA scenarios with respect to swimming performance and escape behaviour from predators. The OA-induced acidification of the haemolymph was larger in boreal *P. maximus* (Norway, previous study) than in temperate *P. maximus* (France, present study) and might explain the lower sensitivity to OA in the temperate population when in the upper thermal pejus range. The impact of pH_e variations on performance capacities merits further investigation to improve our understanding of the mechanisms defining sensitivity towards OWA.

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Ethical standard We hereby declare that the experiments comply with the current laws of the country in which they were performed.

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