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ORIGINAL PAPER

Elevated CO_2 and heatwave conditions affect the aerobic and swimming performance of juvenile Australasian snapper

Shannon J. McMahon[1] · Darren M. Parsons[2,3] · Jennifer M. Donelson[1] · Steve M. J. Pether[4] · Philip L. Munday[1]

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Abstract

As climate change advances, coastal marine ecosystems are predicted to experience increasingly frequent and intense heatwaves. At the same time, already variable CO_2 levels in coastal habitats will be exacerbated by ocean acidification. High temperature and elevated CO_2 levels can be stressful to marine organisms, especially during critical early life stages. Here, we used a fully cross-factored experiment to test the effects of simulated heatwave conditions (+ 4 °C) and elevated CO_2 (1000 µatm) on the aerobic physiology and swimming performance of juvenile Australasian snapper, *Chrysophrys auratus*, an ecologically and economically important mesopredatory fish. Both elevated temperature and elevated CO_2 increased resting metabolic rate of juvenile snapper, by 21–22% and 9–10%, respectively. By contrast, maximum metabolic rate was increased by elevated temperature (16–17%) and decreased by elevated CO_2 (14–15%). The differential effects of elevated temperature and elevated CO_2 on maximum metabolic rate resulted in aerobic scope being reduced only in the elevated CO_2 treatment. Critical swimming speed also increased with elevated temperature and decreased with elevated CO_2, matching the results for maximum metabolic rate. Periods of elevated CO_2 already occur in the coastal habitats occupied by juvenile snapper, and these events will be exacerbated by ongoing ocean acidification. Our results show that elevated CO_2 has a greater effect on metabolic rates and swimming performance than heatwave conditions for juvenile snapper, and could reduce their overall performance and potentially have negative consequences for population recruitment.

Introduction

Accumulation of anthropogenic carbon dioxide in the atmosphere is causing rapid warming at the earth's surface. In the oceans, average sea surface temperature has increased by ~ 0.5 °C since the 1950s (Rhein et al. 2013) and is projected to increase up to 4 °C by the end of the century (Collins et al. 2013). Climate change is also increasing the frequency, intensity and duration of marine heatwaves, which are defined as prolonged periods of anomalously high sea surface temperature (Oliver et al. 2018). Thirty-five percent of coastal marine environments have already experienced more intense and frequent extreme temperatures since the start of the 20th century (Lima and Wethey 2012), with heatwaves expected to further increase in severity and frequency as climate change advances (King et al. 2016; Frölicher et al. 2018). In addition to causing rapid warming, higher atmospheric CO_2 concentrations increase the CO_2 content of seawater, by increasing the uptake of CO_2 at the ocean's surface (Doney et al. 2009). In coastal habitats, this additional CO_2 exacerbates periods of high pCO_2 and low pH that already occur in some nearshore environments

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✉ Shannon J. McMahon
Shannon.mcmahon@jcu.edu.au

[1] ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD 4811, Australia

[2] National Institute of Water and Atmospheric Research, Auckland, New Zealand

[3] Institute of Marine Science, University of Auckland, Auckland, New Zealand

[4] National Institute of Water and Atmospheric Research, Northland Marine Research Centre, Ruakaka, New Zealand

due to upwelling of CO_2-rich water and nutrient inputs that stimulate biological activity (Feely et al. 2008; Hofmann et al. 2011; Green and Zeldis 2015). Consequently, marine organisms in coastal habitats may already be subjected to episodes of high CO_2 that exceed predictions for the open ocean by the end of the century, and which will be exacerbated by the ongoing uptake of CO_2 from the atmosphere (Shaw et al. 2013; Hoegh-Guldberg et al. 2014; Waldbusser and Salisbury 2014).

Most marine organisms are ectotherms, whose physiological functions are affected by temperature change, especially when outside the range usually experienced. Higher temperature increases biochemical reactions and cellular processes, and consequently increases metabolic rate (Gillooly et al. 2001; Schulte, 2015). High seawater pCO_2 can also affect physiological functions of marine organisms because it raises plasma pCO_2, which acts to acidify the organism's blood and tissue (Pörtner et al. 2004). As most cellular processes function optimally within a narrow pH range, many marine organisms actively regulate their acid–base balance to prevent acidosis in high CO_2 conditions (Pörtner et al. 2004; Heuer and Grosell, 2014). However, the process of ion exchange to maintain a stable pH can be energetically costly (Melzner et al. 2009b; Heuer and Grosell, 2016). Therefore, high temperature and elevated CO_2 have the potential to increase the basal energy requirements an organism needs to survive (Pörtner and Farrell 2008; Enzor et al. 2013).

Understanding how environmental stressors, such as elevated temperature and CO_2, affect the metabolic rates of marine organisms is key to determining the impact of climate change on their populations (Pörtner and Knust 2007; Rijnsdorp et al. 2009; Pörtner and Peck, 2010). As metabolism is difficult to directly measure, the rate of oxygen consumption is commonly used as a proxy for metabolic rate (Roche et al. 2013; Rummer et al. 2016). Typically, resting metabolic rate (RMR) of an organism is estimated by measuring resting oxygen consumption (MO_{2rest}) and the maximum metabolic rate (MMR) is estimated by measuring maximum oxygen consumption (MO_{2max}). The difference between maximum and minimum oxygen consumption are used to calculate aerobic scope ($MO_{2max} - MO_{2rest}$ = absolute aerobic scope). Aerobic scope is a proxy for an individual's capacity to undertake aerobic activities, such a swimming and foraging, therefore, reductions in aerobic scope can reduce physical performance (Priede 1985; Pörtner and Farrell, 2008; Johansen and Jones, 2011). For example, aerobic scope in salmon was positively correlated with swimming performance needed during migration to natal spawning sites (Eliason et al. 2011). Generally, increased water temperature raises MO_{2rest}, whereas MO_{2max} increases to an optimal temperature and then declines at higher temperatures as the cardiovascular system is no longer able meet oxygen demands (Pörtner and Knust 2007; Pörtner 2010). Therefore, aerobic scope may initially increase with rising temperature but then declines above the optimum temperature for MO_{2max} (Farrell et al. 2008; Eliason et al. 2013). On the other hand, elevated CO_2 has displayed variable effects on MO_{2rest}, MO_{2max} and aerobic scope. While there appears to be no overall effect of elevated CO_2 on aerobic scope when all studies are considered together (Lefevre 2016; Cattano et al. 2018), different studies have reported increases (MO_{2rest}: Enzor et al. 2013; Laubenstein et al. 2018; MO_{2max}: Silva et al. 2016; Aerobic Scope: Rummer et al. 2013; Gräns et al. 2014), decreases (MO_{2rest}: Rummer et al. 2013; Pimentel et al. 2014; Aerobic Scope: Munday et al. 2009), and no effect (MO_{2rest}: Strobel et al. 2012; Couturier et al. 2013; MO_{2max}: Pope et al. 2013; Aerobic Scope: Laubenstein et al. 2018) on MO_{2rest}, MO_{2max} and aerobic scope. Thus, it seems that the effects of elevated CO_2 on fish metabolic rates can be species-specific.

Coastal habitats are more susceptible to heatwaves and elevated CO_2 events than the open ocean (Hoegh-Guldberg et al. 2014). Additionally, nearshore environments are expected to experience more severe and frequent heatwaves in the future, even under the most conservative CO_2 emission scenarios (King et al. 2016; Frölicher et al. 2018). In the Indo-Pacific region, notable heatwaves have occurred on Ningaloo Reef, Western Australia in 2011 (+3 °C average over 5 weeks) (Pearce and Feng 2013), the northeast Pacific in 2013–2015 (reaching +2.5 °C, February 2014) (Di Lorenzo and Mantua 2016) and across northern Australia in 2016–2017 (reaching +2 °C and lasting for 3 months) (Benthuysen et al. 2018). The 2016–2017 heatwave caused unprecedented back-to-back mass coral bleaching and mortality on the Great Barrier Reef (+1–2 °C for over 4 weeks) (Hughes et al. 2017; Spinks et al. 2019). In the summer of 2017/2018, New Zealand recorded one of the most pronounced and extensive marine heatwaves on record, with water temperatures up to 4 °C higher than average during three distinct peaks, each lasting more than 5 days, and an average 2 °C higher temperature throughout January and February (NIWA 2018: Salinger et al. 2019). Importantly, these heatwave events are becoming more frequent during the critical recruitment times for many fish species (Caley et al. 1996), which could have serious consequences for the replenishment of fish populations.

In contrast to the open ocean, some coastal habitats experience substantial fluctuations in pH, often reaching levels equivalent to worst case climate change scenarios (Hofmann et al. 2011; Price et al. 2012; Law et al. 2018). These fluctuation can be caused by upwelling of CO_2 rich seawater (Feely et al. 2008; Fassbender et al. 2011), nutrient input that enhances biological activity and respiration (Borgesa and Gypensb 2010; Cai et al. 2011; Duarte et al. 2013) and limited water exchange in bays and shallow habitats (Middelboe and Hansen 2007; Feely et al. 2010; Challener et al. 2016).

For example, pH (total hydrogen scale pH_{total}) may range between 7.6 and 8.4 (~ 100–1200 µatm pCO_2) over 24 h in some shallow reef environments (Shaw et al. 2012) and can range between 7.7 and 8.3 (~ 200–1000 µatm pCO_2) in bays and estuaries with low pH events lasting for weeks and, in some cases, becoming persistent over multiple months (Hofmann et al. 2011; Law et al. 2018). The fluctuation in pH and pCO_2 of coastal habitats are also expected to be exacerbated as climate change advances due to the change in the buffering capacity of seawater as it takes up additional CO_2 from the atmosphere (Shaw et al. 2013; McNeil and Sasse 2016). Therefore, marine organisms recruiting into these coastal habitats are expected to be confronted with significantly more extreme pH and pCO_2 in the future.

The Australasian snapper, *Chrysophrys auratus*, is a commercially and recreationally important reef mesopredator found in Australian and New Zealand waters (MPI 2013; GBRMPA 2014). It inhabits nearshore and estuarine environments during its early life stages, utilizing complex habitat structure for protection (Parsons et al. 2016; Lohrer et al. 2018). Early life stages of fish are generally more sensitive to environmental stressors than adults as the demands of growth and maintenance are highest during this stage (Post and Parkinson 2001; Stallings et al. 2010). Additionally, the early juvenile stage is a time when aerobic performance and swimming ability are critically important for migrating to settlement habitat and avoiding predators (Dudley et al. 2000; Almany and Webster 2006). Since juvenile snapper use nearshore and estuarine environments there is a high chance that they will increasingly be exposed to high temperature and elevated pCO_2 levels in the future.

This study aimed to determine how the aerobic capacity and swimming performance of juvenile *C. auratus* is effected by elevated temperature and CO_2 levels that are already occurring in some coastal habitats, and which are predicted to become more frequent and extreme as climate change progresses. For example, the Firth of Thames is a major recruitment habitat for juvenile snapper in northern New Zealand (Parsons et al. 2014). Average summer water temperature is approximately 18 °C in this region but can reach 22 °C under extreme conditions (Evans and Atkins 2013; NIWA 2018). Seawater pH in the Firth of Thames varies from a high around 8.3 down to at least 7.7 (Law et al. 2018), equivalent to a pCO_2 range of approximately 200-1000 µatm. Importantly, while elevated temperature or CO_2 can each affect fish performance, they can have additive, synergistic, or antagonistic effects when they occur together (Côté et al. 2016). Therefore, we used a fully crossed 2 × 2 experiment where we exposed juvenile snapper from the northern New Zealand population to current-day average summer conditions (18 °C and 400 µatm CO_2) and levels possible in near-shore environments during a heatwave (22 °C and 1000 µatm CO_2) for 21 days, from 21–42 days post hatching (dph). The exposure period was chosen to start from 21 dph as this is when juveniles being to settle from the pelagic environment into near-shore habitats (Parsons et al. 2014). We then tested the metabolic performance of juveniles, by measuring oxygen consumption as a proxy for RMR, MMR and absolute aerobic scope. Metabolic rates indicate the energy requirements of an individual that can underpin a number of fitness-related traits (Burton et al. 2011). For instance, swimming performance is positively correlated with MO_{2max} and aerobic scope in a range of fishes (Brett 1964; Eliason et al. 2011; Johansen and Jones, 2011). Therefore, we also tested the maximum swimming performance of juveniles, using a *U*crit test, to determine whether any effects on aerobic performance affected key aspects of the fish's physical performance.

Methods

Aquarium setup

This study was conducted at the National Institute of Water and Atmospheric Research Northland Marine Research Centre (NMRC), in Ruakaka, New Zealand. Brood stock fish ($n = 39$) were captured from the wild population of *C. auratus* by longline fishing in Bream Bay, adjacent to the NMRC, during September of 2017. The brood stock were split between two 20 m^3 circular tanks at the ambient temperature when they were collected (~ 16 °C). Each tank was supplied with 130 L min^{-1} ambient seawater, filtered to 10 µm, and followed the natural temperature increase up to the summer average (18 °C), at which point it was maintained for spawning (Table 1). Spawning occurred naturally within brood stock tanks during January 2018. To maximize genetic variation in the experiment, eggs were collected from both broodstock tanks in even proportions. Eggs were collected using an external egg collector as described by Moran et al. (2007), with a 500 µm mesh net to retain eggs from the surface overflow of each tank. An equal proportion of floating eggs from both contributing tanks were mixed, rinsed with oxygenated seawater for 5 min, and disinfected with Tosylchloramide (chloramine-T) at 50 ppm for 15 min. Eggs were then rinsed with seawater and evenly distributed between two 400 L conical hatching tanks. Each tank was stocked with approximately 100,000 fertilized eggs and received flow-through seawater at ambient temperature (18 °C) at a flow rate of 4 L min^{-1}. Photoperiod was maintained at 14 h light 10 h dark. Snapper eggs hatch in 24–48 h at ambient summer temperatures at Bream Bay. Newly hatched larvae remained in the conical rearing tanks until 2 days post-hatching (dph). Larvae were not fed during this period as they rely on their endogenous reserves (Battaglene and Talbot 1992). Any dead eggs, larvae, and egg shells were removed daily

Table 1 Mean (± SD) of experimental seawater chemistry parameters for Australasian snapper (*Chrysophrys aurtus*) brood stock tank and juvenile treatments

Treatment	Salinity (ppt)	Temperature (°C)	Total Alkalinity (µmol/kg SW)	pH (Total)	pCO_2 (µatm)
Brood stock	35.60 ± 0.05	18.03 ± 0.04	2154 ± 6	7.88 ± 0.01	583 ± 14
Ambient temperature ambient CO_2	35.39 ± 0.29	18.05 ± 0.06	2299 ± 9	8.02 ± 0.02	425 ± 19
Ambient temperature elevated CO_2	35.27 ± 0.28	18.05 ± 0.07	2308 ± 8	7.69 ± 0.02	1011 ± 47
Elevated temperature ambient CO_2	35.34 ± 0.21	22.03 ± 0.07	2313 ± 9	7.99 ± 0.02	465 ± 26
Elevated temperature elevated CO_2	35.29 ± 0.16	21.96 ± 0.20	2316 ± 10	7.69 ± 0.01	1027 ± 32

Brood stock tanks were measured during the week of spawning at the start, middle, and end of the week. Temperature and pH_{total} were measured daily in each rearing tank over the 21 day experiments. Total alkalinity and salinity were measured at the start of the experiment and then every 7 days. pCO_2 was estimated from these parameters in CO2SYS

by draining from an outlet at the bottom of the rearing tank. At 2 dph larvae were transferred to two 1500 L tanks located in the same facility for grow-out. These tanks received flow-through ambient seawater (18 °C, ~ 400 µatmCO_2) at a maximum flow of 20 L min^{-1} per tank. Larvae were grown out at ambient conditions until 21 dph, at which point they were transferred to the experimental treatments. Larvae were fed enriched rotifers (INVE, Selco S.Presso) three times a day (0800, 1200, and 1600) from 2dph. Larvae were transitioned onto enriched artemia between 20 and 26dph with feeding twice a day (0800 and 1600) until 42dph.

Experimental design

At 21 dph larval fish were transferred into a fully crossed experimental design with 2× temperatures and 2 × CO_2 levels. The temperature treatments were 18 °C, which is the temperature where spawning is at its peak for this species (Scott and Pankhurst 1992; Sheaves 2006; Wakefield 2010) and 22 °C, which is close to the maximum temperature recorded in the region (Evans and Atkins 2013) and matching heatwave conditions in 2017/2018 (NIWA 2018). The CO_2 treatments were an unmanipulated ambient of ~ 400 µatm and an elevated treatment of ~ 1000 µatm, which is within the current range of pH fluctuations in habitats used by juvenile *C. auratus* in New Zealand (Law et al. 2018). Treatments were duplicated (four treatments each with two replicate rearing tanks) and each rearing tank had independent temperature and CO_2 control as per best practice (Cornwall and Hurd 2015). Temperature was controlled by 1 Kw bar heaters in 200 L sumps tanks, mixed with recirculating submersible pumps, and maintained to ± 0.1 °C. The elevated ~ 1000 µatm treatment was achieved by dosing CO_2 to the appropriate pH set point in the same 200 L sump tanks. CO_2 dosing was regulated by a pH computer (Aquamedic) connected to a pH probe and a solenoid valve, which maintained the desired pH by slowly dosing CO_2 when pH deviated above the set point. Water was delivered at 4 L min^{-1} from the sump tank to the respective rearing tank.

Approximately 1000 larval snapper (21 dph) were stocked to each rearing tank at ambient conditions. The high temperature and CO_2 treatments were then turned on to produce a gradual change over a 24 h period. Larvae were held under these treatments for a further 21 days to 42 dph, during which they metamorphose into juveniles, at which point they underwent physiological assays. The pH_{total} of each rearing tank was measured daily by spectrophotometry (Hach, DR3900) with cresol purple dye (Clayton and Byrne 1993). Temperature was measured daily with a digital thermometer (Comark C22). Water samples were taken from each tank at the start of the experiment and then every 7 days throughout the experiment (21, 28, 35, 42 dph) for total alkalinity (TA) analysis. Water samples were immediately poisoned with a saturated solution of mercuric chloride (0.05% of the sample volume) and later analysed at the University of Otago Research Centre for Oceanography, Dunedin, New Zealand. Alkalinity was determined by potentiometric titration in a closed cell (Dickson et al. 2007) using a Metrohm Dosimat burette (model 765, Metrohm, Switzerland), a Fluke model 8846A voltmeter, and with 0.2 M HCl (nominal concentration, fortified with NaCl to the ionic strength of seawater) added in 0.1 mL steps. Samples were water-jacketed at 25 °C. TA was determined from the titration data using a least-squares minimisation technique and calibrated with certified reference material (Prof. A.G. Dickson, Scripps Institution of Oceanography, U.S.). The salinity of each sample was measured with a YSI Pro30 salinity probe. The daily pCO_2 of each rearing tank was then calculated in CO2SYS (Pierrot et al. 2006) from the measured values of pH_{total}, temperature, TA and salinity and using the constants of Mehrbach et al. (1973), refit by Dickson and Millero (1987) (Table 1).

Respirometry

Aerobic performance was measured using intermittent flow respirometry (Clark et al. 2013; Svendsen et al. 2016) in 15 fish from each treatment (60 fish total). Fish were fasted for

18 h before testing and were tested in their respective rearing treatment. MO_{2rest} was used as a proxy for RMR and MO_{2max} was used to estimate MMR, whilst absolute aerobic scope was calculated by subtracting MO_{2rest} from MO_{2max} for each fish. Respirometry was conducted in purpose-built intermittent-flow respirometry chambers for juvenile fish (between 13 and 14.5 ml per closed system), submerged in aquaria within the fish's respective experimental treatment water. Submersible pumps fitted to each chamber supplied a continuous water flow from the surrounding water bath through the chambers. Activity was reduced in the respiration chambers using appropriately sized chambers to minimise movement and by shading each chamber from visual simulants. A purpose built python program, AquaResp V3.0, was used to control the timing measurement cycle. This consisted of a 4 min measurement period, 2 min flushing period, and a 1 min wait period, which was repeated over a 4 h trial duration. The O_2 consumption rates were measured during the intervals of interrupted water flow with a Firesting Optical Oxygen Meter (Pyro Science e. K., Aachen, Germany), which the AquaResp program recorded during the measurement periods. The entire measurement period was used to calculate MO2 provided that the slope R^2 was > 0.95. Over 98% for measured slopes across all treatments were above this threshold. Immediately before respirometry commenced, each fish was swum for 5 min at 10 body lengths per second in a swimming flume (see below). Five minutes was enough to illicit unsteady swimming and anaerobic muscle use. Fish were then placed immediately into respirometry chambers allowing for MO_{2max} to be measured immediately following exercise. Fish then remained in the chambers while recovering back to MO_{2rest} over 4 h, with the majority of juveniles reaching stable MO_{2rest} within 1–2 h (Fig. S1). At the end of each trial, wet mass was taken for each individual to adjust the MO_2 calculations for the individual's specific weight.

MO_{2max}, MO_{2rest} and total aerobic scope of individuals in mg O_2 kg^{-1} h^{-1} were calculated using the equation:

$$MO_2 = K * V * \beta / M, \quad (1)$$

where K is the linear rate of decline ($kPah^{-1}$) in the oxygen content over time (h) in the respirometer; V is the volume of the respirometer in L, which is adjusted for the volume of the fish; β is the solubility of oxygen in water at a specific temperature and salinity (mg O_2 L^{-1} kPa^{-1}); and M is the body mass of the fish (kg). Blank measurements were taken for each chamber at the start and end of each trial to calculate any background respiration. Background respiration did not exceed 45 mg O_2 kg^{-1} h^{-1} in any trial. Linear regressions were then used to calculate background respiration over the trial, which was used to adjust the MO_2 measurements for each fish. MO_{2rest} was determined using the mean of the lowest normal distribution for MO_2 values (Behrens and Steffensen 2007; Chabot et al. 2016).

Critical swimming speed

Critical swimming speed (U_{crit}) was measured to compare swimming performance among treatments. Individual fish (13 fish per treatment, 52 fish total) were swum against a water current in a Brett type swimming tunnel (Brett 1964). U_{crit} was measured in different individuals to those used in respirometry trials (above). The water was maintained at the desired temperature and pCO_2 by constant flow-through of the respective treatment water of each fish from the main system. A single fish was placed into the swim tunnel and allowed 10 min to habituate at a water speed of one body length per second (bl s^{-1}). Following standard procedure (Brett 1964), the water flow was then increased by increments of ~ 2 bl s^{-1} (~ 3 cm s^{-1}). Each flow speed was maintained for 10 min, after which the water speed was increased by another 2 bl s^{-1}. These 10 min intervals, increasing by 2 bl s^{-1} each time, were conducted until the fish was no longer able to maintain its position in the water current. The trial was stopped when an individual rested against the rear screen of the flume for 5 s, because fish have the potential to rest momentarily and then burst back into swimming. After fatiguing the water flow was stopped and the fish was allowed 10 min to recover before it was removed from the swim tunnel. U_{crit} was calculated following Brett (1964):

$$U_{crit} = U + U_i * (t/t_i), \quad (2)$$

where U is the penultimate speed before the fish stopped swimming; U_i is the flow speed increment; t is the time elapsed in the final increment during which the fish stopped swimming; and t_i is the amount of time individuals were maintained at each speed.

Statistical analysis

Separate linear mixed-effects models (LMEs) were used to test for differences in MO_{2rest}, MO_{2max}, aerobic scope and U_{crit} across the experimental treatments. Temperature and CO_2 were fixed factors in the models. Rearing tank and testing day were included as random factors. An additional random factor of respiration chamber was used in MO_{2rest}, MO_{2max}, aerobic scope LMEs. Standard length was included as a covariate in the LME for U_{crit}. All assumptions for the LMEs were met. Statistical analysis was conducted with a statistical significance of $\alpha = 0.05$. Analysis was done in SPSS V.25 (IMB).

Results

Aerobic performance

MO_{2rest} was significantly higher at 22 °C compared with 18 °C ($F_{1,53} = 313.01$, $P = < 0.001$) (Fig. 1) (Table S1). MO_{2rest} was ~ 100 mg O_2 kg^{-1} h^{-1} higher at 22 °C, which represented a 21–23% increase from 18 °C. Elevated CO_2 also significantly increased MO_{2rest} ($F_{1,55} = 68.61$, $P = < 0.001$), by ~ 50 mg O_2 kg^{-1} h^{-1} or 9–10% regardless of temperature. There was no interaction between temperature and CO_2 on MO_{2rest} ($F_{1,55} = 1.35$, $P = 0.249$).

MO_{2max} was significantly higher at 22 °C compared with 18 °C ($F_{1,54} = 86.43$ $P = < 0.001$) (Fig. 1) (Table S2). MO_{2max} was 148–187 mg O_2 kg^{-1} h^{-1} higher at 22 °C, which represented a 16–18% increase at the higher temperature. Conversely, elevated CO_2 significantly reduced MO_{2max} by 144–183 mg O_2 kg^{-1} h^{-1} or 14–15% regardless of the temperature ($F_{1,55}, = 80.21$, $P = < 0.001$). There was no interaction between temperature and CO_2 on MO_{2max} ($F_{1,55}, = 0.11$, $P = 0.739$).

Elevated temperature significantly increased aerobic scope by 35–77 mg O_2 kg^{-1} h^{-1}, or 8–13% ($F_{1,53} = 18.73$, $P = < 0.001$) (Table S3). The absolute aerobic scope of juvenile snapper was significantly reduced by elevated CO_2 with fish in the 400 µatm treatment having an aerobic scope of 591–674 mg O_2 kg^{-1} h^{-1}, compared 405–440 mg O_2 kg^{-1} h^{-1} for fish in the 1000 µatm treatment ($F_{1,55} = 261.36$, $P = < 0.001$) (Fig. 2). Consequently, there was a 31–35% reduction in aerobic scope among fish in the elevated CO_2 treatment compared. There was no interaction between temperature and CO_2 ($F_{1,55} = 2.69$, $P = 0.106$).

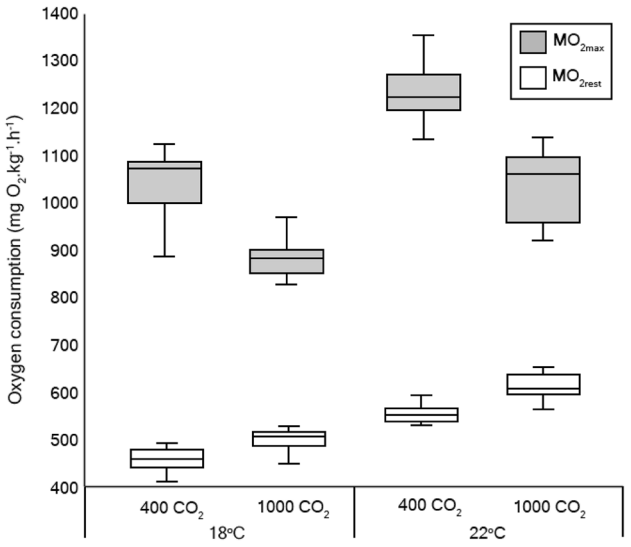

Fig. 1 Oxygen consumption of larval *C. auratus* maintained at ambient and elevated CO_2 (400 and 1000 µatm) and temperature conditions (18 and 22 °C) for 21 days (21–42 dph)

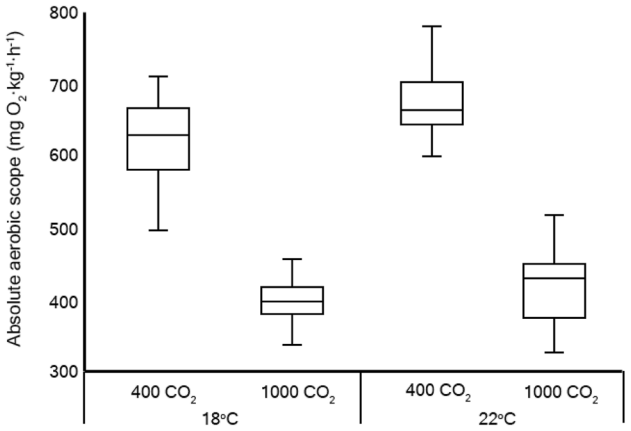

Fig. 2 Absolute aerobic scope of larval *C. auratus* maintained under ambient and elevated CO_2 (400 and 1000 µatm) and temperature conditions (18 and 22 °C) for 21 days (21–42 dph)

Critical swimming speed

The U_{crit} of juvenile snapper ranged from 14 to 21 cm s^{-1} (7 to 10 body lengths s^{-1}) and speed was dependent on both temperate and CO_2, as well as body length (Fig. 3) (Table S4). Specifically, U_{crit} significantly increased by 8–12% or 1.2–2.1 cm s^{-1}, at 22 °C compared with 18 °C ($F_{1,46} = 7.12$, $P = 0.010$) (Fig. 3). Conversely, elevated CO_2 significantly decreased U_{crit}, by 8–11% or 1.3–2.1 cm s^{-1} ($F_{1,46} = 30.60$, $P = < 0.001$). There was no interaction between elevated temperature and CO_2 ($F_{1,46} = 0.67$, $P = 0.414$). Additionally, U_{crit} was found to be significantly affected by length ($F_{1,46} = 19.75$, $P = 0.000$) where increased speed and length were correlated (Fig. 3).

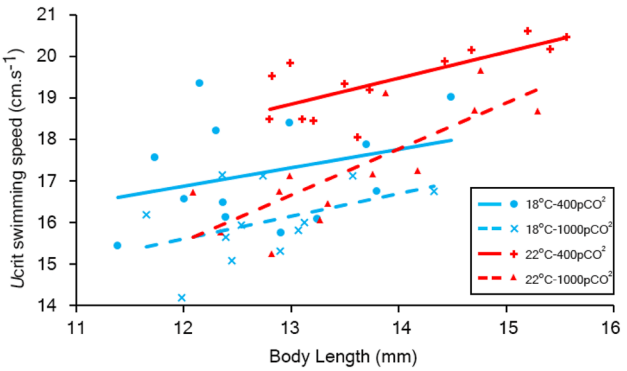

Fig. 3 *U*crit swimming speed of larval *C. auratus*, depending on standard length, in fish exposed for 21 days (21–42 dph) to ambient and elevated CO_2 (400 and 1000 µatm) and temperature conditions (18 and 22 °C)

Discussion

Coastal environments are critical habitats for the early life stages of marine fish, yet they are also susceptible to extreme environmental conditions (Grantham et al. 2004; Hofmann et al. 2011; Lima and Wethey 2012). We found that simulated heatwave temperature and elevated CO_2 both had significant but non-interacting, effects on the metabolic rates and swimming performance of juvenile Australasian snapper, an iconic fish species of high ecological, economic and social importance. Both high temperature and elevated CO_2 increased MO_{2rest} in juvenile snapper, whereas MO_{2max} was increased by elevated temperature and decreased by elevated CO_2. Consequently, aerobic scope decreased in fish exposed to elevated CO_2, but not elevated temperature. U_{crit} swimming followed a similar trend to MO_{2max}, where it increased at high temperature and decreased in elevated CO_2. These results suggest that the aerobic capacity and swimming performance of juvenile snapper in New Zealand are likely to be more vulnerable to elevated CO_2 events (up to 1000 pCO_2) than heatwave events (+4 °C above ambient summer temperature).

MO_{2rest} is indicative of the daily energy expenditure for basic maintenance. As expected, MO_{2rest} increased in the high-temperature treatment. MO_{2rest} was also higher in elevated CO_2, which has implications for juvenile snapper living in locations that naturally experience periods of high pCO2, especially if they coincide with heatwave conditions. The ramifications of 20% higher MO_{2rest} at 22 °C and 10% higher MO_{2rest} in 1000 µatm CO_2 would be substantial, considering juveniles have limited stored energy available (Post and Parkinson 2001; Stallings et al. 2010) and food resources can be naturally patchy (Link et al. 2005; Brown et al. 2010). In cases where both stressors are experienced in tandem, acquiring 30% more energetic resources to support daily energetic costs might be difficult and could result in reduced growth and survival in nature (Mogensen and Post 2012).

MO_{2max} also increased at 22 °C compared with 18 °C, suggesting that 22 °C is still within the optimal range for maximal aerobic capacity in juvenile *C. auratus*. This is not surprising considering the temperature range experienced by this species across its distributional range is from 16 to 25 °C during summer (Sheaves 2006; Wakefield et al. 2015). This result is also consistent with the observation that the thermal niche of temperate species is often wider than tropical species, and that populations of many temperate ectotherms are not living close to their upper thermal limits (Tewksbury et al. 2008; Sunday et al. 2010). Since the increase in MO_{2max} was greater than MO_{2rest} increase, the absolute aerobic scope of these juvenile fish was increased by ~ 11% from 18 to 22 °C. However, the decrease in MO_{2max} and increase of MO_{2rest} under elevated CO_2 ultimately reduced the aerobic scope of juvenile snapper by approximately 30%. Therefore, while an increase in aerobic scope at higher temperature may prove beneficial for juvenile fish, any positive effects would likely be overshadowed by the effects of elevated CO_2 when they occur together. A lower aerobic scope in juvenile fish can potentially affect growth rates, dispersal, settlement rates, and survival (Pörtner and Peck 2010), which would be detrimental to the population, even if later life stages of these species are robust to elevated CO_2. While the link between aerobic scope and fitness-related activities is still debated (Gräns et al. 2014; Norin et al. 2014; Farrell, 2016; Pörtner et al. 2017), reduced MO_{2max} and, thus aerobic scope, could affect swimming performance (see below) and foraging ability, and thus have implications for juvenile snapper living in nearshore habitats.

Swimming performance can be critical to the success of juvenile fish especially near the time of settlement to benthic habitats (May 1974; Fisher 2005). As with other traits, the effect of any particular temperature on swimming speed will depend on where that temperature sits within the thermal performance curve (Wardle 1980; Green and Fisher 2004; Johansen et al. 2014). Increased swimming performance has been observed in a number of temperate fish species at temperatures above their natural ambient conditions (Burst swimming: Batty and Blaxter 1992; U_{crit}: Schurmann and Steffensen 1997; Lee et al. 2003; Routine swimming: Peck et al. 2006), again suggesting that populations of many species may be living below their optimal temperature, at least for maximum swimming performance. As the MO_{2max} of an individual plays a pivotal role in determining the maximum performance of aerobic activities (Metcalfe et al. 2016; Norin and Clark 2016), it is unsurprising that the trend for MO_{2max} and U_{crit} matched in juvenile snapper. Similarly, while increases in aerobic scope do not always represent a benefit to an individual's overall performance (Clark et al. 2013; Gräns et al. 2014), we found that the increase in aerobic scope up at 22 °C correlated with increased swimming performance for juvenile *C. auratus*. It should be noted that juveniles from the elevated temperature treatment were ~ 1 mm longer (7–9%) on average, which also gave them an advantage in swimming performance, but this was accounted for using size as a covariate in the model. Increasing swimming ability within the temperature range tested could be beneficial during the juvenile phase, as it may increase survival and settlement rates (Letcher et al. 1996; Hamilton et al. 2008). However, elevated CO_2 reduced swimming performance in juvenile snapper. The decrease in U_{crit} at 1000 µatm CO_2 was of a similar magnitude to the increase in U_{crit} from 18 to 22 °C; therefore, any benefits of higher temperature on swimming performance would

be offset by elevated CO_2 if both occur simultaneously. Moreover, juvenile snapper may often experience periods of high CO_2 in their natural habitats, even when water temperature is not elevated. Our results suggest that these high CO_2 events, or habitats that sustain elevated CO_2 for long periods of time, such as bay and estuarine systems like the Firth of Thames (Green and Zeldis 2015; Law et al. 2018), could already reduce the swimming performance of juvenile snapper in the wild.

Our observation that elevated CO_2 increased MO_{2rest} in juvenile snapper differs from most previous studies and similarly, our observed reduction of MO_{2max} has only been seen in a few other species (reviewed in Lefevre 2016; Cattano et al. 2018). Interestingly, previous studies that have detected a decline in MO_{2max} under elevated CO_2 have tested juvenile stages of pelagic spawning predatory species (Pope et al. 2014; Laubenstein et al. 2018), akin to this study. In addition, we found that elevated CO_2 reduced swimming performance in juvenile snapper, which is comparable to studies on larval (Pimentel et al. 2014) and juvenile (Bignami et al. 2014) dolphin fish, and juvenile yellowtail kingfish (Watson et al. 2018). However, other studies have found no effect of elevated CO_2 on the swimming performance of juvenile fish (Atlantic cod: Melzner et al. 2009a; sand smelt: Silva et al. 2016; cobia: Bignami et al. 2017), suggesting that sensitivity to elevated CO_2 may be highly species specific. Indeed, Hamilton et al. (2017) showed that elevated CO_2 reduced the swimming performance and aerobic scope of one species of rockfish (*Sebastes caurinus*) but had no effect on a closely related species (*Sebastes mystinus*), showing that sensitivity to elevated CO_2 may differ even between closely related species.

Another consideration is the possibility of varying sensitivity to elevated CO_2 at different life stages. In a meta-analysis of all studies in fish conducted at the time, Lefevre (2016) found no overall effect of elevated CO_2 on MO_{2rest}, MO_{2max}, or aerobic scope. However, when meta-analysis has separated studies into life stages there have been varying effects of elevated CO_2 depending on the life stage at which they were tested (Cattano et al. 2018). This could be due to differences in energetic demands and acid–base regulation capacity between particular life stages. The majority of studies that have reported no effects of elevated CO_2 on oxygen consumption have used more developed stages, from late juveniles to adults, which are better equipped to deal with elevated CO_2 as they have fully developed acid–base regulatory mechanisms (Ishimatsu et al. 2008; Melzner et al. 2009b). There are now a number of species where metabolic rates have been found to be affected by elevated CO_2 during early life history stages (Miller et al. 2013; Pimentel et al. 2014; this study), suggesting that this may be a more susceptible ontogenetic stage. However, there are also a number of species which are not affected by elevated CO_2, even during early life (Lefevre 2016) and the underlying reasons for apparent species-specific differences in sensitivity are unknown.

Changes in aerobic and swimming performance in response to short-term elevated temperature and CO_2, such as those reported in this study, have the potential to affect population dynamics. Adult populations of most fishes are strongly influenced by patterns of growth and mortality in the larval and juvenile phases (Doherty and Williams 1988; Caley et al. 1996; Parsons et al. 2014). We found no interactive effects between temperature and CO_2 on the traits measured, so in this case their combined effect was predictable from each one independently. Additionally, elevated CO_2 (1000 µatm) would likely have more significant negative ecological effects than the high temperature on these juvenile snapper, as the higher temperature appeared to be within the optimal performance range for the traits measured here. However, further increases in temperature may push this species past their optimal range which could add to, or compound, the negative effects of elevated CO_2 on aerobic scope and swimming performance. It is also important to note that mature *C. auratus* have been shown to have their peak spawning in early summer where SST is between 18 and 20 °C, with a marked decline in spawning above this range (Scott and Pankhurst 1992; Francis 1994; Wakefield 2010), suggesting that snapper reproduction may be susceptible to heatwaves. Therefore, the independent effects of higher temperatures and elevated CO_2 may be felt on snapper populations during different parts of their life history, but with both potentially having a negative effect on long-term viability of snapper populations. The next step will be to incorporate our results into numerical population models to evaluate how the independent and combined effects of elevated temperature and CO_2 may influence the dynamics and sustainability of snapper populations.

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Data availability The data sets is available on JCU's Topical data hub. https://doi.org/10.25903/5db68cc96296b.

Compliance of ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This project followed animal ethics guidelines at James Cook University (JCU Animal Ethics No. A2482).

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