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Body size mediated effects of multiple abiotic stressors on the growth and social behaviour of an estuarine fish, Australian Bass (*Macquaria novemaculeata*)

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Body size mediated effects of multiple abiotic stressors on the growth and social behaviour of an estuarine fish, Australian Bass (*Macquaria novemaculeata*)

Abstract

Anthropogenic climate change is expected to result in dramatic shifts in the abiotic conditions within estuaries, including an elevation of temperature and salinity levels. Even so, few studies have addressed the impacts of multiple abiotic stressors on the behaviour and life history of key estuarine species, such as those of biological and commercial importance. Here we used a cross-factored experimental design to tease apart the effects of temperature and salinity on intraspecific aggression and growth rates of a native estuarine fish species, the Australian bass (*Macquaria novemaculeata*). Juvenile bass were exposed to one of four treatment conditions: 1) baseline temperature and salinity, 2) elevated temperature, 3) elevated salinity, and 4) elevated temperature and salinity. Elevated salinity increased rates of aggression, and elevated temperature decreased rates of growth, although the effects of both factors were mediated by the body size of individual bass. These results therefore highlight complex and variable effects of abiotic stressors and body size, emphasising the importance of considering individual-level attributes when evaluating the impacts of climate change on estuarine fishes.

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**BODY SIZE MEDIATED EFFECTS OF MULTIPLE ABIOTIC STRESSORS ON
THE GROWTH AND SOCIAL BEHAVIOUR OF AN ESTUARINE FISH,
AUSTRALIAN BASS (*MACQUARIA NOVEMACULEATA*)**

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ABSTRACT

Anthropogenic climate change is expected to result in dramatic shifts in the abiotic conditions within estuaries, including an elevation of temperature and salinity levels. Even so, few studies have addressed the impacts of multiple abiotic stressors on the behaviour and life history of key estuarine species, such as those of biological and commercial importance. Here we used a cross-factored experimental design to tease apart the effects of temperature and salinity on intraspecific aggression and growth rates of a native estuarine fish species, the Australian bass (*Macquaria novemaculeata*). Juvenile bass were exposed to one of four treatment conditions: 1) baseline temperature and salinity, 2) elevated temperature, 3) elevated salinity, and 4) elevated temperature and salinity. Elevated salinity increased rates of aggression, and elevated temperature decreased rates of growth, although the effects of both factors were mediated by the body size of individual bass. These results therefore highlight complex and variable effects of abiotic stressors and body size, emphasising the importance of considering individual-level attributes when evaluating the impacts of climate change on estuarine fishes.

Keywords: climate change; estuary; temperature; salinity; Australian bass; growth rate; aggression

INTRODUCTION

Estuaries are bodies of water that connect freshwater rivers and creeks to the ocean (Roy et al. 2001). The resulting brackish environment supports a diversity of fishes, including commercially and recreationally important species, which often use estuaries during critical parts of their life cycles (Elliott et al. 2007). Since estuaries are influenced by marine, terrestrial and freshwater processes, they are subject to high annual and seasonal climatic variability, hence the biota within them must be able to tolerate some fluctuations in abiotic conditions (Kench 1999; Roessig et al. 2004). Even so, estuarine fish may be particularly vulnerable to the cumulative effects of multiple abiotic stressors because estuarine ecosystems are disproportionately affected by both increasing development on land and water use (Nelson et al. 2009; Gillson 2011; Pratchett et al. 2011). Therefore, it is important to understand how the modification of estuarine water quality influences the persistence of estuarine fishes within these biologically important ecosystems (Pease 1999; Saintilan 2004; McKinley et al. 2011).

Global climate change is likely to be a key factor causing changes in estuarine physical characteristics, water quality and fish assemblages (Koehn et al. 2011). In response to global climate change, a wide range of abiotic factors are expected to change, including temperature, salinity, dissolved oxygen, CO₂ concentrations and pH (Pratchett et al. 2011). These abiotic variables will not exert their effects in isolation, but rather will interact with each other in potentially complex ways (Pease 1999; Hobday and Lough 2011; Koehn et al. 2011). Although the changes to abiotic variables in coastal ecosystems as a result of climate change have been widely reviewed (Gillanders et al. 2011; Koehn et al. 2011; Pratchett et al. 2011), little is known about the nature and extent of impacts on estuarine fishes relative to studies examining the impacts on marine and terrestrial fauna (Booth et al. 2011).

Amongst the various potential abiotic stressors linked to climate change, elevated salinity is likely to pose problems for fishes through influences on osmoregulation and oxygen consumption (Gillanders et al. 2011; Koehn et al. 2011). The spatial distribution of fish along estuaries can indicate the tolerable salinity range of different species (Cardona 2000; Diouf et al. 2006; Bachman and Rand 2008; Macdonald and Crook 2010), however future changes in salinity may cause conditions to move towards, or away from the optimum conditions for each species (Labonne et al. 2009). For example, large increases in salinity may have negative impacts on freshwater and estuarine resident species through physiological stress (Elliott et al. 2007), particularly where upstream estuarine areas have become hypersaline (Koehn et al. 2011; Pratchett et al. 2011). Extreme increases in salinity can also cause mass fish mortalities, and such extreme events are predicted to increase in frequency and intensity (Gillanders et al. 2011). Extreme events could therefore have severe impacts on estuarine fish communities, particularly in estuaries where physical barriers such as dams restrict the ability of fish to move away from stressful abiotic conditions (Hoeksema et al. 2006; Gillanders et al. 2011).

A compounding potential problem associated with high salinity is an elevation in temperature due to climate change. Direct effects of increased water temperature are generally observed through decrements in growth, reproduction, foraging, immune competence as well as changes in behaviour such as aggression (Pörtner and Knust 2007; Pörtner and Farrell 2008). Increasing water temperatures may affect species differently, depending on whether they are at the extremes of their distribution and temperature tolerance (Koehn et al. 2011). Fish generally occupy thermal preference windows that are narrower than their thermal tolerance range, however additional environmental stress can activate a stress response, for example diverting energy from growth and reproduction to maintenance (Koehn et al. 2011). However, increasing water temperatures may also have positive effects for fish well within

their thermal tolerance range; higher temperatures could accelerate development, with faster larval development and shorter larval duration (Gillanders et al. 2011). Faster development may result in higher survivorship through avoiding predation at smaller sizes, or it could lead to greater susceptibilities to starvation because of higher metabolic rates that require more food and almost constant feeding (Gillanders et al. 2011; Koehn et al. 2011).

There have been few experimental studies specifically investigating how multiple abiotic factors, such as salinity and temperature, influence the life history and behaviour of estuarine fishes, making it difficult to assign causal relationships and formulate effective management and conservation strategies. Moreover, but there have been even fewer investigations into how the physical attributes of individuals could mediate their responses to alterations in multiple abiotic factors. Accounting for individual variation is important, because attributes such as body size, age and sex are known to affect the activity level, time budgets, social behaviours and physiological profiles of fish in general (e.g. Wiegmann and Baylis 1995; Taborky and Grantner 1998; Wong et al. 2012). Therefore, not only is it important to address the interacting effects of multiple stressors, but also how they themselves interact with the physical attributes of organisms.

The overall aim of this study was to address these key knowledge gaps by investigating the impacts of climate change on the life history and behaviour of an estuarine fish, the Australian bass (*Macquaria novemaculata*). Australian bass is a catadromous freshwater fish native to Australia from Queensland to Victoria. Adult fish reside in freshwater upstream but migrate downstream to estuaries in order to spawn between late June and early September (Harris, 1986) – as such, juvenile bass develop in saline estuarine waters before migrating upstream to freshwater (Fielder and Heasman 2011). Australian bass have previously been observed to survive in a wide range of abiotic conditions (Harris 1987): thermal tolerance ranges have been estimated between 3-30°C (Cameron et al. 2012; Grigalchik et al. 2012),

and salinity tolerance ranges from 0-35ppt (Fielder and Heasman 2011). Even so, adult bass do not usually enter water of salinity greater than 20ppt (Fielder and Heasman 2011) and field studies demonstrated that spawning, incubation and larval development occur at salinities of 8-14ppt and temperatures of 11-16°C in the wild (Harris 1986). In temperate East Australian streams, water residence time is expected to increase (Hobday and Lough 2011) and, coupled with an increase in air temperatures, could cause water temperatures to rise to over 30°C in summer months (Hobday and Lough 2011; Koehn et al. 2011). Sea-level rise is also expected to cause ocean water to penetrate further upstream in estuaries, hence, elevating salinity levels (Pethick 2001). Therefore, it could be expected that this key predatory species may be exposed to salinities as high as 35ppt in the future, during either their juvenile phase when undergoing migrations between river systems, or when spawning in estuaries as adults. To date, nothing is known about the impacts of multiple interacting stressors on their growth and behaviour, nor how body size might mediate these effects. This lack of data is alarming, given that Australian bass is endemic to the south-eastern coast of Australia, is a highly prized commercially and recreationally fished species, must migrate to estuaries in order to spawn and a key fish predator in estuarine environments throughout its range (Harris 1986; Hall et al. 2009). These attributes make Australian bass a potentially vulnerable species to future climate change, with knock-on impacts on the recreational, economic and ecological gains from this species.

We conducted a controlled manipulative experiment to determine how elevated temperature (30°C) and salinity (35ppt), as well as their interactions with body size, influence three key life history and behavioural traits: growth rate, aggressive interactions and body condition. We hypothesised that salinity would reduce aggression rates i.e. competition intensity declines with increasing abiotic stress (Alcaraz et al. 2008), and reduce growth rates and body condition, due to increased osmotic stress experienced (Boeuf and Payan 2001). This raised

osmotic stress subsequently diverts energy away from higher level activities like aggression. We also hypothesised that elevated temperature would decrease competitive interactions, overall growth rates and body condition because the increased resting metabolism (Pörtner and Knust 2007) would reduce the energy available for higher level functions like growth and rigorous activities (such as aggression). Larger individuals were also expected to display more aggression, grow faster and have a higher body condition given that size typically reflects dominance in fishes (Wong et al. 2007). We experimentally tested these predictions by maintaining juvenile bass fingerlings under varying degree of temperature and salinity in a cross-factored experimental design to tease apart the relative effects of either abiotic factor, and how they interact with body size, on competitive behaviours (intraspecific aggression) and life history traits, to gain a deeper understanding of how climate change may impact one of the key fish predators within estuaries in Australia.

METHODS

Housing and treatment conditions

All fish were housed in 4 separate recirculating systems located at the University of Wollongong, NSW, Australia. Each system comprised 8 aquaria (60 x 30 x 30cm; approximately 54 litres) containing sand and a PVC pipe for shelter. Juvenile Australian bass (*M. novemaculeata*; mean \pm S.E. standard length = 24.6 ± 0.23 mm) of mixed sex were obtained from a native fish hatchery (Aquablue Seafoods Inc.). To determine initial body size and mass, each fish was measured using callipers (mm standard length (SL) \pm 0.1mm) and weighed using an electronic balance (g \pm 0.1g). Each fish was then tagged using fluorescent elastomer (Northwest Technologies Inc.) injected into the dorsal musculature just under the skin to enable individual recognition. Following this procedure, fish were randomly assigned and placed into an aquarium (4 fish per aquarium). Water conditions within each of the four systems were maintained at 22°C and 10ppt salinity for 2 weeks to allow fish to acclimate to baseline conditions. Light cycles were kept at a constant 12L:12D cycle throughout experiments. Bass were fed to ensure each ate approximately 5-6 pellets each (New Life Spectrum, Homestead FL) and were supplemented with approximately 5-8 frozen blood worms (Hikari Frozen Blood worm, 100g) daily.

After the acclimation period, bass in each system (n = 32 per rack) were acclimated to 4 different water conditions (with one treatment per system): 1) baseline temperature and salinity (22°C and 10ppt); 2) elevated temperature and baseline salinity (30°C and 10ppt); 3) baseline temperature and elevated salinity (22°C and 35ppt); and 4) elevated temperature and elevated salinity (30°C and 35ppt). The adjustments made were gradually over a period of 3 weeks, with temperature increases performed at a rate of approximately 3°C per week for the first two weeks and a further 2°C on the third week so that the maximum temperature of 30°C

was reached. Salinity was raised at a rate of 10ppt per week for the first two weeks and a further 5ppt during the third week (acclimatisation to maximum conditions was performed so that maximum temperatures and maximum salinities were reached at the same time between treatments). Fish were then maintained at these treatment conditions for 4 weeks with no change to the feeding or housing regimes.

Behavioural observations

In order to quantify behaviours, we conducted a pilot observation study of a random subset of 5 individuals to develop an ethogram of the aggressive behaviours exhibited by *M. novemaculeata* (Table 1). Having defined their behaviours in this way, the aggressive behaviours of each fish within each treatment were recorded following the 4 week experimental period to determine the effects of increased temperature and salinity on aggressive social behaviour. The fact that each fish was individually tagged with coloured elastomer not only enabled us to score overall rates of aggression, but to identify the individuals that initiated and received the behaviours within each group i.e. the directionality of aggressive interactions. All behavioural trials were conducted during daylight hours. Each fish in a group was observed one at a time for 10 minutes, following a 5 minute acclimation period per group, during which time they habituated to the presence of the observer (i.e. total of 40 minutes observation per group). Only one person (KO) observed the fish to avoid potential issues with observer bias. It was not logistically possible to observe the fish blind to their respective treatments as each rack had to be designated to one treatment. Following observation of all fish in each group, each fish was captured, re-measured and re-weighed as described above to determine final body size and mass, and hence growth rates and body condition.

Statistical analysis

All statistical procedures were performed using SPSS Statistics Version 21.0 (Armonk, NY: IBM Corp.). Aggressive interactions over the 10-minute observation period were summed for each individual (owing to a low frequency of aggressive encounters within each separate category). To investigate whether bass exhibit size-based dominance, the relationship between summed log-transformed aggression and final body size was assessed using a Linear Regression, using only data from the baseline abiotic conditions (low temperature and salinity). Similarly, the relationship between summed log-transformed aggression and the final size ratio between group members of adjacent size and hence dominance rank (SL subordinate / SL immediate dominant; Wong et al. 2007, 2008) was investigated to determine if aggression was heightened between adjacent ranked individuals. Note that dominance was based on relative body size rather than aggression levels, given that size and aggression were significantly positively correlated (Linear Regression: $N = 106$, $R^2 = 0.29$, $p = 0.004$). A Generalized Linear Mixed Model (GLZ) with backward stepwise elimination was used to investigate the effects of salinity, temperature, final body size and group size (owing to some mortality there were some group size reductions during the experiment) on summed aggression, with a Poisson distribution and loglinear link function owing to the count data. Tank ID was incorporated as a random effect to account for non-independence of fish within each tank. Main effects of each factor and selected 2-way interactions (salinity*temperature, salinity*body size and temperature*body size) were included as predictors in the model.

To investigate the effects of abiotic factors on growth, growth rates were first expressed as a % increase relative to their initial body size (Wong et al. 2007). A General Linear Mixed Model (GLMM) with backward stepwise elimination was used to investigate the effects of salinity, temperature, initial body size and group size on % growth rates, incorporating tank

ID as a random effect. As for aggression, main effects of each factor and selected 2-way interactions (salinity*temperature, salinity*body size and temperature*body size) were included as predictors in the model. Each non-significant factor was sequentially removed at a level of $p > 0.05$.

The following mathematical formula was used to quantify the body condition (K) of fish (Fulton 1902): $K = \text{mass (g)} / \text{total length (cm)}^b * 100$, where b = allometric scaling value. The allometric scaling value was obtained from a regression of the length and mass data from fish in this study (linear relationship with a slope of 0.45, $y = 0.45x - 0.98$, $R^2 = 0.90$) (Ureche et al. 2012). Therefore, a value of $b=1$ was chosen in the equation, which has been previously used when calculating condition of fishes from the Percichthyidae family (Ingram 2009). Total length was used as standard length gives a high K value that is misrepresentative of the proportions and condition of the fish (Barnham and Baxter 1998; Ingram 2009; Vasconcelos et al. 2009; Ureche et al. 2012). K values can range from 0 to 2, where values less than 1 indicate a fish in poor condition and values higher than 1.4 indicate a fish in excellent condition (Barnham and Baxter 1998). As body condition was normally distributed, a GLMM with backward stepwise elimination, incorporating tank ID as a random effect, was used to investigate the main effects of each factor and selected 2-way interactions (salinity*temperature, salinity*body size and temperature*body size) were included as predictors in the model. Each non-significant factor was sequentially removed at a level of $p > 0.05$.

RESULTS

Levels of aggression were significantly positively correlated with final body size (Linear Regression: $N = 106$, $R^2 = 0.29$, $p = 0.004$) (Fig 1a) and weakly positively correlated with the final size ratio between adjacent ranked group members ($R^2 = 0.21$, $p = 0.06$) (Fig 1b), indicating the presence of size-based dominance relationships and potentially heightened conflict between adjacent ranked individuals in bass.

Average rates of aggression differed between the four treatments (Table 1). When investigating the influence of each factor, there was no influence of temperature on levels of aggression (GLZ: $F_{1,97} = 0.33$, $p = 0.57$), nor was there a significant interaction between temperature and salinity ($F_{1,97} = 0.66$, $p = 0.42$) or temperature and final body size ($F_{1,97} = 0.07$, $p = 0.79$) on aggression. There was a significant effect of salinity on aggression ($F_{1,100} = 52.6$, $p < 0.001$) that explained 5.1% of the variation, with less aggression occurring at high salinity. There was a significant interaction between salinity and final body size on aggression ($F_{1,100} = 62.8$, $p < 0.001$) that explained 6.1% of the variation, with aggression increasing with body size under low salinity but not under high salinity (Fig 2). Group size and final body size were also significant predictors of aggression (group size: $F_{2,100} = 8.9$, $p < 0.001$; final body size: $F_{1,100} = 39.5$, $p < 0.001$), explaining 5.6% and 8.2% of the variation respectively, with aggression increasing with group size and final body size.

Average rates of growth differed between the four treatments (Table 1). Temperature was a significant predictor of % growth rates (GLMM: $F_{1,100} = 36.6$, $p < 0.001$), with elevated temperature resulting in lower growth rates (Fig 3) and explaining 17.1% of the variation in growth. In addition, there was a significant interaction between temperature and initial body size ($F_{1,100} = 27.2$, $p < 0.001$) that explained 12.9% of the variation, with growth rates of small fish being higher at low temperatures than at high temperatures, and growth rates of

larger fish being similar under low and high temperatures (Fig 3). Growth rates also showed a significant decline with increasing initial body size ($F_{1,100} = 64.5$, $p < 0.001$) and group size ($F_{2,100} = 7.9$, $p = 0.001$), these factors explaining 35.8% and 6.9% of the variation respectively. Salinity did not significantly predict growth rates, whether as a main effect or an interaction with temperature or initial body size (Salinity: $F_{1,100} = 1.85$, $p = 0.18$; Salinity*Temperature: $F_{1,100} = 0.2$, $p = 0.65$; Salinity*Initial body size = $F_{1,100} = 2.1$, $p = 0.15$).

Although there was a trend towards a significant effect of salinity on body condition (GLMM: $F_{1,104} = 2.9$, $p = 0.09$), no factor was a significant predictor of body condition, either as main or interactive effects (temperature: $F_{1,90} = 0.39$, $p = 0.84$; group size: $F_{2,93} = 0.25$, $p = 0.78$; tank ID: $F_{7,95} = 1.1$, $p = 0.37$; final body size: $F_{1,102} = 1.3$, $p = 0.26$; salinity: $F_{1,104} = 3.0$, $p = 0.09$). Finally, there were a total of 22 deaths during the experiment ($n = 5$ in treatment 1; $n = 5$ in treatment 2; $n = 7$ in treatment 3; $n = 5$ in treatment 4), however there was no significant difference in the frequency of deaths between the four treatments (Chi-squared test: $\chi^2 = 0.15$, $p = 0.7$).

DISCUSSION

Anthropogenic climate change is expected to result in dramatic alterations to the estuarine environment, including an elevation of temperature and salinity levels. To our knowledge, we provide the first experimental assessment of the interplay between multiple abiotic factors and body size on intraspecific aggression and growth rates of an Australian native estuarine fish, the Australian bass. We found that intraspecific aggression within groups was size-related, with larger bass being more aggressive than smaller bass, and that bass tended to be more aggressive to those similar in size to themselves, supporting the occurrence of size-based dominance relationships within groups. Interestingly, this size-related variation in aggression disappeared under high salinity levels, and salinity had no impact on growth rates. High temperatures did not influence levels of aggression, but did affect growth rates - at high temperatures, bass grew slower than at low temperatures, and elevated temperatures had a greater negative impact on the growth rate of smaller fish than on larger fish. These results point to complex and variable interactions between salinity, temperature and body size on the behaviour and life history of bass, emphasising the importance of considering individual body size in the evaluation of climate change impacts on estuarine fishes.

Intraspecific competition is dependent on abiotic (e.g. temperature, water level, pollutants etc) as well as biotic factors (e.g. individual body size or environmental resource availability) (Dunson and Travis 1991; Taniguchi and Nakano 2000; Thomas and Holway 2005; Scott & Sloman 2004). Here we provide further support for the role of abiotic and biotic factors in influencing competition and aggression, since salinity mediated by body size influenced aggression and competition in bass. So far, there is mixed evidence, with competition becoming either less or more intensified under stressful abiotic conditions (Lortie and Callaway 2006; Maestre et al. 2006; Alcaraz et al. 2008). For the endemic Australian bass,

we found that salinity but not temperature influenced levels of aggression. In other words, larger fish, which are typically more aggressive than smaller fish, became less aggressive under salinity conditions resembling those expected under future climate change. The consequences of such alterations are unclear, but one possibility could be that larger fish would become less capable of maintaining their dominance over smaller fish given they exhibit less aggression under higher salinities. Further experimental work is required to address this interesting possibility.

In contrast to aggression, salinity had no effect on the growth rates of juvenile bass. This is a surprising result, given that salinity is considered an important determinant of performance in aquatic organisms (Boeuf and Payan 2001; Chen et al. 1996; Tsuzuki et al. 2003; Varsamos et al. 2005; Bachman and Rand 2008; Nordlie 2006). Salinity is expected to affect estuarine fish via an increased energy expenditure required for osmoregulation under hypo- and hyper-osmotic conditions (Swanson 1998; Bachman and Rand 2008), in turn affecting higher level activities such as growth and activity (Boeuf and Payan 2001). For bass, juveniles remain in estuaries where costs of osmoregulation can be minimised, hence fluctuations in salinity, for example due to increases in tidal influx from sea level changes and storm surges, are expected to negatively impact fitness of non-resident estuarine fishes by elevating salinity levels in estuaries to that of sea water (Burke 1992). While support for the energetic burden of high salinity comes from the fact that larger fish were unable to maintain high levels of aggression under high salinity in the current study (i.e. they showed a reduced activity rate in the form of aggression), the lack of an effect on growth rate appears contradictory. However, it is possible that juvenile bass are more tolerant of an increase (compared to a decrease) in salinity levels, given that hatching and larval survival rates of bass increase with incubation salinities of up to 35 ppt (Van der Wal 1985). Therefore, increasing salinities may exert an impact on behavioural rather than growth rate changes in bass, although further work

investigating the influence of developmental stage of exposure (Bachman et al. 2008) and rate of salinity increases (Nordlie 2006) on growth rates would be important to confirm this suggestion.

In contrast, elevated temperature resulted in a substantial reduction in the growth rates of bass although the effect was dependent on initial body size. The overall negative relationship however was expected given that high temperatures result in an elevation in resting metabolic rate (Munday et al. 2008; Pörtner and Knust 2007) and food availability was held constant so bass could not sustain the increased metabolic demands (Jobling 1997). Interestingly, body size mediated the effect of elevated temperatures on growth rates, with increasing temperatures having a greater negative effect on the growth rates of smaller compared to larger fish. This suggests that increased temperatures expected under climate change may differentially affect smaller and larger juveniles, with smaller individuals losing their growth rate advantage under high temperatures. This in turn could lead to greater size heterogeneity amongst juvenile and adult cohorts, in other words, a greater variation in body size between individuals from the same cohort, which in turn may result in differential adult growth rates, survival and reproductive output in response to climate change.

Temperature did not have any impact on levels of aggression. This was contrary to our prediction of reduced aggression under high temperatures, which was expected given the temperature increase was to an extreme level expected under a future climate change scenario. The fact that this elevated temperature did not reduce aggression therefore suggests that individual were able to maintain original levels of aggression despite the energetic demands of an increased resting metabolism. It is possible that aggressive interactions are not as costly as was initially expected, or because other behaviours that were not quantified, such as overall swimming speed or distance were reduced to compensate for maintaining

aggression. Our finding also contrasts with that of other studies reporting increased aggression with temperature in fishes (Ratnasabapathi et al 1992; Sakakura and Tsukamoto 1997; Biro et al. 2010). Under high temperatures, the acceleration of metabolism can only be translated into an acceleration in activity (including aggressive activity) if there is sufficient food to support this increased activity (Jobling 1997). Given that growth rates in the current study declined under high temperature, it is likely that food was limiting hence not surprising that aggression did not increase in response to elevated temperature. In support of this, the bass in our study finished the food provided to them within 1 minute, suggesting that they were not fully satiated. Further, Grigaltchik et al. (2012) reported that bass made fewer attacks on mosquitofish (*Gambusia holbrooki*) at temperatures of 30°C and without any increase in food availability, demonstrating that aggression (in the context of predation) did not increase towards heterospecifics at high temperatures.

In conclusion, temperature and salinity are known to influence behaviour and life history of fishes as well as having complex interactions between each other. For example, the effect of salinity is often dependent on temperature (Boeuf and Payan 2001). Therefore, it is important to clearly separate out the effects of salinity and temperature when considering the impacts of climate change on aquatic organisms. Here we showed that although salinity and temperature did not interact to influence behaviour and growth of bass, their effects were distinctly and independently mediated by a third key factor, body size. Therefore, our study highlights the importance of considering not only the potential interactions between multiple abiotic factors but also between those and properties of the individuals themselves, such as their body size. Doing so will enable us to provide a more detailed picture of the likely impacts of climate change on estuarine fishes. Future work would also benefit from examining the prolonged consequences of environmental stressors on behavioural and growth rate differences, for example, whether the conditions experienced during the juvenile phase remain throughout

adulthood and even exerting an effect across generations (reviewed by Burton and Metcalfe, 2014).

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Table 1: Mean \pm S.E. of aggression rate (number of acts per 10 minutes), growth rate (% growth rate), initial body size (mm SL) and final body size (mm SL), within each treatment.

Treatment	Aggression rate	Growth rate	Initial body size	Final body size
Baseline temperature Baseline salinity	7.93 \pm 2.5	18.82 \pm 1.61	23.2 \pm 0.3	27.5 \pm 0.31
Elevated temperature Baseline salinity	9.96 \pm 2.19	6.48 \pm 0.72	24.83 \pm 0.44	26.38 \pm 0.39
Baseline temperature Elevated salinity	5.32 \pm 1.63	17.16 \pm 1.0	24.37 \pm 0.29	28.5 \pm 0.24
Elevated temperature Elevated salinity	7.33 \pm 2.49	7.37 \pm 0.8	26.0 \pm 0.57	27.8 \pm 0.53

FIGURES

Fig. 1 a

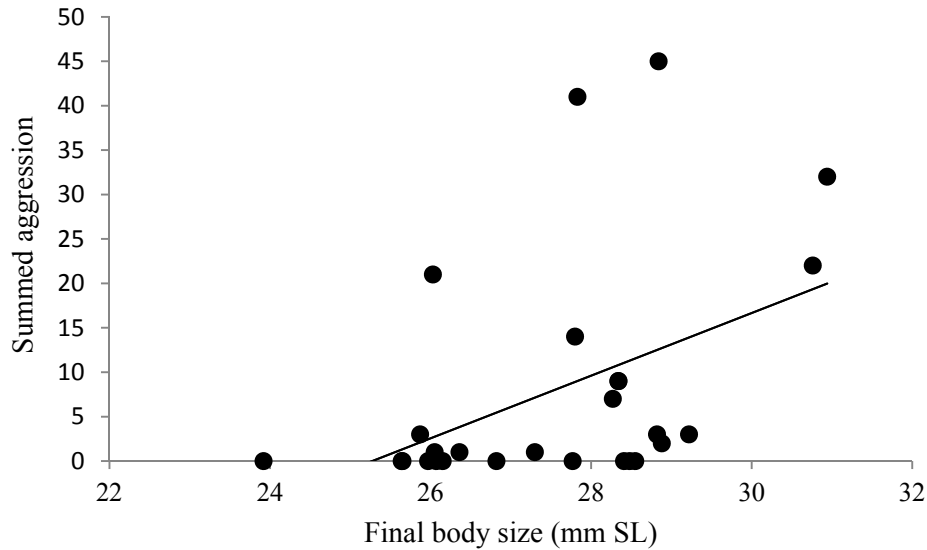


Fig. 1 b

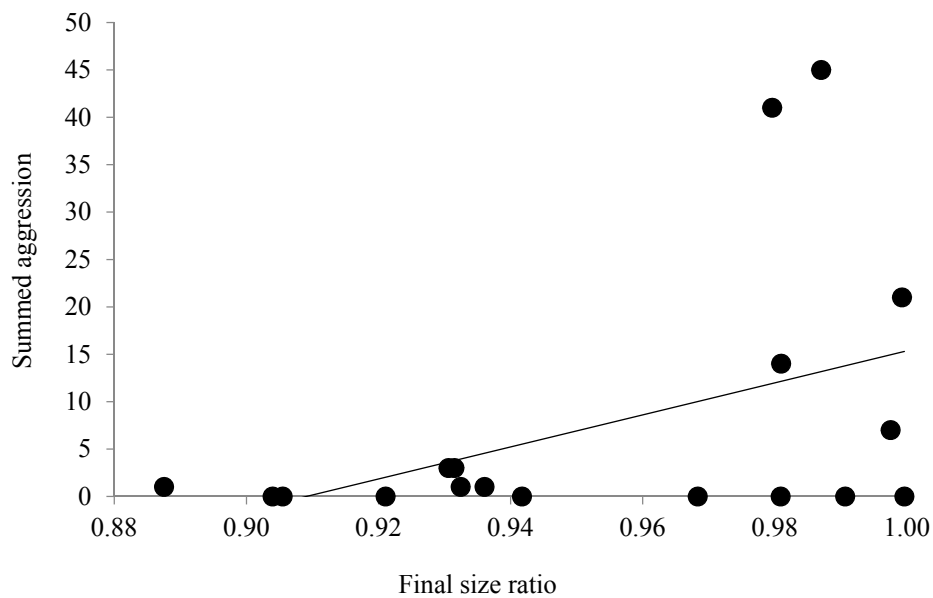


Fig 1 a) Relationship between final body size (mm SL) and summed aggression ($y = 3.53x - 89.11$), expressed as total number of acts during 10-minute observation period; and **b)** relationship between final body size ratio (SL subordinate / SL immediate dominant) and summed aggression ($y = 168.99x - 153.62$).

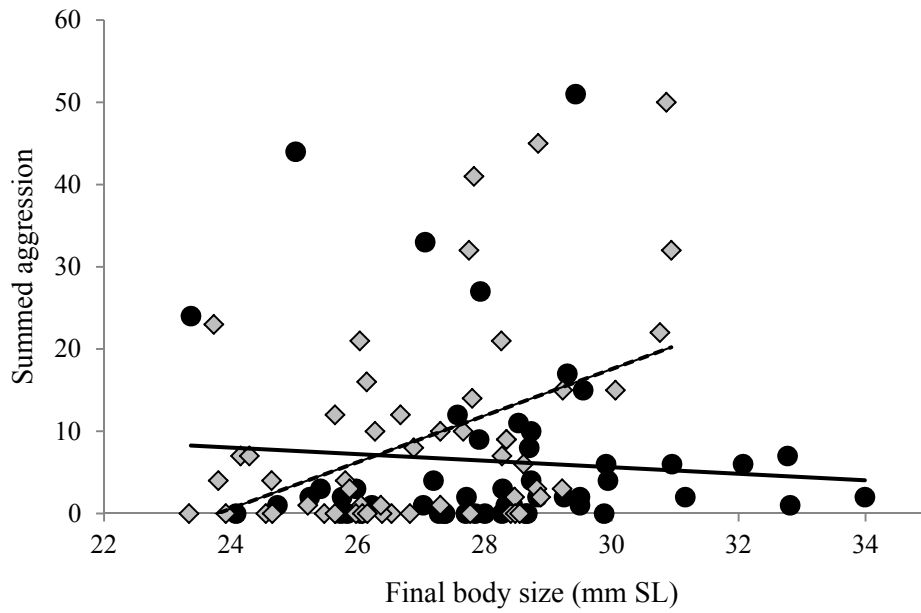


Fig 2 Relationship between final body size (mm SL) and summed aggression, expressed as total number of acts during a 10-minute observation period, under conditions of high salinity (black circles) ($y = -0.40x + 17.56$) and low salinity (grey triangles) ($y = 2.83x - 67.25$).

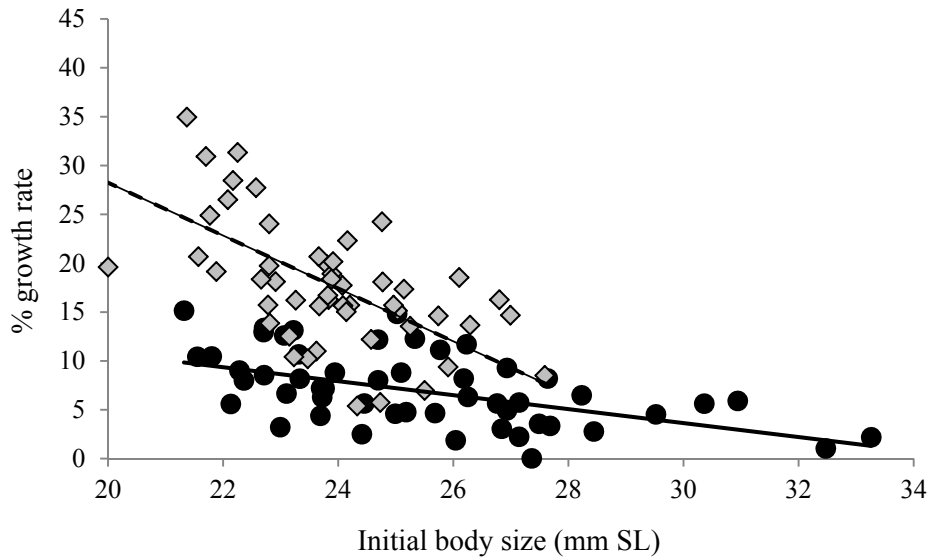


Fig 3 Relationship between initial body size (mm SL) and % growth rate (expressed as % increase relative to initial body size), under conditions of high temperature (black circles) ($y = -0.71x + 25.07$) and low temperature (grey triangles) ($y = -2.71x + 82.37$).