

Response of estuarine fishes to elevated temperatures within temperate Australia: Implications of climate change on fish growth and foraging performance

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ABSTRACT

Range shifts of marine fishes are well documented to respond to climate change, however the physiological mechanisms linked to these shifts are poorly understood. Responses of estuarine fishes, which have limited scope to shift, are particularly lacking. We tested the influence of present (18 °C, 22 °C) and predicted near-future (26 °C) water temperature on the growth and foraging performance of five common co-occurring fish: eastern trumpeter *Pelates sexlineatus* (Quoy & Gaimard 1824), eastern forscue *Centropogon australis* (White 1790), yellowfin bream *Acanthopagrus australis* (Owen, 1853), fan-belly leatherjacket *Monacanthus chinensis* (Isbeck 1765), bridled leatherjacket *Acanthaluteres spilomelanurus* (Quoy & Gaimard 1824), from an urbanised, temperate estuary near Sydney. Growth performance was quantified as instantaneous growth rate over a two-week period, whilst foraging performance was assessed on bite rate, time to feeding, boldness and also escape response. Growth patterns were significantly species-specific, and all species except for *M. chinensis* (high within-treatment variance) exhibited significant growth differences among the temperature treatments. The growth of *P. sexlineatus* and *A. australis* increased with temperature, *A. spilomelanurus* lost weight with temperature and *C. australis* exhibited a hump-shaped performance curve with the highest growth occurring at 22 °C. Bite rate, boldness, and escape response increased, and time to feeding decreased with higher water temperature in *P. sexlineatus*, *A. australis* and *M. chinensis*. Surprisingly, there was no significant association between these foraging characteristics and growth rate of individuals within each temperature treatment. This study validates the hypothesis that species within temperate estuaries will be significantly, and differently, affected by the isolated impact of water temperature rise, culminating in changes in local fish assemblages. These changes may include shifts in species dominance, trophic interactions, and migration, as well as changes to the productivity of fisheries that rely on these populations.

1. Introduction

As poikilotherms, the physiology and behaviour of teleost fish are impacted by external thermal fluctuations, making them especially susceptible to climate change (Angilletta Jr et al., 2002; Boltaña et al., 2017; Cheung et al., 2013). Fishes generally have a specific thermal range in which they express their maximum aerobic scope and performance, with decreasing performance as temperature approaches the upper and lower thermal limits (Angilletta Jr et al., 2002; Diamond et al., 2017). If species do not have the correct genes or morphological adaptations to appropriately thermoregulate outside this range, they may attempt to migrate to remain in preferred ambient temperatures

(Booth et al., 2014). In a number of scenarios however, migration is impossible due to physical constraints such as geographical barriers, or the risks associated with migration (e.g. predation) (IPCC, 2019).

Given that estuaries are typically isolated by coastal seas, estuarine fishes may have reduced ability to migrate large-distances latitudinally to seek thermal refuge, meaning in-situ strategies may be needed to maintain fitness if climate change affects the environmental characteristics of these systems (McMahon et al., 2020; Rodríguez-Domínguez et al., 2019). Estuarine fish within south-eastern (SE) Australia reside in a biogeographical region that is experiencing rates of oceanic warming that is among the highest in the world (Booth et al., 2014; Djurichkovic et al., 2019). Indeed, the waters within SE Australia have increased

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0.023 °C per year over the past decade (Booth et al., 2014). Despite the fact that these predicted changes in water temperature appear to be small in magnitude, the impacts are severe, especially when compounded by additional anthropogenic stressors such as urbanisation (Lough and Hobday, 2011; Scanes et al., 2020). This is because the metabolic compromise that occurs when fish are forced to exist outside their thermal optimum may result in reduced aerobic capacity, energy production or circulation efficiency, all culminating in a loss of physiological function (Booth et al., 2014; Cheung et al., 2013; Donelson et al., 2010; Laubenstein et al., 2018).

An example of this loss in physiological function under increased ambient temperatures include changes to the growth potential of fishes (Booth et al., 2014; Cheung et al., 2013). Current predictive models suggest that the isolated impact of climate change-induced warming will reduce the growth rates and carrying capacities of fish assemblages in the near future (excluding aquaculture populations where food is unlimited) (Cheung et al., 2013; Feary et al., 2010). Because most food webs can be summarised by the notion that larger organisms eat smaller organisms, changes in growth rates will therefore not only have implications for the fitness of individuals but will also re-shape the ecological processes that underpin system health (Cheung et al., 2016; Roy et al., 2001). For example, individuals with their growth rates reduced will spend greater time at a smaller size class, thereby being more prone to predation-related mortality (Djurichkovic et al., 2019; Feyrer et al., 2015). Temperature rise can also affect both physical (e.g., aerobic, and anaerobic capacity and muscle development) and behavioural (e.g., boldness and responsiveness) characteristics that will influence foraging success and subsequently long-term survival (Donelson et al., 2010; Nowicki et al., 2012; Pimentel et al., 2016). Knowledge of the impact rising temperatures will have on the growth and foraging performance of fish species will therefore be invaluable in predicting the ecological changes aquatic systems may undergo in the future (Booth et al., 2014; Lefevre, 2016; Rodriguez-Dominguez et al., 2019; Westhoff and Paukert, 2014).

Understanding these relationships within Australian estuarine fish assemblages is important as a third of the \$390 million value of the country's aquaculture stocks is derived from estuaries (Booth et al., 2014; Cottingham et al., 2018; Scanes et al., 2020; Sheaves et al., 2015). Estuaries house complex organisations of seagrass, sand banks and mangroves that provide juveniles of a number of commercially valuable or keystone species with an abundance of food and shelter that is unavailable offshore (Gillanders et al., 2011; Scanes et al., 2020). As such, estuarine fish communities include both permanent residents and marine species that will migrate into the ocean after maturing, meaning shifts in population dynamics among these assemblages may have socioeconomic implications on both estuarine and oceanic aquaculture stocks (Lough and Hobday, 2011). Estuaries within SE Australia also contain species of different biogeographical affinities and origins (Gillanders et al., 2011; Scanes et al., 2020). Since the biogeographical ranges and thermal tolerance of species are interrelated (e.g., low-latitude species will generally have narrower thermal performance curves compared to mid-latitude species), we might expect that elevated temperature will affect species differently and accordingly disrupt local food webs both within and well beyond the estuaries themselves (Boltaña et al., 2017; Neubauer and Andersen, 2019). This is all combined with the notion that the rise of water temperatures in eastern Australian estuaries is double that of Australia's oceans and atmosphere. The average water temperature of eastern Australian estuaries have increased by 2.16 °C over the last 12 years (0.2 °C per year), meaning the thermal resilience of fish species occupying these ecosystems is essential to their future fitness (Scanes et al., 2020).

Despite the well-established environmental and socio-economic importance of estuaries, empirical data into thermoregulatory performance is not available for the majority of residing species (Booth et al., 2014; Scanes et al., 2020). The ability to track the acclimation of these populations in response to climate change is accordingly limited (Booth

et al., 2014). The current prediction by scientists is that by residing in a thermally dynamic environment, estuarine fishes will exhibit greater resilience to thermal fluctuations compared to other marine species (Booth et al., 2014; Cheung et al., 2013; Lefevre, 2016). Indeed, when comparing studies, we see that that estuarine species will typically exhibit greater thermo-regulatory performance compared to fishes from more stable environments (e.g., tropical reefs) (Audzijonyte et al., 2020; Booth et al., 2014; Coleman et al., 2019; Figueira et al., 2019; Rodriguez-Dominguez et al., 2019; Shultz et al., 2016). Recent studies however have proposed instead that organisms residing in fluctuating environments such as estuaries may actually be closer to their upper thermal limits than organisms from stable environments (Gunderson and Stillman, 2015; Shultz et al., 2016). This research therefore investigated the potential role of elevated ambient temperatures on the growth and foraging performance of the following common estuarine species; eastern trumpeter *Pelates sexlineatus*, eastern forscue *C. australis*, yellowfin bream *A. australis*, fan-belly leatherjacket *M. chinensis*, bridled leatherjacket *A. spilomelanurus* to elevated water temperatures. The abundance of these species within local estuaries means that they are key elements in these systems, as well as the socioeconomic relationship these systems have with local human populations (Sheaves et al., 2015). The response of these fishes to ambient water temperature is therefore an appropriate model for understanding climate change impacts on estuaries (Coleman et al., 2019). This study was divided into three sub-aims: (1) to compare growth rates of these species across a thermal gradient reflective of current and predicted future water temperatures, (2) to quantify different characteristics of foraging performance across this same thermal gradient and (3) to assess the association between foraging performance and growth rate over current and predicted water temperatures. Three predictions were made. Firstly, trends in the growth response across temperature treatments will differ between species and will be reflective of these species' respective latitudinal ranges. Second, due to increased metabolic demands caused by elevated temperatures, individuals will engage in compensatory behaviour that will result in reduced time to feeding and increased bite rate, boldness, and escape response in the highest temperature treatment. And lastly, those individuals that demonstrate either greater bite rates, boldness, escape response, or reduce time to feeding will also have greater growth rates, over and above temperature effects.

2. Methods

2.1. Fish capture

Fish were collected three times on the 1st of March, 30th of March, and 4th of May 2020 at Careel Bay (33° 37' 02.80 S; 151° 18' 25.24 E). 40 km north of Sydney, along the eastern shoreline of Pittwater, Careel Bay is around 2.5 km in length and covers an area of 1.5 km². It supports a number of wetland vegetative communities, as well as sandy habitats such as beaches and mudflats, and is subject to high recreational fishing pressure (Hutchings and Rainer, 1979). Fish were collected using a 10 m long seine net (mesh size 16 mm) that was drawn for short (< 20 m) deployments through sand and seagrass (*Posidonia australis* and *Zostera* species) banks in shallow water (water depth < 2 m). Any required species were collected into a holding bucket whilst other fish were immediately released, in accordance with NSW DPI permit and University of Technology (UTS) Animal Ethics requirements. Once adequate sample sizes were reached, these collected species were immediately transported live to the UTS aquarium facilities. In total, 125 individuals across five species were captured and used for this study. Based on size, all captured individuals were deemed to be juveniles. Since one of the main functions of estuaries is as a nursery, performance assessments of juveniles are important to predicting the health of these ecosystems under climate change. The five species sampled were *P. sexlineatus* (*n* = 46), *C. australis* (*n* = 27), *A. australis* (*n* = 24), *A. spilomelanurus* (*n* = 12) and *M. chinensis* (*n* = 15). *P. sexlineatus*, *C. australis*, *A. australis* have a

range extending from far north Queensland (sub-tropical) to southern Victoria (temperate). *A. spilomelanurus* is distributed further south, exhibiting its greatest abundance around southern-Victoria and Tasmania, with Sydney serving as the northern-boundary of its range. *M. chinensis* has a similar range to *P. sexlineatus*, and *C. australis*, *A. australis*, but can also be found along the northern coastline of Australia (Booth et al., 2014; Curley et al., 2013). Approximate latitudinal ranges and other characteristics of test species are provided in Table 1.

2.2. Aquarium experimental setup

All captured individuals were first housed in groups ($n = 10\text{--}20$ fish per group) in 40 L tanks at ambient Sydney estuary temperatures (22°C). In these tanks, each group was then acclimatized over a 7-day period to one of the three treatment temperatures (18°C , 22°C , 26°C) by daily 0.5°C changes in tank temperature, except the group that remained at 22°C . 18°C and 22°C are reflective of the average sea surface temperatures (SST) in winter (May–June) and summer (December – February) in SE Australia, respectively (Booth et al., 2014; Djurichkovic et al., 2019). 26°C represents predicted summer SST by 2100 in the same region (Booth et al., 2014). For further reference, estuaries within SE Australia may reach minimum and maximum temperatures of approximately 17°C and 31°C , respectively, during short-term extreme thermal events (Scanes et al., 2020).

Sea water flowed from holding tanks located in the UTS building, sourced from local estuaries, and water temperature was controlled using 300 W aquarium glass heaters. To ensure appropriate oxygen saturation, PO_2 levels were maintained through using a combination of air stones and powerhead pumps. Shelter was provided in the form of 5 cut-off sections of PVC pipes. Water temperature was measured twice daily to ensure temperature changes were occurring at a suitable rate to allow for acclimation without overly stressing the fish. Fish were fed Aqua One® tropical fish flakes twice daily to satiation. Fish flakes were chosen because they provided the correct nutrient requirements, they kept well and produce relatively little ammonia waste, assisting in tank maintenance throughout the experimental period. Any uneaten food and faeces were siphoned off on a daily basis. Water was topped up with clean water (approximately 1/3 of the tank capacity) that had been pre-heated to the temperature of the tank in which it is being placed. Water ammonia, phosphate and nitrate was measured twice during the acclimation period using water quality test strips.

After this period, fish were randomly assigned and transferred to individual 10 L tanks. Individuals were also measured to the nearest mm [total (LT) and standard (LS) lengths (mm)] and weighed to the nearest 0.0001 g (wet mass). Similar to during the acclimation period, each tank contained its own 55 W aquarium glass heater to maintain water temperature, a section of PVC pipe for shelter and an air stone for aeration. Those tanks that were kept at 18°C had their temperatures controlled by the air-conditioning system of the laboratory, but still contained non-functioning heaters to ensure secondary treatment effects were controlled. The protocol for feeding and tank maintenance was kept the

same for fish during the experimental period as it was during the acclimation period. The observation period from this point was 14 days for each experimental block. The sides and back of each tank throughout both the acclimation and experimental period were covered with black paper to reduce the risk of external disturbance.

2.3. Experimental protocols

Growth was measured across the 14-day experimental period. The growth response of species is an effective ecological metric when assessing physiological performance because conceptually it integrates energy uptake by an organism, and accordingly relates to its fitness (Cottingham et al., 2018). Somatic growth was estimated as the instantaneous growth rate (G_{INST}) based on the mass (wet mass) of each individual fish at the beginning (M_1) and the end (M_2) of the interval of length t ($t = 14$ days), using eq. 1 (Booth et al., 2014):

$$G_{\text{INST}} = [\ln (M_2 M_1^{-1})] \Delta t^{-1}$$

Foraging performance experiments were recorded over the last two days of the two-week period (20–21 days after capture), so as to ensure that individuals were exposed to the different temperature treatments for as long as possible (within the timeframe fish were ethically permitted to be held for) before behavioural assessments were conducted. Feeding activity was tested on day one of the foraging experiments (20 days after capture), and boldness and escape response were tested on the second day (21 days after capture), and these were separated by two hours. This spreading of experiments was to minimize any disturbance effects from the previous test.

Feeding activity and boldness experiments occurred at approximately 1 pm both days, and escape response experiments at 3 pm, 3 and 5 h after feeding, respectively. The same order of tanks was followed for each repeat to minimize any possible effects of the time of day on experiments (this order was non-randomised). Experiments were filmed using a GoPro® 4 that was positioned outside the front of each tank at the same height of the base of the tank. Observation period was three minutes, and this was preceded by an acclimation period of three minutes where the camera was positioned in front of the tank. This acclimation period was done to minimize any disturbance effects of the presence or placing of the camera (Djurichkovic et al., 2019).

Foraging performance was tested for 3 species (*P. sexlineatus*, *A. australis* and *M. chinensis*). *C. australis*, and *A. spilomelanurus* did not feed during the viewing period nor did they react to the introduction of the Lego® structure or sinker. For these two species, it should be noted that food was not present when tank checks were made the following morning, indicating these species fed overnight. To assess the influence of water temperature on the foraging activity of the remaining species, approximately 1 g of fish flakes was introduced to each tank through the use of a siphon, 3 h after last feeding. Over the observation period, bite rate (total number of feeding strikes) and time to feeding (time taken from food introduction to first feeding strike (sec)) were recorded. A feeding strike was defined as a clear action by the individual fish to

Table 1
Latitudinal range, maximum size, diet, habitat, and commercial value of test species.

Species	Latitudinal range	Maximum size	Diet	Habitat	Commercial value
<i>P. sexlineatus</i>	27° 14'S - 35° 03'S	15 cm	Carnivore	Bays, estuaries, and coastal waters, often over seagrass beds near estuary mouths.	No commercial value; only caught as bycatch
<i>C. australis</i>	25° 13'S - 38° 34'S	14 cm	Demersal carnivore	Estuary and Bays up to a depth of 30 m	No commercial value; only caught as bycatch
<i>A. australis</i>	19° 15'S - 38° 00'S	56 cm	Omnivore	Estuaries, coastal rivers, creeks, lakes, and bays.	High commercial and recreational value
<i>A. spilomelanurus</i>	28° 38' S - 42° 52'S	14 cm	Omnivore	Estuarine and inshore waters in seagrass beds	No commercial Value
<i>M. chinensis</i>	10° 40' S - 34° 24' S	40 cm	Omnivore	Coastal and offshore reefs, estuaries, typically over seagrass beds.	Little recreational value

lunge towards the delivered food. Any fish that did not feed during this observation period had bite rate and time to feeding recorded as 0 and 180 (sec), respectively.

Because successful foraging is a compromise between the time spent foraging and predator avoidance/vigilance, measures of feeding activity alone are not an adequate measure of foraging performance in a real-world scenario (Pistevos et al., 2015). Fish that feed at greater rates will not necessarily experience greater survival and reproductive fitness, particularly in habitats with high predator density (White et al., 2013). For this reason, boldness (i.e. propensity of an individual to take risks (White et al., 2013)) and escape response (i.e. movements performed by an animal in response to possible predation (Domenici and Hale, 2019)) were also measured. To test the boldness of the test animals, each tank was provided with a miniature structure of red and yellow Lego® blocks (2 cm × 2 cm × 3 cm size) to represent a novel structure. These were placed at the centre of each tank with as minimal disturbance as possible. Lego® blocks have previously been used by White et al. (2013) to test the boldness of the lemon damselfish *Pomacentrus moluccensis* within the Great Barrier Reef because they do not imitate any natural structure that these fish may have experienced in the wild, so are truly novel and appear un-threatening. A reaction score that summarised boldness was recorded on an 0–3 ordinal scale with 1 scale increments, where 0 - Hiding in refuge or fleeing away from structure, 1- Not responding to structure in any manner, 2- No investigation of structure until >30s into the viewing period, 3- Immediate or almost immediate investigation of structure that includes physical contact with structure (e.g., bumping or feeding strikes).

To measure the escape response of individuals, a sudden disturbance was added to each tank to simulate predator appearance (e.g., Figueira et al. 2009). Given the nature of the tanks and test species, this was achieved through dropping a lead sinker within two body lengths of the fish to elicit a burst swim response similar to fleeing a predator (Djurichkovic et al., 2019). The simplicity of such a method means that assessments can be completed on the test species without the added complexity, variability and ethical issues in the use of a live predator to elicit this response (Domenici and Hale, 2019; Figueira et al., 2019). Like boldness, a reaction score that summarised overall escape response behaviour was recorded on an ordinal 1–3 scale with 1 scale increments, where 1- No visible response to disturbance, 2- Initial escape response that consists of increase in swimming acceleration and shift in swimming angle is followed by an immediate return to normal behaviour and 3- Large increase in swimming acceleration and erratic shift in swimming angle that continues for at least 20 s after initial disturbance and may be followed by freezing behaviour.

2.4. Data analysis

Statistical analyses were performed using R-studio®. Prior to analysis, all data was pooled across each species and temperature treatment and tested for normality and homogeneity of variance using a Shapiro-Wilks test and a Levene's test, respectively, and transformed appropriately. $P < 0.05$ was the defined level of significance for all analyses.

A two-factor analysis of variance (ANOVA) was first used to determine whether initial body sizes (wet mass(g)) were significantly different between temperatures and species. Because of unequal sample sizes between species, this and future two-factor ANOVA's were conducted using the *car* package in R studio, using a Type-III sums of squares (Fox and Weisberg, 2018). One factor ANOVA's were also used on each species separately to determine if initial body sizes were different between treatments. This found that there were no significant differences in the initial sizes of individuals between temperature treatments and species ($P > 0.05$; Appendix B). A separate linear regression across each species and temperature treatment was used to determine the association between bite rate and time to feeding with G_{INST} . Because boldness and escape response were quantified on a ranked ordinal scale, a separate ordinal regression across each species

and temperature treatment was done to test the association between boldness and escape response with G_{INST} . This found that in all temperature treatments for all test species, there was no significant association of bite rate, time to feeding, boldness or escape response with G_{INST} (Linear Regression: $P > 0.05$ and Ordinal Regression: $P > 0.05$; Appendix C-E).

Consequently, a two-factor ANOVA was used to determine the effect of temperature (fixed factor) and species (fixed factor) on G_{INST} , and a one-factor ANOVA was completed on each species separately to compare the effect of temperature on G_{INST} . The interaction between temperature and species on G_{INST} was also tested. A one-factor ANOVA was conducted on *P. sexlineatus*, *A. australis* and *M. chinensis* separately to compare the effect of temperature on bite rate and time to feeding. Where results indicated significant differences, Tukey's *post-hoc* tests were used to compare difference in significance between temperature treatments within each species. The effect of temperature on boldness and escape response on *P. sexlineatus*, *A. australis* and *M. chinensis* was tested using a Kruskal Wallis test on each species separately, with Pairwise Wallis *post-hoc* tests used to compare significance between temperature treatments within each species.

3. Results

3.1. Effect of water temperature on growth rate

A. australis juveniles were the largest at collection ($3.45 \text{ g} \pm 1.1$), followed by *A. spilomelanurus* ($2.368 \text{ g} \pm 0.6$), *M. chinensis* ($1.52 \text{ g} \pm 0.8$), *C. australis* ($1.22 \text{ g} \pm 0.6$) and *P. sexlineatus* ($1.05 \text{ g} \pm 0.43$) (Table 2 and Appendix A). Instantaneous growth rate (G_{INST}), based on the change in individual mass over the 14-day period differed significantly

Table 2

Mean (\pm SE) total length (mm) and wet mass (g) of *P. sexlineatus* (n: 18 °C = 15, 22 °C = 15, 26 °C = 16), *C. australis* (n: 18 °C, 22 °C, 26 °C = 9), *A. australis* (n: 18 °C, 22 °C, 26 °C = 8), *A. spilomelanurus* (n: 18 °C, 22 °C, 26 °C = 4), *M. chinensis*, (n: 18 °C, 22 °C, 26 °C = 5) at initial capture across the temperature treatments. Also provided are sample sizes of each treatment (n) and the life stage of each test species.

Species	Temperature treatment	n	Life stage	Wet mass (g)	Length (mm)
<i>P. sexlineatus</i>	18	15	Juvenile	1.00 \pm 0.2	40.2 \pm 3.8
	22	15	Juvenile	0.99 \pm 0.6	43.3 \pm 3.0
	26	16	Juvenile	1.10 \pm 0.5	44.7 \pm 3.6
<i>C. australis</i>	18	9	Juvenile	1.31 \pm 0.5	45.2 \pm 6.9
	22	9	Juvenile	1.20 \pm 0.3	44.6 \pm 3.5
	26	9	Juvenile	1.17 \pm 0.3	46 \pm 4.8
<i>A. australis</i>	18	8	Juvenile	2.89 \pm 0.3	72.6 \pm 5.7
	22	8	Juvenile	2.64 \pm 0.4	73.5 \pm 6.1
	26	8	Juvenile	2.64 \pm 0.4	72.4 \pm 6.0
<i>A. spilomelanurus</i>	18	4	Juvenile	1.86 \pm 0.2	54.9 \pm 1.2
	22	4	Juvenile	1.96 \pm 0.6	58.3 \pm 5.9
	26	4	Juvenile	1.89 \pm 0.7	58 \pm 7.3
<i>M. chinensis</i>	18	5	Juvenile	1.66 \pm 0.6	41 \pm 4.0
	22	5	Juvenile	1.36 \pm 0.7	44.6 \pm 3.7
	26	5	Juvenile	1.40 \pm 0.8	47 \pm 2.1

among temperature treatments (ANOVA: $P = 0.01$) and species (ANOVA: $P < 0.0001$; Table 3). There was also a significant interaction between species and temperature on G_{INST} ($P < 0.0001$) indicating the presence of species-specific growth responses across the thermal gradient used in this study (18 °C - 26 °C).

G_{INST} of all species except for *M. chinensis* differed significantly among temperature treatments (*A. australis*: $P < 0.001$, *C. australis*: $P < 0.001$, *P. sexlineatus*: $P = 0.001$, *A. spilomelanurus*: $P = 0.01$ and *M. chinensis*: $P > 0.05$). Based on Tukey's HSD tests, G_{INST} was greatest at 26 °C and lowest at 18 °C for *P. sexlineatus* (Fig. 1A) and *A. australis* (Fig. 1C) and vice-versa for *A. spilomelanurus* (Fig. 1D). *C. australis* exhibited its highest G_{INST} at 22 °C and lowest at 26 °C (Fig. 1B). The G_{INST} of *P. sexlineatus* and *A. australis* juveniles was 0.002 g and 0.003 g higher at 26 °C compared to 18 °C whilst the G_{INST} of *C. australis* and *A. spilomelanurus* juveniles at 18 °C was 0.003 g and 0.007 g higher than individuals at 26 °C.

3.2. Effect of water temperature on foraging activity

There was a significant difference in bite rate among temperature treatments in *P. sexlineatus* and *A. australis* (ANOVA: $F = 6.920$, $P < 0.005$ and $F = 7.958$, $P < 0.005$, respectively), but not *M. chinensis* ($P > 0.05$) (Fig. 2). Bite rates of juvenile *P. sexlineatus* and *A. australis* increased with water temperature (the same trend was observed to occur with *M. chinensis*, though it was not significant). More specifically, bite rates of *P. sexlineatus* and *A. australis* were approximately 72% and 92% higher at 26 °C compared to 18 °C, respectively. The only significant change in the bite rate of *P. sexlineatus* between temperature treatments was between 18 °C and 26 °C (Tukey's HSD; 18–26 °C, $P < 0.05$). The bite rate of *A. australis* in the 18 °C treatment was significantly lower than both the 22 °C and 26 °C treatment (Tukey's HSD; 18–22 °C, $P < 0.05$; 18–26 °C, $P < 0.01$).

There was a significant difference in time to feeding among temperature treatments in *P. sexlineatus*, *A. australis* and *M. chinensis* (ANOVA: $F = 6.417$, $P < 0.01$; $F = 4.937$, $P = 0.01$ and $F = 4.685$, $P < 0.05$, respectively). Time to feeding of all species decreased with water temperature (Fig. 3). More specifically, time to feeding of *P. sexlineatus*, *A. australis* and *M. chinensis* were approximately 127%, 99% and 70% lower at 26 °C compared to 18 °C, respectively. There was a significant change in the time to feeding of *P. sexlineatus* between 18 °C to 22 °C (Tukey's HSD; 18–22 °C, $P < 0.01$) and between 18 °C and 26 °C (Tukey's HSD; 18–26 °C $P < 0.05$) for *A. australis* and *M. chinensis*.

3.3. Effect of water temperature on foraging behaviour

There was a significant difference in the boldness of *M. chinensis* among temperatures treatments (Kruskal-Wallis: $\chi^2 = 7.191$, $P < 0.05$) (Fig. 4). There was no significant difference in the boldness of *P. sexlineatus* and *A. australis* among temperature treatments (Kruskal-Wallis: $P > 0.05$). The boldness of juvenile *M. chinensis* was approximately 46% and 89% greater at 22 °C and 26 °C compared to 18 °C (boldness of *P. sexlineatus* and *A. australis* were also observed to increase

with temperature). The only significant difference between temperature treatments was between 18 °C and 26 °C (Pairwise Wallis; 18–26 °C, $P < 0.01$).

There was a significant difference in the escape response among temperature treatments of *P. sexlineatus*, *A. australis* and *M. chinensis*, (Kruskal-Wallis: $\chi^2 = 9.579$, $P < 0.01$; $\chi^2 = 8.741$, $P = 0.01$, and $\chi^2 = 8.68$, $P = 0.01$, respectively) (Fig. 5). The escape response of *P. sexlineatus*, *A. australis* and *M. chinensis* was greatest at higher water temperatures. The escape response of *P. sexlineatus*, *A. australis* and *M. chinensis* was approximately 34%, 53% and 74% greater in the 26 °C temperature treatment compared to the 18 °C temperature treatment. There was a significant difference in the escape response of *A. australis* and *M. chinensis* between 22 °C and 26 °C (Pairwise Wallis; 22–26 °C, $P < 0.01$; 22–26 °C, $P < 0.05$) and between 18 °C and 26 °C for *P. sexlineatus* (Pairwise Wallis; 18–26 °C, $P < 0.01$).

4. Discussion

This study shows that elevated water temperatures may alter estuarine fish growth and foraging performance, and thus affect population and community dynamics within estuaries. Herein we have observed that increased water temperatures reflective of future climate change had a negative influence on the growth performance of *A. spilomelanurus*, a positive influence on *P. sexlineatus* and *A. australis*, and a mixed effect on *C. australis*, which demonstrated the greatest growth in the 22 °C treatment. Whilst the observed growth response, based on instantaneous growth rate, was significantly species-specific, there was little difference between the foraging performance of the three species over the thermal gradient. Higher temperatures promoted individuals of *P. sexlineatus*, *A. australis* and *M. chinensis* to feed at a greater rate, have higher observed boldness and a more severe escape response. Over the 8 °C temperature range, bite rate, boldness and escape response increased by 116.1% and time to feeding decreased by 68.6% in all species. Surprisingly, these behavioural indicators were observed to be unrelated to individual growth rate. This research therefore extends our knowledge of the thermal response of temperature estuarine fish, demonstrating that temperature rise may impact individual physiological and behavioural performance.

As expected, trends in growth were associated with the biogeographic range of the species. Given *A. spilomelanurus* primarily resides in cooler temperate regions where the average SST in summer ranges between approximately 20 °C to 22 °C, and was captured at the northern limit of its latitudinal range, it is unsurprising that its growth was significantly reduced at the higher temperature treatments (Booth et al., 2014; Shultz et al., 2016). The increased growth of *P. sexlineatus* and *A. australis* under elevated temperatures was also expected because these species have ranges that extend into sub-tropical regions where water temperatures exceed 26 °C for a large part of the year and typically experience greater growth within these sub-tropical regions and during summer (Coleman et al., 2019). By not being at their thermal threshold, these species would have experienced greater metabolism at higher temperatures without any physiological constraints (Coleman et al., 2019; Diamond et al., 2017; Pörtner and Knust, 2007). It is possible therefore that warming associated with climate change will improve the growth performance of these and other similar species within a temperate region. The hump-shaped performance of *C. australis* was surprising given these species have a latitudinal range similar to *P. sexlineatus* and *A. australis*, however the findings of this study align almost identically with those of Booth et al. (2014).

Because trophic interactions are mediated by the body size of both predators and prey, even small differences in the growth response of species to ambient temperatures may shift the organization of marine systems as water temperatures rise (Audzijonyte et al., 2020; Booth et al., 2014). If species across trophic levels grow at different rates, then changes may occur to the energetic demands, preferred prey and top-down control of apex or meso-predators, as well as the susceptibility

Table 3

Analysis of Variance (ANOVA) for the effect of temperature and species on instantaneous growth rate (G_{INST}). G_{INST} is defined as the change in individual mass over the 14-day experimental period, based on eq. 1.

Source	SS	MS	F	d.f.	P
Temperature	2.6×10^{-5}	1.4×10^{-5}	2.99	2	< 0.05
Species	1.4×10^{-5}	6.9×10^{-5}	8.66	4	< 0.01
Temperature: Species	7.2×10^{-5}	1.8×10^{-5}	9.36	8	< 0.0001
<i>P. sexlineatus</i>	3.01×10^{-5}	1.5×10^{-5}	7.18	2	0.001
<i>C. australis</i>	2.6×10^{-4}	1.3×10^{-4}	19.64	2	< 0.001
<i>A. australis</i>	3.6×10^{-5}	1.8×10^{-5}	23.6	2	< 0.001
<i>A. spilomelanurus</i>	1.1×10^{-4}	5.6×10^{-5}	6.984	2	0.01
<i>M. chinensis</i>	3.2×10^{-5}	1.6×10^{-5}	0.869	2	0.444

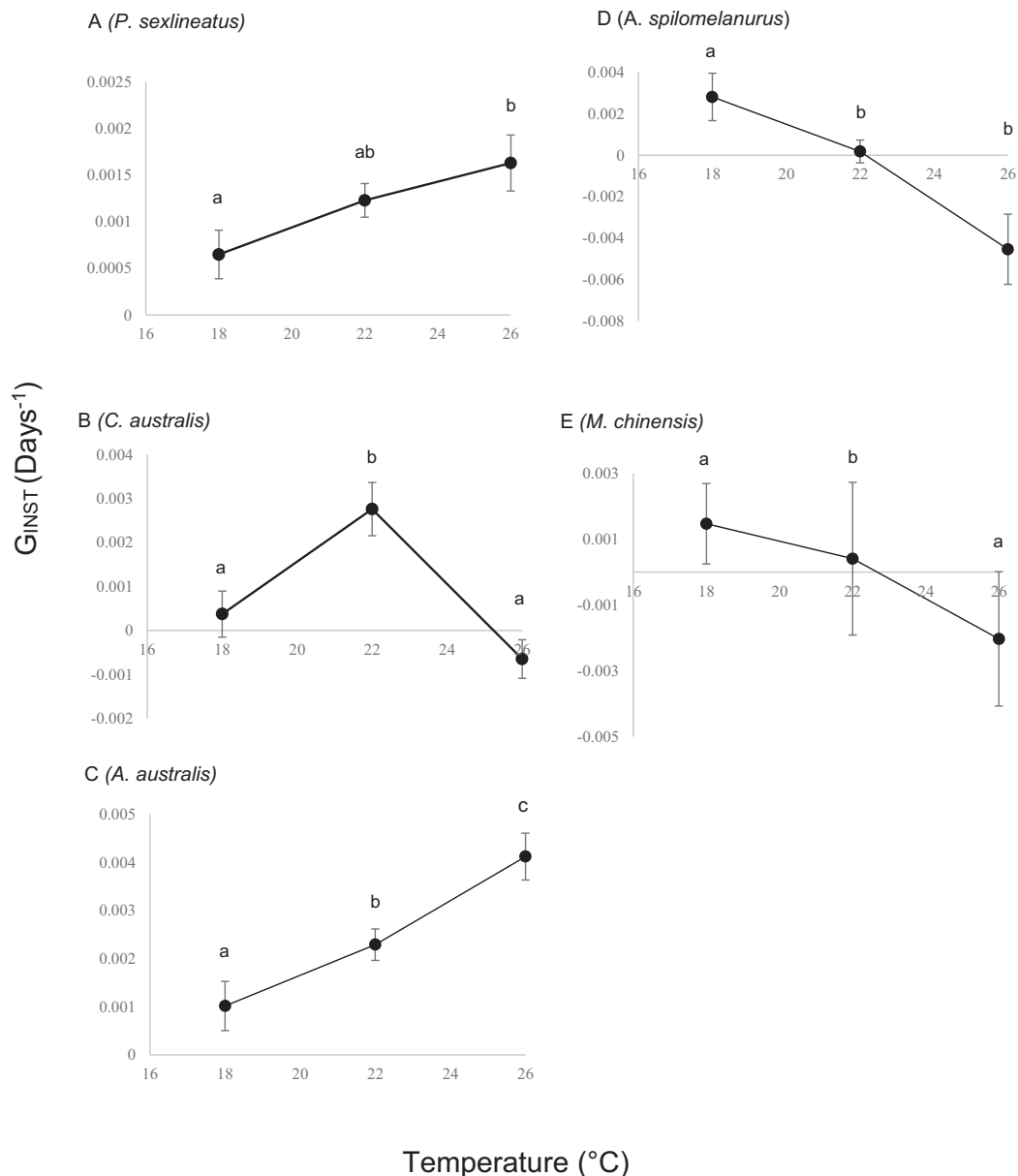


Fig. 1. Mean (\pm SE) instantaneous growth rate (G_{INST}) across temperature treatments (18 $^{\circ}\text{C}$, 22 $^{\circ}\text{C}$, 26 $^{\circ}\text{C}$) for (a) *P. sexlineatus* (n: 18 $^{\circ}\text{C}$ = 15, 22 $^{\circ}\text{C}$ = 15, 26 $^{\circ}\text{C}$ = 16), (b) *C. australis* (n: 18 $^{\circ}\text{C}$, 22 $^{\circ}\text{C}$, 26 $^{\circ}\text{C}$ = 9), (c) *A. australis* (n: 18 $^{\circ}\text{C}$, 22 $^{\circ}\text{C}$, 26 $^{\circ}\text{C}$ = 8), (d) *A. spilomelanurus* (n: 18 $^{\circ}\text{C}$, 22 $^{\circ}\text{C}$, 26 $^{\circ}\text{C}$ = 4), (e) *M. chinensis*, (n: 18 $^{\circ}\text{C}$, 22 $^{\circ}\text{C}$, 26 $^{\circ}\text{C}$ = 5). Different letters indicate significant difference between temperature treatments (Tukey's HSD: $P < 0.05$). Data for *P. sexlineatus* and *C. australis* are $\log(x + 1)$ transformed. G_{INST} is defined as the change in individual mass over the 14-day experimental period, based on eq. 1.

of species to predation leading to a cascading of effects throughout an ecosystem (Pistevos et al., 2015).

Shifts in organization may be further exacerbated if the foraging performance of fish species also changes with temperature, since even slight differences to this behaviour is an important determinant of overall survival. It has been well established that fish raised in elevated temperatures will exhibit greater aggression, feeding rates, foraging excursions, and escape responses (Domenici, 2010; Domenici and Hale, 2019; Warren et al., 2017). Our results concur with these findings. This increased activity under elevated temperatures is likely linked to increasing metabolic activity, muscle development and contraction speed caused by temperature rise (Basford et al., 2016; Bignami et al., 2017; Grigaltchik et al., 2012; Heuer and Grosell, 2014; Rodriguez-Dominguez et al., 2019; Warren et al., 2017). Neural conduction speed of fishes has also been found to increase with temperatures, which may explain shorter feeding and escape latencies (Domenici et al., 2019). In a

real-life scenario, our findings may translate to foraging strategies that accommodate greater energetic demands, such as larger prey selection and more aggressive strategies (e.g., daytime and/or open water feeding) that in turn may alter individual survival. Biro et al (2007) for example showed that increased boldness of whole-lake populations of rainbow trout *Oncorhynchus mykiss* at higher temperatures led to these populations being more susceptible to predator-related mortality compared to their counterparts at a lower temperature. To improve the applicability of our findings, other components of foraging performance require attention (e.g., feeding and escape directionality, shoal foraging performance, prey selection etc).

We found no significant association between foraging and growth, an unexpected finding since individuals that exhibit greater feeding rates and aggression are usually also those that grow quicker and larger, due to a reduced perceived risk of predation, increased metabolic demands, and increased competitive ability and processing capacities (Grigaltchik

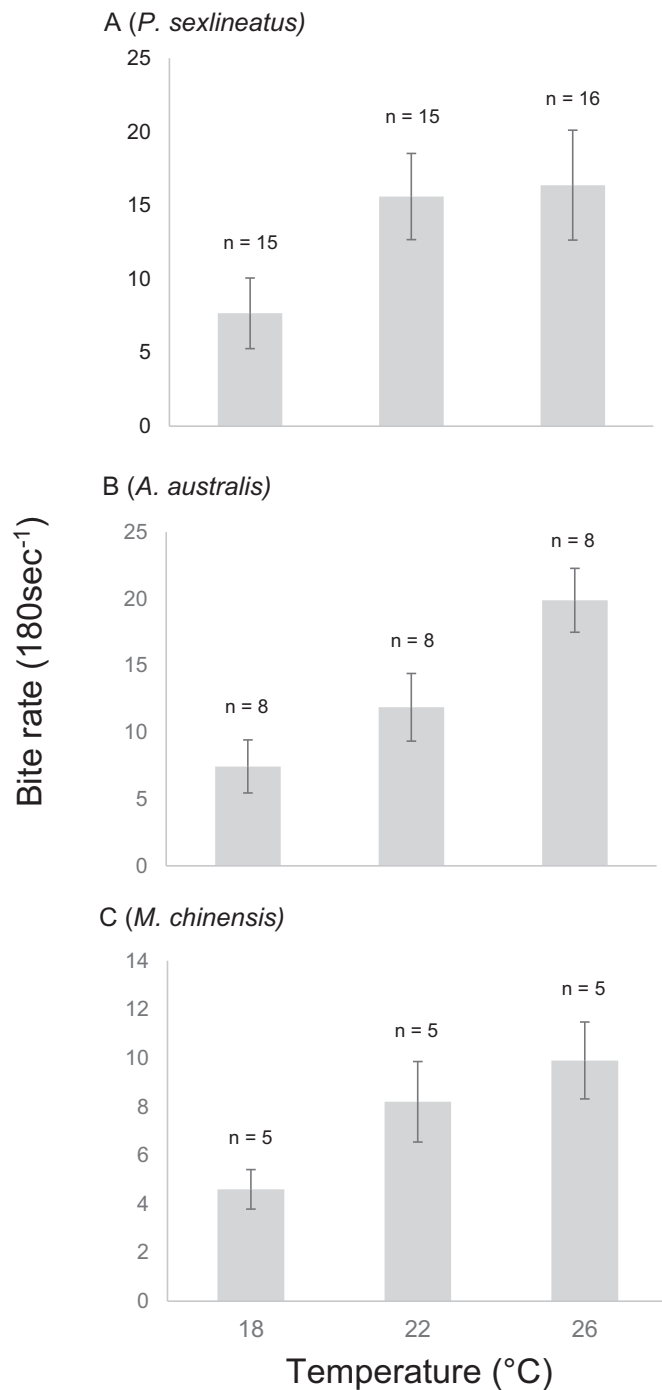


Fig. 2. Mean (\pm SE) bite rate of (a) *P. sexlineatus* (n: 18 °C = 15, 22 °C = 15, 26 °C = 16), (b) *A. australis* (n: 18 °C, 22 °C, 26 °C = 8) and (c) *M. chinensis* (n: 18 °C, 22 °C, 26 °C = 5) over 18 °C, 22 °C and 26 °C. Bite rate is defined by the number of feeding strikes recorded during a 180 s time period.

et al., 2012; O'Mara and Wong, 2016; Rodriguez-Dominguez et al., 2019). A lack of relationship may have been because of inter-individual behavioural variation, relatively low sample numbers or because of laboratory conditions, most likely the high food availability (Killen et al., 2011; Liu and Fu, 2017). Killen et al. (2011) only found an association between metabolism and boldness in European seabass *D. labrax* when fish were food deprived, and Liu and Fu (2017) found no relationship between growth and behaviour in grass carp *C. idella*, reasoning that high food availability removed the typical metabolic compromise between growth and behaviour. In the context of climate

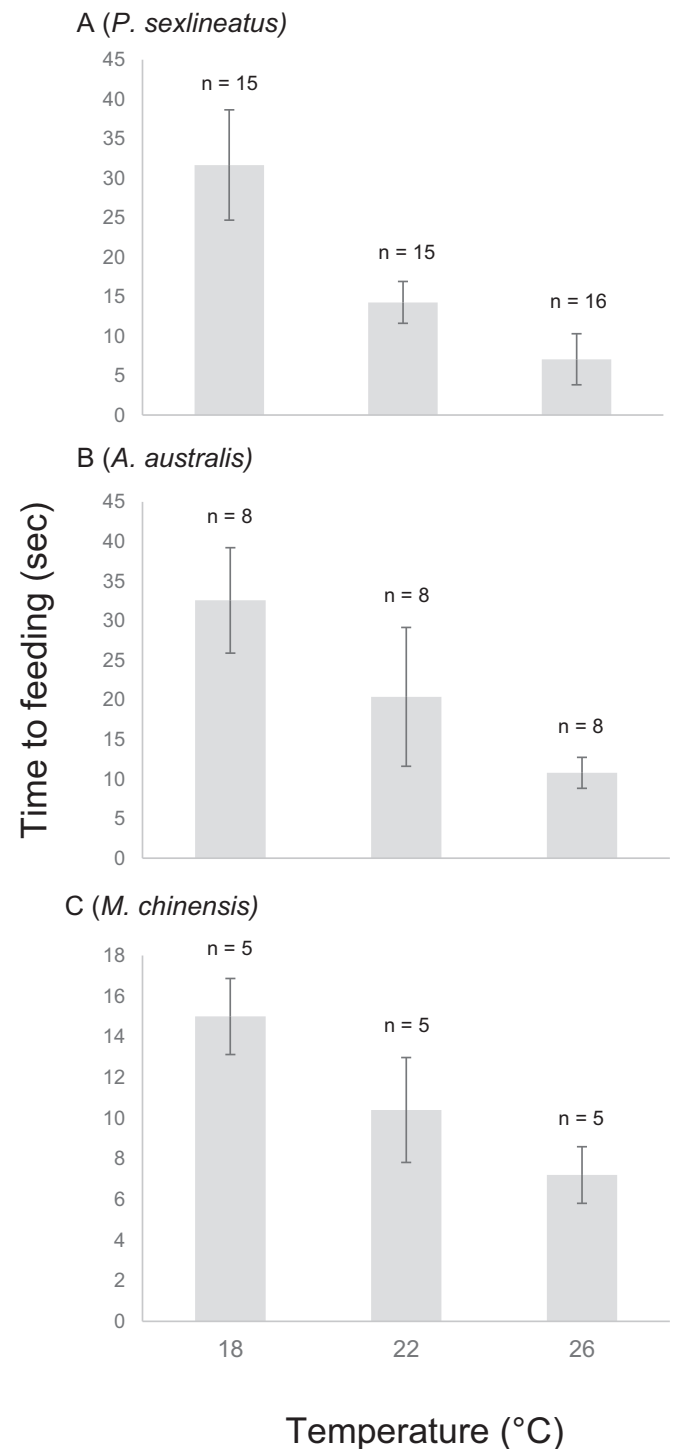


Fig. 3. Mean (\pm SE) time to feeding of (a) *P. sexlineatus* (n: 18 °C = 15, 22 °C = 15, 26 °C = 16), (b) *A. australis* (n: 18 °C, 22 °C, 26 °C = 8) and (c) *M. chinensis* (n: 18 °C, 22 °C, 26 °C = 5) over 18 °C, 22 °C and 26 °C. Time to feeding is determined by time taken from the introduction of food to the first feeding strike (sec).

change, that may also indicate that rising temperatures will have a similar effect on foraging activity and behaviour across fishes, albeit with different magnitudes of response, irrespective of individual body-size.

This study reinforces that the complexity of the relationship between environmental variation and the physiology of fish species must be considered to predict future response to climate-change (Feary et al.,

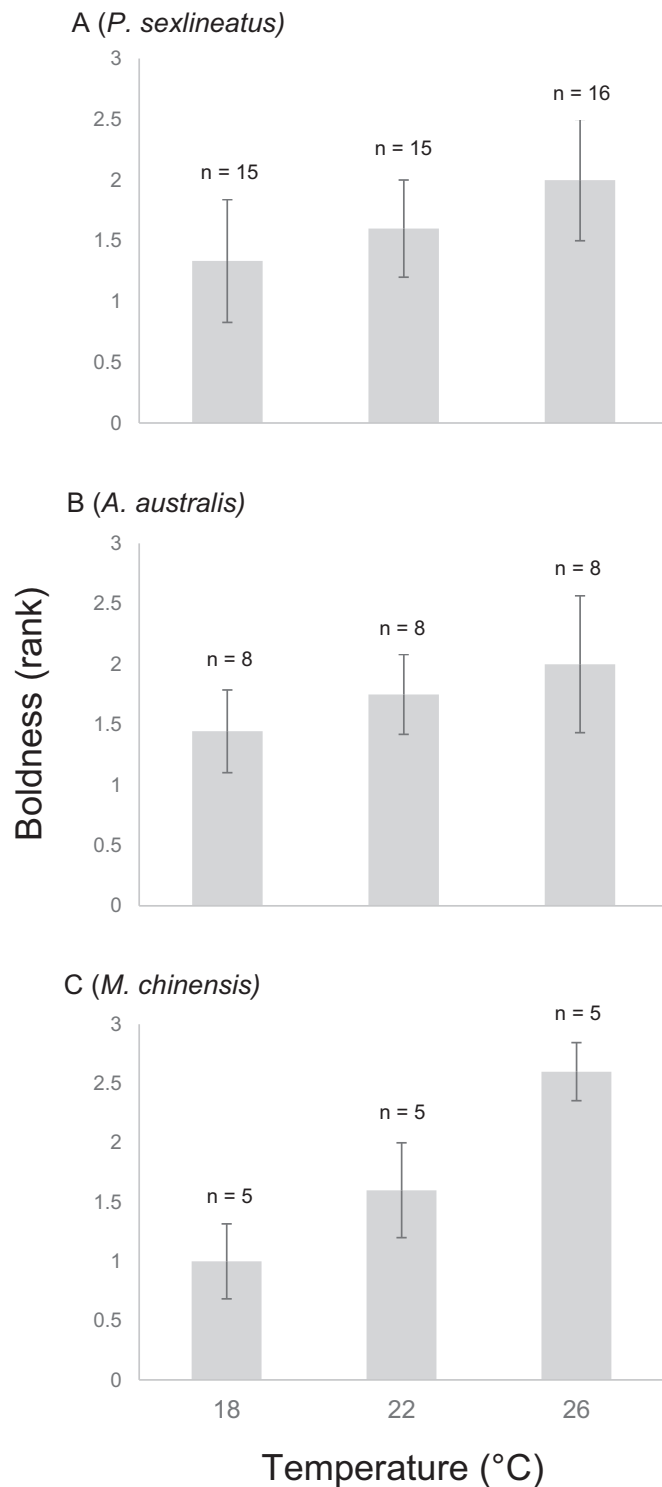


Fig. 4. Mean (\pm SE) boldness (rank) of (a) *P. sexlineatus* (n: 18 °C = 15, 22 °C = 15, 26 °C = 16), (b) *A. australis* (n: 18 °C, 22 °C, 26 °C = 8) and (c) *M. chinensis* (n: 18 °C, 22 °C, 26 °C = 5) over 18 °C, 22 °C and 26 °C. Boldness is defined on an ordinal scale from 0 to 3 with increasing value corresponding to increased boldness.

2010; Sheaves et al., 2015). Experimentation in the field, or greater replication with longer experiment periods and integrated complexity in laboratory experiments would further indicate whether species possess the physiological capacity to maintain the demands of this increased body size over a lifetime, the possibility of developmental or trans-generational acclimation, and how other climate change related threats

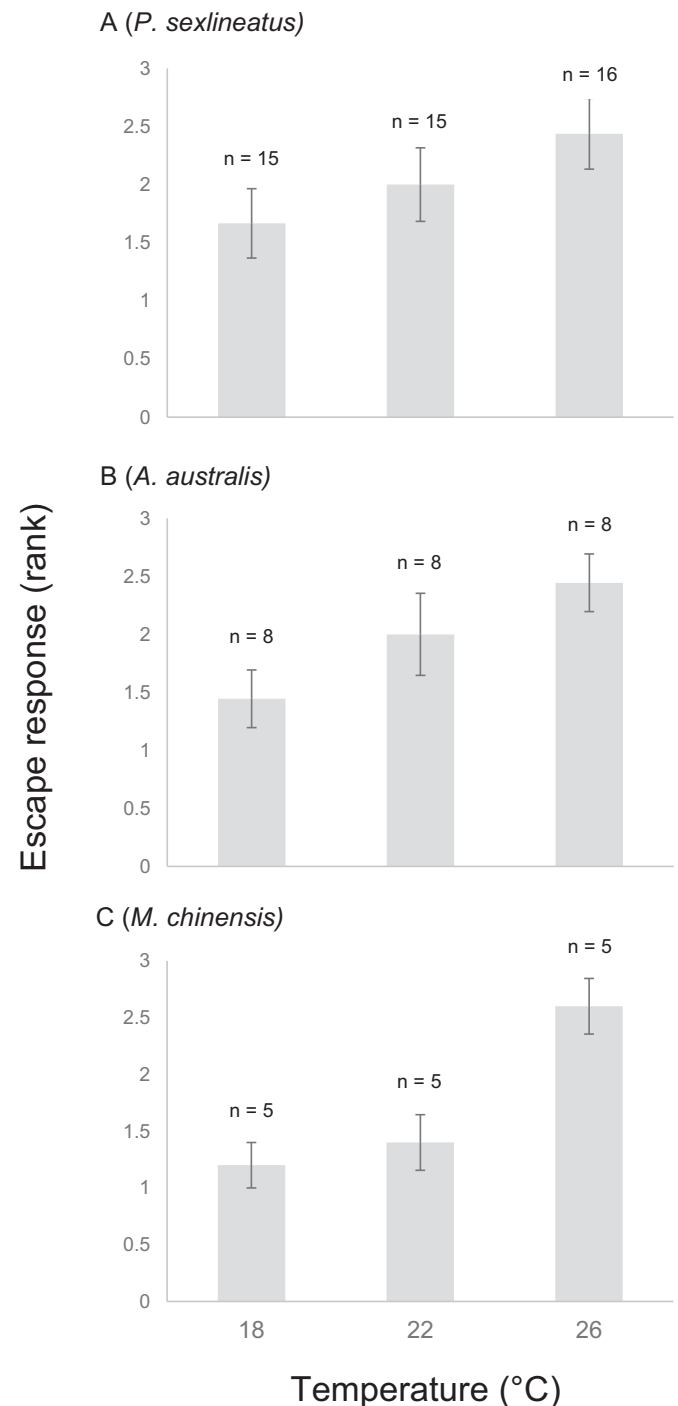


Fig. 5. Mean (\pm SE) escape response (rank) of (a) *P. sexlineatus* (n: 18 °C = 15, 22 °C = 15, 26 °C = 16), (b) *A. australis* (n: 18 °C, 22 °C, 26 °C = 8) and (c) *M. chinensis* (n: 18 °C, 22 °C, 26 °C = 5) over 18 °C, 22 °C and 26 °C. Escape response is defined on an ordinal scale from 1 to 3, with increasing value corresponding to increased escape response.

(e.g. less water discharge into estuaries, loss of habitat and greater frequency of high-magnitude climatic events) will affect fish performance response (Djurichkovic et al., 2019; Warren et al., 2017). Furthermore, to place these findings in a larger ecological context, studies are required to assess whether growth patterns measured in this study in juveniles will be continue as these individuals mature (juveniles typically exhibit greater growth rates compared to sub-adult and adults), and to include species of difference life history strategies, trophic and habitat niches (Ong et al., 2015). Importantly, results of this study may not be

applicable at different latitudes where species are adapted to different ambient temperatures (e.g., *A. australis* individuals that reside at lower latitudes may have a different thermal reaction norm compared to the individuals that we assessed) (Donelson et al., 2010).

5. Conclusion

Near-future summer water temperatures (26 °C) led to decreased growth rates of *A. spilomelanurus* and *C. australis*, and increased growth rates of *P. sexlineatus* and *A. australis* from temperate estuaries. These same temperatures led to increased observed feeding rates, boldness, and escape response (and decreased time to feeding) in *P. sexlineatus*, *A. australis* and *M. chinensis* individuals, irrespective of growth performance. Rather than a consistent response across species, our results highlight that a possible decrease in the physiological performance of some estuarine fish may parallel the thermal resilience of others with the appropriate physiological adaptations (Audzijonyte et al., 2020; Coleman et al., 2019). The broad thermo-tolerance ranges of estuarine fish (particularly those with a biogeographical range that extends into sub-tropical or tropical climates) that allow them to reside in such dynamic systems may therefore help maintain the health and productivity of estuaries under climate change, and the fisheries industries that rely on them (Booth et al., 2014).

Species resilient to elevated water temperatures will likely maintain or increase their dominance in these systems, whilst those unable to acclimate appropriately may instead experience diminished physiological capabilities, and as a result may inhabit these systems less frequently or will be absent in the future (Crozier and Hutchings, 2014; Gunderson and Stillman, 2015). Continued research into the effect of environmental variation on key ecological processes of fishes may help identify performance response trends to climate change, and therefore support a number of conservation strategies (Booth et al., 2014).

Declaration of Competing Interest

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Declaration of Competing Interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jembe.2021.151626>.

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