

DR. MELINDA A COLEMAN (Orcid ID : 0000-0003-2623-633X)

DR. BRENDAN KELAHER (Orcid ID : 0000-0002-7505-4412)

Article type : Primary Research Articles

Climate change does not affect seafood quality of a common targeted fish

Running heading: Climate change and seafood quality

Coleman MA^{1,2}, Butcherine P³, Kelaher BP^{2,3}, Broadhurst MK¹, March DT², Provost EJ²,
David J², Benkendorff K³

¹ NSW Department of Primary Industries, National Marine Science Centre, 2 Bay Drive,
Coffs Harbour, NSW 2450, Australia

² National Marine Science Centre, Southern Cross University, 2 Bay Drive, Coffs Harbour,
NSW 2450, Australia

³ Marine Ecology Research Centre, School of Environment, Science and Engineering,
Southern Cross University, 2480 Lismore, NSW, Australia

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1111/gcb.14513](https://doi.org/10.1111/gcb.14513)

This article is protected by copyright. All rights reserved

Corresponding author: Melinda Coleman. PH: +61 266568937,
Melinda.coleman@gmail.com

Keywords: climate change, fish, nutrition, seafood, temperature, acidification, lipid, fatty acid, fishery, yellowfin bream, *Acanthopagrus australis*

Paper type: Primary research article.

Abstract

Climate change can affect marine and estuarine fish via alterations to their distributions, abundances, sizes, physiology and ecological interactions, threatening the provision of ecosystem goods and services. While we have an emerging understanding of such ecological impacts to fish, we know little about the potential influence of climate change on the provision of nutritional seafood to sustain human populations. In particular, the quantity, quality and/or taste of seafood may be altered by future environmental changes with implications for the economic viability of fisheries. In an orthogonal mesocosm experiment, we tested the influence of near-future ocean warming and acidification on the growth, health and seafood quality of a recreationally and economically important fish, yellowfin bream (*Acanthopagrus australis*). The growth of yellowfin bream significantly increased under near-future temperature conditions (but not acidification), with little change in health (blood glucose and haematocrit) or tissue biochemistry and nutritional properties (fatty acids, lipids, macro- and micronutrients, moisture, ash, and total N). Yellowfin bream appear to be highly resilient to predicted near-future ocean climate change, which might be facilitated by their broad spatio-temporal distribution across habitats and broad diet. Moreover, an increase in growth, but little change in tissue quality, suggests that near-future ocean conditions will benefit fisheries and fishers that target yellowfin bream. The data reiterate the inherent resilience of yellowfin bream as an evolutionary consequence of their euryhaline status in often environmentally challenging habitats, and imply their sustainable and viable fisheries into the future. We contend that widely-distributed species that span large geographic areas and habitats can be “climate-winners” by being resilient to negative direct impacts of near-future oceanic and estuarine climate change.

53

54 **Introduction**

55 Climate change will have various direct and indirect impacts on marine and estuarine species
 56 and ecosystems. Climate stressors, including warming and acidification, can directly impact
 57 species physiologies (Davis *et al.*, 2017, Deutsch *et al.*, 2015, Portner & Knust, 2007),
 58 phenology (Asch, 2015, Edwards & Richardson, 2004) and distributions e.g. (Cetina-Heredia
 59 *et al.*, 2015, Coleman *et al.*, 2017, Perry *et al.*, 2005, Sunday *et al.*, 2015) that can cascade
 60 through indirect effects to alter entire ecosystems (Nagelkerken & Connell, 2015, Provost *et*
 61 *al.*, 2017, Vergés *et al.*, 2016, Wernberg *et al.*, 2016, Wernberg *et al.* 2018). While we have
 62 an emerging understanding of these ecological impacts, we know less about the effects of
 63 climate change on the provision of ecosystem goods and services to human populations.

64

65 Oceans and estuaries provide many beneficial goods and services, worth trillions of dollars
 66 (Costanza *et al.*, 2014), with the production of seafood among the most important for
 67 sustaining growing human populations. Seafood production and consumption is not only
 68 socially and culturally important, but sustains the economies of many global communities
 69 and industries. With a predicted increase in the reliance of seafood as a source of protein
 70 under climate change (Delgado *et al.*, 2003, Gerland *et al.*, 2014), understanding potential
 71 climate-induced alterations to seafood quality and quantity will be vital for ensuring long-
 72 term resource viability (Cooley *et al.*, 2012, Lloret *et al.*, 2015).

73

74 There is general consensus that future ocean conditions will negatively impact fish
 75 production (quantity) via different pathways, including decreases in species body size
 76 mediated by physiological constraints (Sheridan & Bickford, 2011), ability to locate prey,
 77 and altered defence mechanisms (Cripps *et al.*, 2011, Pauly & Cheung, 2018, Pistevos *et al.*,
 78 2015). However, relatively fewer studies have examined the potential for impacts of climate
 79 change on fish tissue quality and nutritional benefits. Changes in tissue quality could manifest
 80 as altered tissue biochemistry, including the composition of fatty acids (particularly
 81 polyunsaturated fatty acids; PUFAs), micronutrients and protein. Although there are no
 82 studies on fish, near-future warming and acidification decreased the nutritional quality of
 83 marine mollusc flesh through reduced proteins and lipids (Tate *et al.*, 2017), and altered fatty-

acid profiles (Anacleto *et al.*, 2014, Valles-Regino *et al.*, 2015) and concentrations of micronutrients, including copper and arsenic (Tate *et al.*, 2017). Such changes not only affect the nutritional benefits of seafood, but could also manifest as altered palatability (i.e. taste and/or texture) or visual appeal. For example, for oysters (*Crassostrea gigas*), warming and acidification under future climate scenarios tended to increase appeal in some sensory properties (meat appearance and degustation), but failed to significantly impact palatability or appearance (Lemasson *et al.*, 2017). Any substantial change in the nutritional quality and appeal of seafood may have implications for providing health benefits and sustenance to humans into the future.

For the first time, we examine the interactive effects of near-future climate change (warming and acidification) on the growth, health and nutritional properties of a recreationally and economically important fish; yellowfin bream (*Acanthopagrus australis*). This species occurs throughout southeastern Australia (southern Queensland to southern New South Wales/Victoria; Iwatsuki 2013, Stewart *et al.* 2015) where as a panmictic stock (Roberts & Ayre, 2010) they undertake migrations from estuarine to oceanic areas for spawning (Curley *et al.*, 2013, Pollock, 1984). Such movements are facilitated by wide salinity (<10–35 PSU) and temperature tolerances (19–38°C) (Froese & Pauly, 2017, Gray, 2015, Uhlmann *et al.*, 2015). Along with numerous closely related congeners, which are distributed more broadly throughout the Indo-Pacific (Iwatsuki 2013), yellowfin bream have a relatively higher market value than many co-harvested species (Curley *et al.*, 2013, Froese & Pauly, 2017). Given their wide distribution and putative tolerance to a range of abiotic conditions, we suggest yellowfin bream and species of *Acanthopagrus* in general, may be relatively resilient to near-future warming and acidification.

MATERIALS AND METHODS

To test whether the growth, health and tissue quality of yellowfin bream may be impacted by climate change, an experiment utilising twenty independent 230-L round outdoor mesocosms (80 cm diameter × 45 cm high) was configured at the National Marine Science Centre (NMSC) aquaria, Coffs Harbour, Australia (30°16'3.70"S, 153° 8'15.31"E). The mesocosms were arranged to have an orthogonal combination of ambient ('current') and future $p\text{CO}_2$ (~430 and ~960 ppm, respectively) and temperatures (~22 and 25 °C, respectively) ($n = 5$

mesocosms per treatment; Table S1). These treatments corresponded to 2100 predictions for climate change scenario RCP 8.5, a high emissions trajectory prediction (IGBP *et al.*, 2013).

Seawater from the adjacent ocean was pumped into the NMSC flow-through aquarium system and filtered at 50 μm prior to entering each mesocosm at 2.5 L min⁻¹. Water temperatures in the mesocosms were controlled using heater-chiller units (Aquahort Ltd., Omana Beach, New Zealand). The $p\text{CO}_2$ concentrations were manipulated by bubbling CO_2 -enriched air via a gas mixer (PEGAS 4000MF) through the CO_2 -enriched header tanks, while ambient air was diffused through stones in the current treatment header tanks. Water temperature, conductivity (units) and pH were measured daily (Hach HQ40d multi probe; Table S1). Total alkalinity for each treatment was measured weekly using a potentiometric titration (888 Titrand, Metrohm, USA) of 40 μm filtered, Hg fixed water samples. These water quality measurements were then used to calculate the partial pressure of CO_2 ($p\text{CO}_2$) using the CO2SYS program (Pierrot *et al.*, 2009).

Before starting the experiment ~230 yellowfin bream (~20–26 cm total length; TL) were collected from the middle of its range in eastern Australia at Maclean, New South Wales (NSW, -29.464° E, 153.172° S) during short (~15 min) deployments of paired penaeid trawls fitted with codends made from 27 mm knotless netting (Broadhurst & Millar, 2009). Catches were emptied on to a wet sorting tray and yellowfin bream were collected, transported and placed into multiple 3000-L aerated and flow-through holding tanks at the NMSC for an acclimation period (>6 mo). During this period, fish were fed a diet of school prawns (*Metapenaeus macleayi*) and 4 mm commercial pellets at a rate ~1% biomass day⁻¹. The ambient water temperature (17.6–20.7°C; mean \pm SD of 19.1 \pm 0.9°C), salinity (33.5–37.0; 34.9 \pm 0.1 ppt) and DO (6.7–8.1; 7.5 \pm 0.4 mg L⁻¹) in the holding tanks remained within the tolerance ranges for yellowfin bream. In total, 13% of fish died and all within the first two weeks of confinement, with no subsequent mortality.

The experiment commenced on 27 September 2017, well after the known spawning period (Curley *et al.*, 2013) to avoid confounding results with reproductive factors or sexes of fish, although most were juveniles based on established size at maturity (20–24 cm fork length; FL). On the first day of the experiment, yellowfin bream in two of the 3000-L holding tanks were anaesthetized using 30 mg L⁻¹ Aqui-S in seawater. Twenty individuals were randomly selected across both holding tanks, measured to the nearest 0.1 mm for TL, FL and standard

length (SL) and weighed (nearest 0.1 g) by being secured in a foam mount on a digital benchtop scale before being transferred to the mesocosms (one fish per mesocosm). Only one fish was placed in each mesocosm to avoid competitive interactions.

Each fish was acclimatised in its new environment (i.e. a mesocosm) for one week, prior to beginning gradual commencement of the seawater manipulations to treatment levels over a two-day period. Fish were fed school prawns to satiation throughout the experiment. After 40 days, each fish was again anaesthetised with 30 mg.L⁻¹ Aqui-S solution, removed from their tanks and secured in a foam block before an ~1 ml blood sample (0.4–2.5 ml) was collected using a heparinised syringe and 23 gauge needles following Broadhurst *et al.* (2005). Immediately following blood collection, two microhematocrit tubes were filled for each individual and centrifuged for 120 seconds at 15,800 rpm/13,700 g to calculate the haematocrit (Hct) packed cell volume (PCV) and a glucometer (TruTrack, Nipro, Australia) was used to determine blood glucose levels.

After being blood sampled, fish were euthanised (150 mg L⁻¹ Aqui-S), weighed and measured for TL, FL and SL as above and dissected for tissue and organ sampling as below. Sex was noted where possible (although many fish were juveniles and could not reliably be sexed). Among those individuals that could be reliably sexed, ratios were roughly 1:1. Fish were then filleted and subsamples of the flesh were snap frozen in liquid nitrogen and transferred to –80°C prior to lipid analysis and the remaining flesh was stored at –20°C until further processing for proximate and elemental analyses.

Samples of the flesh (1 g) were weighed on an analytical balance (\pm 0.0001 g) then dried in the oven at 60°C until they obtained a stable weight, then reweighed and the difference used to calculate moisture content. The dry samples were then transferred to a muffle furnace (Bainstead thermolyne 30400 furnace) at 400°C for 4 hours to obtain the ash content. The Kjeldahl nitrogen method was used to calculate total nitrogen, according to standard protocols (AOAC, 1995), with a factor of 6.25 to convert to crude proteins.

Lipids were extracted from the flesh using 1:2 chloroform: methanol according to standard procedures (Folch *et al.*, 1957) in analytical grade solvents (Sigma-Aldrich). Separation of

the polar layer was induced using 0.9% NaCl solution in a separating funnel. The lipophilic (chloroform) layer was then dried on a Buchi rotary evaporator (470 mbar, 40°C). The extract was transferred to a pre-weighed vial in a small volume of hexane and dried under a stream of high purity N₂ gas, then re-weighed to obtain the weight of lipid extract. The total lipid concentration for each extracted sample was determined as percent lipid in the fresh weight (% g/g).

Subsamples of the total lipid extract (200 µL suspended at 25 mg/mL in isopropanol) were analysed by liquid chromatography-mass spectrometry (LC-MS) using a Phenomenex Synergi C18 (5 µm, 250 mm × 4.6 mm) LC column in an Agilent Technologies 1260 Infinity series HPLC with attached mass spectrometry unit (Agilent Technologies 6120 Quadrupole LC/MS). The mobile phase consisted of a solvent gradient of methanol and isopropanol (IPA) with 0.05% trifluoroacetic acid (TFA) added to both solvents at a flow rate of 300 µL min⁻¹. The gradient started with 10% IPA, increasing to 25% over 25 min, then up to 95% at 40 min, then held for 10 min before dropping back to 10% and held for 5 mins. UV detection was set 210, 230, 280 and 360 nm, while total ion current was set to positive ion mode in the MS. Major peaks were compared to lipid standards with characteristic fragment ions from the total ion current (TIC) used to assist identifying free fatty acids and phospholipids, whilst TIC was characteristically suppressed for di- and tri-glycerides.

A 200 µL subsample of the lipid extract was derivatised using BF₃ in methanol for fatty acid methyl esters (FAMES) analysis according to Valles-Regino *et al.* (2015). Fatty-acid composition was analysed using gas chromatography (GC) (Agilent 6890N) on a BPX 70 capillary column (70% cyanopropyl polysilphenylene-siloxane, 50 m × 0.22 mm × 0.25 µm), coupled with a flame ionization detector (FID). The GC oven temperature was programmed at 100°C, held for 5 min and then increased at 5°C min⁻¹ until the final temperature 240°C was obtained, with high-purity helium as the carrier gas at a linear flux of 1 ml min⁻¹. Identification of FAMES was based on retention time, peak and elution order compared to FAMES standard test mix (SUPELCO 37-Component FAME Mix) and marine-test mix PUFA No.1 (Marine Source, Analytical Standards, Sigma-Aldrich). To identify unmatched peaks including docosapentadecanic acid, supplementary analysis using gas chromatography mass spectrometry (GCMS) was undertaken using an Agilent 6890 GC coupled to Agilent

5973 mass spectrometer (Valles-Regino *et al.*, 2015) and matched to the NIST14 and Wiley275 mass spectral libraries.

The total elemental analysis of flesh sub-samples (1 g) was undertaken by the Environmental Analysis Laboratory (EAL), Southern Cross University (National Association of Testing Authorities, Australia (NATA); Accreditation Number 14960). Samples were digested in a mixture of HNO₃ (25%) and HCl (75%) (1:3, v/v) using a hot-block acid digestion procedure. Elemental concentrations were analysed on an inductively-coupled plasma (ICP) spectrometer (NexION 300 D series) with ESI SC-FAST Auto Sampler (Perkin Elmer, Waltham, Massachusetts, U.S.A.) and were determined on a wet-weight basis.

Statistical analyses

Multivariate and univariate analyses were done using PERMANOVA in the PRIMER 6.0 & PERMANOVA+ add-on package (Anderson *et al.*, 2008). For each individual variable, data were analysed using Euclidian distances with 9999 permutations and pairwise tests used to ascertain the nature of any significant differences. Multivariate analyses were also done for lipid and fatty acid composition (standardized) and macro- and micro-elements (normalised) using Euclidean distance. For all analyses there were two orthogonal, fixed factors; temperature (ambient 22 °C and future 25 °C) and acidification (ambient and future) with $n = 5$ replicate tanks.

RESULTS

All fish survived the duration of the experiment, ate well and were in visible good health. There were significant increases in TL, FL and SL (PERMANOVA $p \leq 0.05$) and a marginally non-significant ($p = 0.07$) but biologically large (50%) increase in weight under elevated temperature treatments (Table 1, Fig. 1). After 40 days, fish were, on average, about 10 g heavier and 4 mm longer in tanks at 25°C than those in tanks at 22°C (Fig. 1). There was no effect of acidification on changes in fish morphometrics, or an interaction with temperature (PERMANOVA, $p > 0.05$, Table 1).

There was no influence of either temperature or acidification (or their interaction) on blood haemolysis (haematocrit PCV) or glucose levels (PERMANOVA, $p > 0.05$; Table 1). The proximate composition of the flesh was also unaffected (Table 1) with an average of $75.0 \pm 1.0\%$ moisture content and $5.8 \pm 0.7\%$ ash per g wet weight (PERMANOVA, $p > 0.05$). The protein content varied from 18–22g/100g dry flesh with no significant difference under elevated temperature or $p\text{CO}_2$ conditions (PERMANOVA, $p > 0.05$, Table 1).

The total extracted lipids comprised on average $1.3 \pm 0.4\%$ per g wet weight, with no difference according to experimental conditions (PERMANOVA, $p > 0.05$, Table 1). There was a non-significant trend for a higher percentage of phospholipids and free-fatty acids relative to triglycerides in the total lipid composition under elevated temperature treatments (Figure 2). The fatty-acid profile was dominated by saturated and monounsaturated fats ($>70\%$), with a high proportion of steric and oleic acids (Table 2). The dominant PUFA was linoleic (C18:2; $\sim 10\%$), with low levels of all other omega 6 (n-6) and omega 3 (n-3) PUFAs, and an n-3:n-6 ratio < 1 (Table 2). There was no change in the proportion of SFA, MUFA and PUFAs or fatty-acid composition under elevated temperature or acidification (PERMANOVA, $p > 0.05$, Table 1 and 2).

The dominant macroelements in the flesh were potassium ($>4 \text{ mg g}^{-1}$), phosphorous, sulfur and sodium (on average $>1 \text{ mg g}^{-1}$), followed by magnesium ($>0.4 \text{ mg g}^{-1}$), calcium, silicon (on average $>0.1 \text{ mg g}^{-1}$), iron and aluminium ($0.002\text{--}0.4 \text{ mg g}^{-1}$) (Table S2). There were no significant effects of elevated temperature or acidification on the overall macroelemental composition (PERMANOVA, $p > 0.05$ for all factors; Table 1) or any individual macroelement (Table S2). All microelements were recorded at below maximum recommended limits for seafood, with the exception of vanadium (average $1.5 \pm 0.03 \text{ mg Kg}^{-1}$ vs. upper limit of $0.01 \text{ mg Kg}^{-1} \text{ day}^{-1}$ ATSDR, 2015). There was a slight tendency for temperature to change the composition of microelements overall (PERMANOVA, $p = 0.06$, Table 1) and this was likely affected by significant decreases in copper and increases in arsenic at elevated temperatures and non-significant trends for decreases in lead at elevated temperatures (Table S2). No other microelement or macroelement showed differences between treatments (PERMANOVA, $p > 0.05$, Table S2).

Discussion

Although there is a consensus that future ocean conditions will likely evoke decreases in the production and sizes of marine fish, few studies have examined the influence of predicted increases in temperature and acidification on the quality and nutritional value of tissue. The data here show that elevated temperatures and $p \text{ CO}_2$ induced acidification predicted under conditions of near-future ocean warming increased the growth of yellowfin bream, and there was little change in their health or the quality and nutritional properties of muscle tissue. These results imply that this species and the fishery it underpins, may be resilient to changes throughout oceans in the near future.

Effects of climate change on fish health and seafood quality

The finding that near-future ocean warming (an increase in 3°C from ambient as forecast for the end of this century) had little impact on the health and seafood quality of yellowfin bream is likely due to this species having a wide latitudinal range and inhabiting a variety of marine

and estuarine habitats, that naturally vary greatly in their abiotic characteristics (Curley *et al.*, 2013, Froese & Pauly, 2017, Gray, 2015). Although the increase in temperature simulated here was above that usually experienced by yellowfin bream in the open ocean in the region where the experiment was completed (and where these fish were collected), it is well within the thermal range of the species as a whole (Curley *et al.*, 2013) and within the range that can be experienced within individual estuaries. Moreover, acoustically tagged bream from nearby areas have been known to migrate up to 250 km, including between estuarine and inshore open coastal habitats (Lowry *et al.*, 2017). Thus, a 3°C temperature increase is likely well within the range yellowfin bream can tolerate more broadly, and suggests that near-future climate change may have negligible direct impacts on this widely-distributed species, except perhaps near its low latitude limit. Indeed, modelling studies have shown that ecological generalists (e.g. species that display characteristics including omnivory and/or large latitudinal range size etc.) are most likely to have already undergone climate-induced range extensions (Sunday *et al.*, 2015), suggestive that such species are tolerant to the changing abiotic conditions expected in coming decades.

In contrast to our previous studies on a harvested gastropod, which incurred large reductions in protein and lipid content relative to moisture under near-future ocean conditions (Tate *et al.*, 2017), we detected little change in the tissue chemistry of yellowfin bream. Unlike the gastropods, yellowfin bream do not need to catabolise their tissue to provide energy to cope with stress from future conditions of temperature and acidification. Nonetheless, we did find a non-significant trend for the percentage of triglycerides in yellowfin bream to be lower (relative to phospholipids and free fatty acids) under elevated temperature treatments, which is consistent with a weak stress response. Triglycerides are important energy reserves in fish (Bennett *et al.*, 2007) and are likely to be utilised by increased metabolism and higher growth rates observed at elevated temperature.

An increase in saturated relative to unsaturated fatty acids is a common consequence of organismal exposure to elevated temperatures, as a result of homeoviscous adaptation to maintain appropriate fluidity in cell membranes (Neidleman, 1987). However, unlike previous studies investigating ocean warming on molluscs (Anacleto *et al.*, 2014, Martino & Cruz, 2004, Valles-Regino *et al.*, 2015), yellowfin bream had no significant differences in

their fatty acid composition. Previous studies on fish indicate that they also adapt to lower temperatures by increasing unsaturation in tissue lipids (Patton, 1975) and desaturase activity can be inhibited at higher temperatures (De Torrenço & Brenner, 1976, Qiang *et al.*, 2017). However, the fish here had a relatively low proportion of polyunsaturated fatty acids (<30% vs >40% in molluscs), and they contained very low levels of long-chained highly saturated omega 3 or omega 6 acids such as arachidonic acid (ARA C20:4), eicosapentaenoic acid (EPA C20:5) or docosapentaenoic acid (DPA C22:5), which are most susceptible to warming (Valles-Regino *et al.*, 2015). Owing to relatively low omega 3 and 6 polyunsaturated fatty acids, and an n-3:n-6 ratio <1, yellowfin bream do not provide a premium source of fish oils that are good for human health (Simopoulos, 1991, Simopoulos, 2008, Swanson *et al.*, 2012). Nevertheless, they do provide a good source of linoleic (C18:2) and monounsaturated fatty acids, which were not impacted under near-future ocean conditions.

There was also a slight tendency for temperature to change the composition of micronutrients overall, and this was driven by significant decreases in copper and increases in arsenic at elevated temperatures. The decrease in copper was in contrast to Tate *et al.* (2017), who found that elevated temperatures significantly increased copper content in the foot meat of a harvested predatory whelk (*Dicathais orbita*). We also found increases in arsenic and non-significant trends for a decrease in lead at elevated temperatures, but levels of these elements remained within safe levels (NHMRC, 2006). Again, this is in contrast to Tate *et al.* (2017) who found decreases in lead due to acidification (but not warming). Whelks are sedentary compared to yellowfin bream, and have a narrower distributional range, which may explain why they generally responded more strongly to near-future ocean conditions. Nevertheless, these minor changes in mineral elements are unlikely to significantly impact the nutritional content of yellowfin bream tissue, but instead highlight that the influence of future oceans on seafood nutritional values will be species-specific and may be difficult to predict.

Effects of climate change on fish growth

The increase in growth of yellowfin bream under near-future ocean temperatures is in contrast to the literature that generally predicts fish production will decline due to a combination of decreases in body size (Sheridan & Bickford, 2011) associated with size-related physiological constraints, and changes in distributions and abundances (Cheung *et al.*,

2012, Pauly & Cheung, 2018, Portner & Knust, 2007), as well as survival (Rosa *et al.*, 2014). Because the yellowfin bream in our study were not near their critical upper temperature threshold in the elevated temperature treatment, it is likely that they experienced increased metabolism and certainly ate more (with fish fed to satiation) while remaining within size-related physiological constraints (Cheung *et al.*, 2012, Pauly & Cheung, 2018, Portner & Knust, 2007). Previous studies have shown that yellowfin bream grow faster during summer and at their northern range (Curley *et al.*, 2013). Moreover, our study resulted in relatively rapid increases in weight and size over a short period (40 days), which may not be sustained over longer time periods, as increasing body size and demand for oxygen goes beyond physiological limits of supply due to gill surface area (Pauly and Cheung 2018). Nonetheless, there is uncertainty in how any inherent positive temperature effects on growth might translate in terms of climate change. Specifically, increased growth may not be realised if prey respond negatively to ocean changes or if yellowfin bream foraging efficiency is compromised (Gardiner *et al.*, 2014, Munday *et al.*, 2013). However, the omnivorous diet of yellowfin bream (Froese & Pauly, 2017) may facilitate adaptability to changing ecological landscapes.

It will be important to quantify if the increased growth of yellowfin bream found here was in the form of muscle, fat or other tissue because this has important implications for seafood quality and production. Similarly, given the sustainable harvesting of yellowfin bream is based on relationships between size, age and sex, understanding how the increases in size relates to maturation rates will be key for developing robust strategies for a sustainable fishery in a future of ocean change (Stewardson *et al.*, 2016). Nevertheless, intuitively, any realised increases in growth rates are likely to be positive in terms of life history (Curley *et al.*, 2013) and may translate to greater absolute productivity in coming years.

Conclusion

Near-future changes to oceans predicted for the end of the century had few impacts on the health or nutritional quality of yellowfin bream, a recreationally and economically important fish species from eastern Australia. Indeed, contrary to theory that predicts future oceans will decrease the size, production and nutritional quality of fish lipids, elevated temperatures

increased the growth of yellowfin bream suggesting that short term exposure to predicted near-future increases in ocean temperature are well within current physiological thresholds. We contend that fish species that have broad geographic ranges and habitats may sometimes be climate winners because they have plastic responses and can tolerate a range of abiotic conditions. The maintenance of seafood nutritional properties of such species will contribute to their fisheries viability in a future of increasing ocean climate change.

Acknowledgments

We thank Ashley Dowell, Analytical Research Laboratory, SCPS for facilitating the fatty acid and lipid analyses. Sean Blake is thanked for collecting the fish. Financial support was received through a SCU MERC Grant to KB and BPK and through the Australian Research Council via DP150104263 to BPK.

REFERENCES

- Anacleto P, Maulvault AL, Bandarra NM, Repolho T, Nunes ML, Rosa R, Marques A (2014) Effect of warming on protein, glycogen and fatty acid content of native and invasive clams. *Food Research International*, **64**, 439-445.
- Anderson M, Gorley R, Clarke K (2008) PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. . In: *PRIMER-E*. pp Page, Plymouth, UK.
- Aoac (1995) *Official Methods of Analysis. (16th ed.)*, Washington, DC, Association of Official Analytical Chemists.
- Asch RG (2015) Climate change and decadal shifts in the phenology of larval fishes in the California Current ecosystem. *Proceedings of the National Academy of Sciences*, **112**, E4065-E4074.
- Bennett PM, Weber LP, Janz DM (2007) Comparison of Chloroform–Methanol-Extracted and Solvent-Free Triglyceride Determinations in Four Fish Species. *Journal of Aquatic Animal Health*, **19**, 179-185.
- Broadhurst MK, Gray CA, Reid DD, Wooden MEL, Young DJ, Haddy JA, Damiano C (2005) Mortality of key fish species released by recreational anglers in an Australian estuary. *Journal of Experimental Marine Biology and Ecology*, **321**, 171-179.
- Broadhurst MK, Millar RB (2009) Square-mesh codend circumference and selectivity. *Ices Journal of Marine Science*, **66**, 566-572.
- Cetina-Heredia P, Roughan M, Seville E, Feng M, Coleman MA (2015) Strengthened currents override the effect of warming on lobster larval dispersal and survival. *Global Change Biology*, **21**, 4377-4386.
- Cheung WWL, Sarmiento JL, Dunne J *et al.* (2012) Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. *Nature Climate Change*, **3**, 254.
- Coleman MA, Cetina-Heredia P, Roughan M, Feng M, Seville E, Kelaher BP (2017) Anticipating changes to future connectivity within a network of marine protected areas. *Global Change Biology*, **23**, 3533-3542.
- Cooley SR, Lucey N, Kite-Powell H, Doney SC (2012) Nutrition and income from molluscs today imply vulnerability to ocean acidification tomorrow. *Fish and Fisheries*, **13**, 182-215.
- Costanza R, De Groot R, Sutton P *et al.* (2014) Changes in the global value of ecosystem services. *Global Environmental Change*, **26**, 152-158.
- Cripps IL, Munday PL, McCormick MI (2011) Ocean Acidification Affects Prey Detection by a Predatory Reef Fish. *Plos One*, **6**, e22736.
- Curley BG, Jordan AR, Figueira WF, Valenzuela VC (2013) A review of the biology and ecology of key fishes targeted by coastal fisheries in south-east Australia: identifying critical knowledge

- gaps required to improve spatial management. *Reviews in Fish Biology and Fisheries*, **23**, 435-458.
- Davis KL, Coleman MA, Connell SD, Russell BD, Gillanders BM, Kelaher BP (2017) Ecological performance of construction materials subject to ocean climate change. *Marine Environmental Research*, **131**, 177-182.
- De Torrenço MP, Brenner RR (1976) Influence of environmental temperature on the fatty acid desaturation and elongation activity of fish (*Pimelodus maculatus*) liver microsomes. *Biochimica et Biophysica Acta (BBA) - Lipids and Lipid Metabolism*, **424**, 36-44.
- Delgado CL, Wada N, Rosegrant MW, Meijer S, Ahmed M (2003) Fish to 2020: supply and demand in a changing world. pp Page, Washington, DC, IFPRI.
- Deutsch C, Ferrel A, Seibel B, Pörtner H-O, Huey RB (2015) Climate change tightens a metabolic constraint on marine habitats. *Science*, **348**, 1132-1135.
- Edwards M, Richardson AJ (2004) Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature*, **430**, 881.
- Folch J, Lees M, Sloane Stanley GH (1957) A simple method for the isolation and purification of total lipides from animal tissues. *J Biol Chem*, **226**, 497-509.
- Froese R, Pauly D (2017) Fishbase. www.fishbase.org. pp Page.
- Gardiner JM, Atema J, Hueter RE, Motta PJ (2014) Multisensory Integration and Behavioral Plasticity in Sharks from Different Ecological Niches. *Plos One*, **9**, e93036.
- Gerland P, Raftery AE, Ševčíková H *et al.* (2014) World population stabilization unlikely this century. *Science*, **346**, 234-237.
- Gray CA (2015) Spatial variation in demography of an estuarine teleost: implications for population and fishery assessments. *Aquatic Biology*, **23**, 209-223.
- Igbp, loc, Scor (2013) Ocean acidification summary for policymakers - Third symposium on the ocean in a high co2 world. In: *International Geosphere-biosphere programme*. pp Page, Stockholm, Sweden.
- Lemasson AJ, Kuri V, Hall-Spencer JM, Fletcher S, Moate R, Knights AM (2017) Sensory Qualities of Oysters Unaltered by a Short Exposure to Combined Elevated pCO2 and Temperature. *Frontiers in Marine Science*, **4**.
- Lloret J, Sabatés A, Muñoz M *et al.* (2015) How a multidisciplinary approach involving ethnoecology, biology and fisheries can help explain the spatio-temporal changes in marine fish abundance resulting from climate change. *Global Ecology and Biogeography*, **24**, 448-461.

- Lowry M, Becker A, Folpp H, Mcleod J, Taylor MD (2017) Residency and movement patterns of yellowfin bream (*Acanthopagrus australis*) released at natural and artificial reef sites. Marine and Freshwater Research, **68**, 1479-1488.
- Martino RC, Cruz GMD (2004) Proximate composition and fatty acid content of the mangrove oyster *Crassostrea rhizophorae* along the year seasons. Brazilian Archives of Biology and Technology, **47**, 955-960.
- Munday PL, Pratchett MS, Dixon DL, Donelson JM, Endo GKG, Reynolds AD, Knuckey R (2013) Elevated CO₂ affects the behavior of an ecologically and economically important coral reef fish. Marine Biology, **160**, 2137-2144.
- Nagelkerken I, Connell SD (2015) Global alteration of ocean ecosystem functioning due to increasing human CO₂ emissions. Proceedings of the National Academy of Sciences, **112**, 13272-13277.
- Neidleman SL (1987) Effects of Temperature on Lipid Unsaturation. Biotechnology and Genetic Engineering Reviews, **5**, 245-268.
- Nhmrc (2006) Nutrient reference values for Australia and New Zealand: including recommended dietary intakes. pp Page, Commonwealth of Australia, Canberra, Australia), (National Health and Medical Research Council).
- Patton JS (1975) The effect of pressure and temperature on phospholipid and triglyceride fatty acids of fish white muscle: A comparison of deepwater and surface marine species. Comparative Biochemistry and Physiology Part B: Comparative Biochemistry, **52**, 105-110.
- Pauly D, Cheung WWL (2018) Sound physiological knowledge and principles in modeling shrinking of fishes under climate change. Global Change Biology, **24**, e15-e26.
- Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate Change and Distribution Shifts in Marine Fishes. Science, **308**, 1912-1915.
- Pierrot D, Neill C, Sullivan K *et al.* (2009) Recommendations for autonomous underway pCO₂ measuring systems and data-reduction routines. Deep Sea Research Part II: Topical Studies in Oceanography, **56**, 512-522.
- Pistevos JCA, Nagelkerken I, Rossi T, Olmos M, Connell SD (2015) Ocean acidification and global warming impair shark hunting behaviour and growth. Scientific Reports, **5**, 16293.
- Pollock BR (1984) Relations between migration, reproduction and nutrition in yellowfin bream (*Acanthopagrus australis*). Marine Ecology Progress Series, **19**, 17-23.
- Portner HO, Knust R (2007) Climate change affects marine fishes through the oxygen limitation of thermal tolerance. Science, **315**, 95-97.

- 497 Provost EJ, Kelaher BP, Dworjanyn SA *et al.* (2017) Climate-driven disparities among ecological
498 interactions threaten kelp forest persistence. *Global Change Biology*, **23**, 353-361.
- 499 Qiang J, Bao WJ, Tao FY, He J, Li XH, Xu P, Sun LY (2017) The expression profiles of miRNA-mRNA of
500 early response in genetically improved farmed tilapia (*Oreochromis niloticus*) liver by acute
501 heat stress. *Scientific Reports*, **7**, 8705.
- 502 Roberts DG, Ayre DJ (2010) Panmictic population structure in the migratory marine sparid
503 *Acanthopagrus australis* despite its close association with estuaries. *Marine Ecology Progress*
504 *Series*, **412**, 223-230.
- 505 Rosa R, Baptista M, Lopes VM *et al.* (2014) Early-life exposure to climate change impairs tropical
506 shark survival. *Proceedings of the Royal Society B: Biological Sciences*, **281**.
- 507 Sheridan JA, Bickford D (2011) Shrinking body size as an ecological response to climate change.
508 *Nature Climate Change*, **1**, 401.
- 509 Simopoulos AP (1991) Omega-3 fatty acids in health and disease and in growth and development.
510 *The American Journal of Clinical Nutrition*, **54**, 438-463.
- 511 Simopoulos AP (2008) The Importance of the Omega-6/Omega-3 Fatty Acid Ratio in Cardiovascular
512 Disease and Other Chronic Diseases. *Experimental Biology and Medicine*, **233**, 674-688.
- 513 Stewardson C, Andrews J, Ashby C *et al.* (2016) Status of Australian fish stocks reports. . pp Page,
514 Fisheries Research and Development Corporation, Canberra. .
- 515 Sunday JM, Pecl GT, Frusher S *et al.* (2015) Species traits and climate velocity explain geographic
516 range shifts in an ocean-warming hotspot. *Ecology Letters*, **18**, 944-953.
- 517 Swanson D, Block R, Mousa SA (2012) Omega-3 Fatty Acids EPA and DHA: Health Benefits
518 Throughout Life. *Advances in Nutrition*, **3**, 1-7.
- 519 Tate RD, Benkendorff K, Ab Lah R, Kelaher BP (2017) Ocean acidification and warming impacts the
520 nutritional properties of the predatory whelk, *Dicathais orbita*. *Journal of Experimental*
521 *Marine Biology and Ecology*, **493**, 7-13.
- 522 Uhlmann SS, Broadhurst MK, Millar RB (2015) Effects of Modified Handling on the Physiological
523 Stress of Trawled-and-Discarded Yellowfin Bream (*Acanthopagrus australis*). *Plos One*, **10**,
524 e0131109.
- 525 Valles-Regino R, Tate R, Kelaher B, Savins D, Dowell A, Benkendorff K (2015) Ocean Warming and
526 CO₂-Induced Acidification Impact the Lipid Content of a Marine Predatory Gastropod.
527 *Marine Drugs*, **13**, 6019.
- 528 Vergés A, Doropoulos C, Malcolm HA *et al.* (2016) Long-term empirical evidence of ocean warming
529 leading to tropicalization of fish communities, increased herbivory, and loss of kelp.
530 *Proceedings of the National Academy of Sciences*, **113**, 13791-13796.

531 Wernberg T, Bennett S, Babcock RC *et al.* (2016) Climate-driven regime shift of a temperate marine
532 ecosystem. *Science*, **353**, 169-172.

533 Wernberg T, Coleman, MA, Bennett S, Thomsen M, Tuya F, Kelaher BP (2018) Genetic diversity and
534 kelp forest vulnerability to climate stress. *Scientific Reports*, 8, 1851.

535

536

Author Manuscript

Table 1. PERMANOVA Pseudo-*F* and *P* values for analyses of change in morphometrics, blood parameters and biochemical flesh quality (upon conclusion of the experiment only). ^a = multivariate analysis. Significant values in bold.

	Temperature		<i>p</i> CO ₂		Temperature × <i>p</i> CO ₂	
	Pseudo F	<i>P</i>	Pseudo F	<i>P</i> value	Pseudo F	<i>P</i> value
Morphometrics						
Weight	4.03	0.07	0.66	0.42	0.19	0.19
TL	9.31	0.01	0.55	0.45	0.33	0.57
FL	4.11	0.05	0.09	0.56	0.09	0.78
SL	6.13	0.02	0.00	0.94	0.00	0.93
Blood analysis						
Haematocrit PVC	0.14	0.73	0.14	0.74	0.46	0.52
Glucose	0.54	0.49	0.01	0.92	0.67	0.45
Proximate composition						
Moisture	1.48	0.26	0.20	0.71	0.07	0.84
Ash	0.06	0.82	0.38	0.55	3.28	0.09
Total protein	3.73	0.08	0.62	0.44	0.10	0.76
Total lipids	0.01	0.91	0.00	0.96	1.38	0.25
Lipid composition^a	0.93	0.47	1.02	0.40	0.93	0.46
Free fatty acids	1.90	0.21	0.01	0.91	0.01	0.92
Phospholipids	1.33	0.31	0.49	0.53	1.04	0.38
Triglycerides	2.48	0.15	0.41	0.56	0.70	0.44
Fatty acids composition^a	0.25	0.83	0.30	0.79	0.66	0.55
Saturated fatty acids	0.16	0.68	0.29	0.59	0.59	0.47
Monounsaturated fatty acids	0.21	0.66	0.10	0.76	1.21	0.30
Polyunsaturated fatty acids	0.01	0.91	0.40	0.55	0.15	0.70
n-3	0.01	0.92	0.46	0.53	0.09	0.78
n-6	0.30	0.58	0.12	0.74	0.23	0.63
n-3/ n-6 ratio	0.25	0.64	0.49	0.52	0.02	0.89
Macroelements^a	0.17	0.87	0.23	0.82	0.04	0.99
Microelements^a	3.12	0.06	0.65	0.51	0.68	0.48

Author Manuscript

540 **Table 2.** Mean (\pm SE) fatty acid composition of yellowfin bream in temperature and acidification treatments upon conclusion of the experiment.

541 All values are non-significant (see Table 1).

Fatty acid	Trivial name	Ambient temperature (22°C)		Elevated temperature (25°C)	
		Current $p\text{CO}_2$	Future $p\text{CO}_2$	Current $p\text{CO}_2$	Future $p\text{CO}_2$
C14:0	Myristic	3.07 \pm 0.63	2.91 \pm 0.61	2.86 \pm 0.12	2.82 \pm 0.31
C16:0	Palmitic	25.02 \pm 2.74	24.23 \pm 2.83	24.67 \pm 0.99	24.54 \pm 1.14
C18:0	Stearic	7.03 \pm 0.51	6.74 \pm 1.09	6.54 \pm 0.28	7.01 \pm 0.39
Total SFA		35.59 \pm 3.81	33.88 \pm 3.99	34.06 \pm 1.25	34.36 \pm 1.50
C16:1	Palmitoleic	7.20 \pm 0.55	7.32 \pm 1.1	7.34 \pm 0.30	6.86 \pm 0.36
C18:1(n-9)	Oleic	31.85 \pm 3.61	32.96 \pm 4.76	34.16 \pm 1.64	32.40 \pm 1.02
Total MUFA		39.04 \pm 3.61	40.28 \pm 5.76	41.50 \pm 1.68	39.25 \pm 1.19
C18:2(n-6)	Linoleic (LA)	10.62 \pm 1.14	10.97 \pm 1.39	10.50 \pm 0.83	10.28 \pm 0.76
C18:3(n-3)	α -Linoleic (ALA)	1.23 \pm 0.19	1.36 \pm 0.36	1.13 \pm 0.14	1.11 \pm 0.17
C20:2 (n-6)	Eicosadienoic	2.53 \pm 0.36	2.28 \pm 0.52	2.34 \pm 0.28	2.24 \pm 0.45
C20:4(n-6)	Arachidonic (AA)	1.96 \pm 0.89	1.77 \pm 1.14	1.61 \pm 0.42	2.36 \pm 0.20
C20:5(n-3)	Eicosapentaenoic (EPA)	1.92 \pm 0.69	1.97 \pm 0.73	1.70 \pm 0.25	2.19 \pm 0.14
C22:5(n-3)	Docosapentaenoic (DPA)	1.78 \pm 0.64	1.64 \pm 0.68	1.82 \pm 0.56	1.89 \pm 0.29
C22:6(n-3)	Docosahexaenoic (DHA)	5.33 \pm 2.4	5.85 \pm 3.70	5.13 \pm 0.99	6.21 \pm 0.43
Total PUFA		25.37 \pm 5.52	25.84 \pm 6.25	24.43 \pm 0.79	26.38 \pm 1.55
n-3		10.26 \pm 3.82	10.82 \pm 5.08	9.98 \pm 1.22	11.41 \pm 0.85
n-6		15.12 \pm 1.81	15.02 \pm 1.85	14.45 \pm 0.46	14.98 \pm 1.06
n-3:n-6		0.66 \pm 0.19	0.71 \pm 0.29	0.69 \pm 0.11	0.76 \pm 0.07

Figure captions

Figure 1. Change in yellowfin bream morphometrics (growth) under ambient and elevated temperature treatments. TL = total length, FL = fork length, SL = standard length. * = significant difference at $P < 0.05$.

Figure 2. Percentage of major lipid classes and free fatty acids after methylation in yellowfin bream tissue under ambient (A) and elevated (E) temperature (T) and acidification (C).

Figure 3. Concentrations of arsenic and copper in yellowfin bream after being subjected to ambient and elevated temperature treatments. * = significant difference at $P < 0.05$.





