



Size-dependent thermal limits in Australian hybrid abalone: implications for productivity shifts with ocean warming

Owen J. Holland · Callum Smythe · Timothy D. Clark · Norman L. C. Ragg · Julie Mondon · Patricia Corbett · Adam D. Miller

Received: 5 April 2023 / Accepted: 6 October 2023 / Published online: 13 November 2023
© The Author(s) 2023

Abstract Ocean warming and extreme heatwaves threaten marine species supporting commercial fisheries and aquaculture. Predicting the responses of these industries to chronic and acute warming depends on understanding which life stages are most vulnerable, the potential for stocks to adapt to changing thermal environments, and the availability of thermally adapted genotypes to help enhance stock resilience through strategic interventions. Here, we shed light on some of these knowledge gaps by quantifying the critical thermal maximum (CT_{max}) of ~10–210 g hybrid abalone (*Haliotis rubra* × *H. laevigata*) from two farms representing contrasting thermal environments from south-eastern Australia. CT_{max} was not dependent on body size or provenance (farm) when heating rates were rapid (1 °C per h), but a significant relationship between CT_{max} and body size was observed when heating rates were slower and more

ecologically realistic (1 °C per 12 h). Histological analyses revealed a negative relationship between CT_{max} and the stage of gonadal development when abalone were exposed to chronic thermal stress conditions. These results suggest that marine heatwaves and ongoing ocean warming might favour smaller, less fecund animals in natural and farm settings. This could potentially impact future harvestable biomass, recruitment and population dynamics in wild-capture fisheries, and production of larger, high-value animals in farm settings. This study adds to a growing body of literature pointing to complex and often negative effects of climate change on commercial fisheries, and the potential need for interventions aimed at bolstering fisheries resilience against the effects of ocean warming.

Keywords Abalone · CT_{max} · Ocean warming · Body size · Fisheries · Aquaculture

Owen J. Holland and Callum Smythe: Joint first authors.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s11160-023-09812-4>.

O. J. Holland · C. Smythe · T. D. Clark · J. Mondon · P. Corbett · A. D. Miller (✉)
School of Life and Environmental Sciences, Deakin University, Warrnambool, VIC, Australia
e-mail: a.miller@deakin.edu.au

N. L. C. Ragg
Cawthron Institute, Nelson, New Zealand

Introduction

Climate change is recognised as a growing threat to commercial fisheries around the world (Cheung et al. 2010; Cochrane et al. 2009; Free et al. 2019; Worm and Lotze 2021). In particular, rising ocean temperatures (Hoegh-Guldberg and Bruno 2010), ocean acidification (Doney et al. 2009), reduced oxygen levels (Breitburg et al. 2018), and shifts in oceanic currents (Hays 2017) pose a direct threat to many

commercially important species. These risks are most pronounced in ocean warming hotspots, such as south-eastern Australia (Hobday and Lough 2011), a region prone to marine heatwaves (Oliver et al. 2017, 2018; Roberts et al. 2019), and where sea surface temperatures (SSTs) are rising at four times the global average (Frusher et al. 2014; Hobday and Pecl 2014). Here, fisheries and aquaculture are already showing signs of climate stress (Holbrook and Johnson 2014; Pecl et al. 2014; Wernberg et al. 2011), with declines in productivity linked to direct physiological stress (Martino et al. 2019; McLeay et al. 2019; Wade et al. 2019), distributional shifts (Champion et al. 2018; Gervais et al. 2021a; Ramos et al. 2018; Robinson et al. 2015), habitat modifications (Johnson et al. 2011; Ling 2008) and disruption of trophic interactions (Holland et al. 2021; Ling et al. 2009; Vergés et al. 2016). Impacts of climate change are expected to intensify over the coming decades (IPCC 2021; Pereira et al. 2010), causing significant concern for industry viability, threatening food security, human health, and socio-economic values (Rice and Garcia 2011; Sumaila et al. 2011; Vianna et al. 2020). Future adaptive management of commercial fisheries and aquaculture in south-eastern Australia, and other regions of the world impacted by climate change hinges on our ability to predict how these industries will respond to future climate challenges and interventions capable of enhancing fisheries resilience (Bryndum-Buchholz et al. 2021).

South-eastern Australia is home to the world's largest wild-capture abalone fishery, primarily targeting blacklip abalone (*Haliotis rubra*), as well as a rapidly expanding aquaculture industry which predominantly farms greenlip (*H. laevis*) and hybrid abalone (*H. rubra* × *H. laevis*; Cook 2019; Mayfield et al. 2012). Combined annual harvests exceed 3000 tonnes valued at approximately AUS\$120 million (Tuynman and Dylewski 2022). Some wild abalone fisheries in the region have suffered significant declines in recent decades, due to overexploitation (Gorfine et al. 2001), disease (Mayfield et al. 2011) and invasive urchin species (Ling 2008). However, recent evidence now points to declining wild abalone stocks independent of fishing pressure, disease exposure and urchin activity, with ocean warming implicated as an additional driver of biomass reductions (Young et al. 2020). A recent study demonstrated that ocean warming is likely to be decoupling critical trophic interactions

supporting the wild *H. rubra* fisheries, causing reductions in abalone biomass (Holland et al. 2021). However, evidence also suggests that ocean warming is likely to be directly impacting the health and development of *H. rubra* and contributing to declines in some fisheries (Dang et al. 2012; Morash and Alter 2016; Young et al. 2020). Farm fisheries are also expected to become increasingly threatened by ocean warming, due to their dependency on coastal water inputs, leading to reduced growth rates and elevated risks of mortality and disease outbreaks (Hooper et al. 2014; Morash and Alter 2016; Stone et al. 2014).

Abalone are poikilothermic and thermally sensitive marine organisms (Morash and Alter 2016). Elevated SSTs have been shown to compromise all life stages, suppressing larval development (McCormick et al. 2016), delaying gonad maturation (Sukhan et al. 2021), reducing fecundity (Rogers-Bennett et al. 2010), stunting growth (Vilchis et al. 2005), and increasing susceptibility to disease (Dang et al. 2012; Raimondi et al. 2002). Extreme marine heat wave events have decimated abalone stocks in northern California (Rogers-Bennett and Catton 2019), and in Western Australia (Caputi et al. 2019; Kajtar et al. 2021; Pearce and Feng 2013), and at least one marine heatwave event has been linked to declines in *H. rubra* stocks in Tasmania (Oliver et al. 2017). Parts of south-eastern Australia are projected to experience an increase in warming of 1.5–3 °C by the year 2070, depending on the severity of ongoing carbon emissions (Hobday and Lough 2011). Understandably, fisheries managers and industry stakeholders in south-eastern Australia are concerned about these projections and future threats to the abalone industry, as well as knowledge gaps that currently hinder adaptive management.

Across the animal kingdom, early life-history stages (gametes and larvae), and larger, mature individuals are thought to be more vulnerable to thermal stress (Clark et al. 2012; Klockmann et al. 2017; Leiva et al. 2019; Peck et al. 2009). The mechanisms underpinning these ontogenetic patterns are not clear, but have previously been attributed to size-dependent oxygen transport limits (Clark et al. 2008; Peck et al. 2004, 2013). Evidence suggests that these patterns are strongest in aquatic species (Horne et al. 2015; Pinsky et al. 2019), with several studies demonstrating strong linear relationships between body size and thermal stress tolerance in a range of marine vertebrates and

invertebrates (Clark et al. 2017; Di Santo and Lobel 2017; Illing et al. 2020; Messmer et al. 2017; Peck et al. 2013). Body size also generally correlates with reproductive output in fishes, with smaller individuals often producing fewer or smaller offspring (Barneche et al. 2018; Clark et al. 2013a, b). Consequently, it has been suggested that ocean warming may impact the future productivity of some fisheries around the world by selecting for smaller and less fecund individuals (Audzijonyte et al. 2013; Baudron et al. 2014; van Rijn et al. 2017). However, it is not well understood if such allometric patterns apply to marine invertebrates such as abalone, where studies of this nature remain limited (Díaz et al. 2000; Gilroy and Edwards 1998; Hecht 1994). This highlights the need for further research geared toward improving our understanding of potential climate change effects on marine invertebrates, specifically those of commercial importance in climate change ‘hotspots’ such as south-eastern Australia.

Whilst studies suggest that patterns of vulnerability across developmental life stages persist across species distributions (Daufresne et al. 2009; Leiva et al. 2019), critical thermal limits among populations from contrasting thermal environments can differ significantly due to adaptive genetic differences (Eliason et al. 2011; Howells et al. 2012; Newton et al. 2010). Species with wide latitudinal ranges often exhibit genetically determined clines across thermal gradients (Aitken and Bemmels 2016; Halbritter et al. 2018; Jeffery et al. 2017; Miller et al. 2020). Abalone species from south-eastern Australia are widely distributed spanning strong thermal gradients, particularly *H. rubra* which has a latitudinal range of over 1500 km where annual average SST range from 14 to 22 °C (Huang et al. 2017), suggesting that adaptive differences among abalone populations may exist. Previous population genomic studies have demonstrated adaptive genetic structure relating to temperature in *H. rubra* (Miller et al. 2019) and *H. laevisgata* (Sandoval-Castillo et al. 2018), as well as haliotids from the northern hemisphere (De Wit and Palumbi 2013; Yu et al. 2021a). However, functional validation of adaptive genetic differences among populations from contrasting thermal environments has only been demonstrated in a single haliotid from China, which has since been further characterised using transcriptomic

and metabolomic data (*H. discus hannai*; Yu et al. 2021a; b, 2023). Similar quantitative experiments are needed to provide functional validation of adaptive genetic differences among Australian abalone relating to temperature. Such studies are critical for identifying vulnerable wild and farm fishing stocks (Gervais et al. 2021a, b), understanding the potential for abalone stocks to evolve and adapt to future environments (Miller et al. 2020; Waldvogel et al. 2020), and identifying temperature tolerant genotypes that can be used to enhance the resilience of both wild and farm stocks through strategic translocation activities and breeding programs (Turko et al. 2021).

In this study, controlled trials were used to test the effects of body size and provenance (two farm sites) on maximal thermal limits of Australian farmed hybrid abalone. Specifically, critical thermal maximum (CT_{max}) was measured in abalone from different life stages and thermal environments, using both acute (1 °C per h) and chronic (1 °C per 12 h) heating rates. The inclusion of two heating rates is uncommon in studies of this nature (Díaz et al. 2000; Gilroy and Edwards 1998; Searle et al. 2006), but was deemed important for understanding differential impacts of acute versus chronic thermal stress on abalone resilience. This study was limited to the use of farmed hybrid abalone, which may not accurately reflect the thermal maxima of wild, pure-bred animals. However, this approach provides a necessary first step into investigating the effects of size and provenance on the critical thermal maxima of Australian abalone broadly, as well as a baseline for how farmed animals may respond to ongoing ocean warming. Based on the findings of previous correlative (De Wit and Palumbi 2013; Miller et al. 2019; Sandoval-Castillo et al. 2018; Yu et al. 2021a) and quantitative (Yu et al. 2021b) genetic research, we hypothesise that significant differences in CT_{max} will be observed between abalone from different thermal environments (farm sites). Furthermore, given the existing knowledge from the literature, and anecdotal reports from abalone farms reporting higher mortalities in larger size classes following marine heatwave events, we hypothesise that a negative linear relationship between body size and CT_{max} will be observed at both heating rates.

Methods

Animal selection and collection

Experimental trials were performed on farmed hybrid abalone (female *H. rubra* × male *H. laevisigata*) from south-eastern Australia. Hybrid abalone exhibit heterosis (also known as ‘hybrid vigour’) providing growth and behavioural advantages and possibly enhanced resilience to thermal stress (Alter et al. 2017; Li 2008; Tripp-Valdez et al. 2021; Xiao et al. 2022), although they are rarely encountered in the wild (Brown 1995). While conducting experimental trials on pure line animals sourced from the wild would help to maximise the translation of research findings to natural settings, replicated sampling of wild specimens across developmental life stages is logistically difficult due to the cryptic nature of juveniles (Prince et al. 1988), and time constraints involved with the project.

A total of 324 hybrid abalone were sourced from two aquaculture farms from south-eastern Australia, with 162 animals collected on October 25th 2021 for an acute thermal stress trial and an additional 162 animals collected on November 25th 2021 for a chronic thermal stress trial. The two farms were Southern Ocean Mariculture (SOM) from Port Fairy (38° 23' 25.5" S, 142° 10' 43.5" E) and Jade Tiger Abalone (JTA) from Avalon (38° 4' 50.4" S, 144° 27' 18.2" E), and were selected based on their contrasting thermal environments. The average summer sea surface temperature (SST) and average annual range recorded at SOM (summer mean = 19.11 °C, annual range = 11.53 °C) are considerably lower than those from JTA (summer mean = 22.51 °C, annual range = 17.371 °C), providing a strong thermal gradient for experimental tests of provenance effects on maximum thermal limits. Each experimental trial (acute and chronic thermal stress conditions) used a gradient of animal size classes to investigate the effect of body size and ontogeny on thermal tolerance. Eighteen individuals were selected from each of four size/age classes from each farm (wet weight and age: 10–20 g, ~1.0–1.5 years; 40–50 g, ~2.0 years; 70–80 g, ~2.5–3.0 years; 100–110 g, ~3.5 years), while a fifth size/age class was included from SOM (200–210 g, ~4 years), providing a total of 72 animals from JTA and 90 animals from SOM (n = 162) for each of the acute and chronic experiments. Experimental abalone from SOM were progeny of

F4 broodstock of mixed genetic backgrounds originally sourced in 2006, with male *H. rubra* broodstock sourced from Port Phillip Bay and female *H. laevisigata* sourced from Tasmania, as well as Port Lincoln, South Australia. Animals from JTA were also progeny of broodstock initially sourced from local and non-local sources and bred in captivity for several generations. However, exact details could not be shared due to intellectual property constraints.

Abalone were removed from farm grow-out tanks and transported to Deakin University's Warrnambool campus according to standard industry practices and translocation requirements (Victorian Fisheries Authority, Permit Number RP1445). To prevent physical harm to abalone, tanks were initially drained of seawater, and abalone were gently pried off the tank surface using a blunt spatula. Animals were subsequently weighed and transferred into live export baskets, before being placed into polystyrene foam boxes with absorbent pads, ice and oxygen for transport to Deakin University. The total time from abalone collection to arrival was 3 h for each farm.

Acclimation and animal husbandry

Upon arrival at Deakin University's research facilities, the shell of each abalone was briefly dried and labelled for diagnostic purposes with Glue-on Shellfish Tags (Hallprint, Hindmarsh Valley, South Australia, Australia), according to the manufacturer's instructions. Labelled abalone were returned to export baskets and submerged in a 900 L recirculating aquaculture system (RAS) at a temperature of 14 °C ± 1 °C, consisting of two experimental aquaria and one sump tank, filled with seawater collected locally from Lady Bay, Warrnambool. After 24 h, 12 animals per size class, per farm, were transferred and distributed evenly across two 450 L RASs, also at a temperature of 14 °C ± 1 °C, each including two experimental aquaria and one sump tank. Even distributions of size classes and farms were employed intentionally to control for potential tank effects during the experimental trials. Additionally, 5 animals per size class per farm were transferred to a single aquarium in the 900 L RAS at a temperature of 14 °C ± 1 °C to be used as experimental control animals.

In each RAS, flow was regulated at 750 L h^{-1} by AquaPro® AP3000 Water Feature Pumps (Aquatec Equipment Pty Ltd., Perth, Western Australia, Australia), and constant aeration was provided by UniStar® Tornado 150-LM Air Pumps (UniStar Australia Pty Ltd., Brisbane, Queensland, Australia). All RASs contained biofiltration media, which was established eight weeks prior with Seachem Stability® (Seachem Laboratories Inc., Madison, Georgia, USA). Animals were acclimated for two weeks at $14 \text{ }^{\circ}\text{C} \pm 1 \text{ }^{\circ}\text{C}$ as this approximated the water temperature at each farm at the time of animal collection (H. Ebery, SOM & J. McIntyre, JTA, pers. comm., Oct 2021), with water temperatures maintained using a Hailea® HC-1000 A IHP Chiller (Guangdong Hailea Group Co., Ltd., Chaozhou, Guangdong, China). Abalone were kept in constant darkness as they are photophobic (Shepherd and Turner 1985), except during animal husbandry procedures and experimental observation which utilised red coloured lighting to minimise disturbance.

All animals were starved for a period of five days to facilitate purging of feed consumed prior to collection. Abalone are able to endure weeks of starvation before depletion of body reserves occurs (Carefoot et al. 1993), and a loss of appetite and reduced feed intake are common in the days following movement and physical handling (Hooper et al. 2011). Additionally, the majority of faecal matter is voided between 12 and 60 h for adults (Shipton and Britz 2001), and total gut content accounts for 6% of body mass in juveniles (Britz et al. 1996). This starvation period controlled for any dietary discrepancies between individual animal responses from each farm (Stone et al. 2014).

Following the five-day starvation period, abalone were fed an artificial diet of Aquafeeds® 3 mm Abalone Food (Aquafeeds Pty Ltd., Mount Barker, South Australia, Australia) to satiety every 24 h. For each day of the acclimation period, nitrogenous waste levels and pH were measured with an API® Saltwater Master Test Kit (Mars Inc., Chalfont, Pennsylvania, USA), and dissolved oxygen and salinity were monitored with a YSI® Pro2030 (YSI Inc., Yellow Springs, Ohio, USA). Waste was siphoned from aquaria and a third of the total water volume in each RAS was replaced with fresh seawater daily.

Acute and chronic thermal limit trials

Twenty-four hours prior to the commencement of the experiments, aquaria were drained, and the abalone were removed from their resting position using a blunt spatula and temporarily held in separate, aerated aquaria. PVC pipe frames lined with 100 mm nylon gutter-brush (Sello Products, Oakleigh, Victoria, Australia) were fitted around all edges of each aquarium, including the control aquaria, to prevent animal movement from vertical to horizontal surfaces during the experiment (Fig. 1). Aquaria were subsequently refilled with seawater and animals were returned to their aquaria, allocating an even number of animals of each size class from each farm to the front and back vertical walls of each tank. Abalone were left to habituate for 12 h overnight in a vertical position prior to the thermal ramping trials commencing.

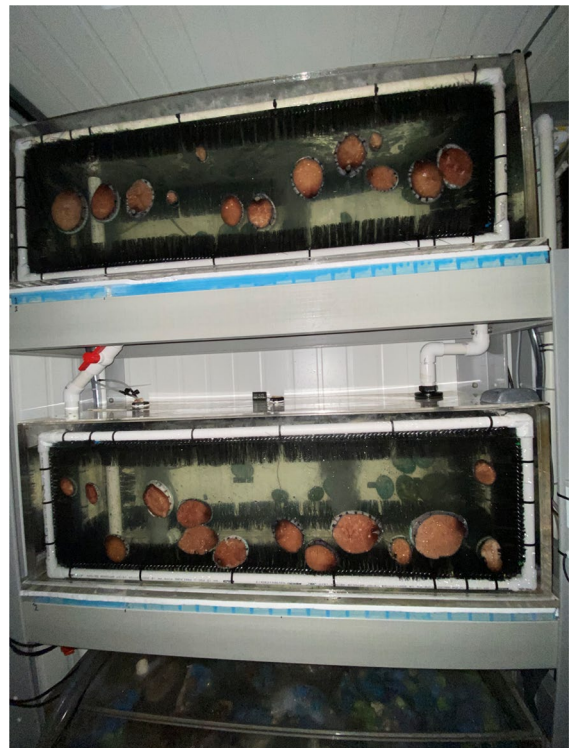


Fig. 1 Single experimental aquarium from experimental system (2 × 150 L aquaria and 1 × 150 L sump), with nylon gutter brush attached to PVC pipe frames, restricting animal movement to faces of the aquaria. Abalone are adhered to the front (ventral view) and back (dorsal view) aquaria faces

Two separate experimental trials were performed to test the effects of provenance and body size on CT_{max} achieved under fast (herein ‘acute’) and slower (herein ‘chronic’) thermal ramping. Both experiments started from a base temperature of 14 °C, with acute and chronic thermal ramping trials consisting of temperature ramping rates of 1 °C per hour and 1 °C per 12 h, respectively. Chronic heating rates of this nature reflect observed rates of summer temperature change at JTA and SOM, where water temperatures can shift by 1–2 °C in a single day, with changes in the nursery and during heatwave events being more intense (H. Ebery, SOM and J. McIntyre, JTA, pers. comm., Feb 2021). Heating was controlled using Schego® 2400 W Titanium Heaters (Schego Schemel & Goetz Electrical Appliance Co., Offenbach, Hessen, Germany) programmed by Aqua Logic® Digital Thermostat Controllers (Aqua Logic Inc., San Diego, California, USA). In contrast, control animals were maintained at a constant temperature of 14 °C. Abalone responses and tank conditions were monitored every 30 min for the acute trial and every 6 h for the chronic trial. The temperature at which an abalone lost pedal adherence to the vertical surface was deemed its critical thermal maximum (CT_{max}), an endpoint used in previous abalone thermal stress studies (Díaz et al. 2000; Gilroy and Edwards 1998; Hecht 1994; Searle et al. 2006). The measure of loss of pedal adherence has previously been demonstrated to be a reliable physiological indicator of CT_{max} in abalone. Chen et al. (2020) observed sharp declines in the heart rates in *H. gigantea*, *H. discus hannai*, and the hybrid *H. d. hannai* × *H. fulgens* during controlled thermal challenges, correlating strongly with the loss of adhesion. Additionally, exposure to high temperatures is known to cause reduced function in mucous production and physical degradation in *H. discus hannai* pedal tissue, leading to loss of adherence (Park et al. 2015). The CT_{max} temperature was recorded to 0.1 °C with a YSI® Pro2030 (YSI Inc., Yellow Springs, Ohio, USA) and was cross-validated using digital thermometer probes. For a schematic of this experimental process, refer to Figure S1.

For both the acute and chronic thermal ramping trials, total ammonia (NH_4^+/NH_3), nitrite (NO_2^-), and nitrate (NO_3^-) did not exceed 0.5 mg L⁻¹, 1.0 mg L⁻¹ and 20.0 mg L⁻¹, respectively, and pH remained

stable at 8.0. Salinity was maintained in the range of and 33.7–35.6 ppt. Dissolved oxygen concentration steadily decreased for the duration of the experiment as a result of the increasing temperature, with a maximum saturation of 8.2 mg L⁻¹ and a minimum saturation of 7.5 mg L⁻¹.

Sample processing and histological analysis

Individual abalone were removed from experimental aquaria upon reaching their CT_{max} , with the water temperature and time of detachment recorded. Abalone were subsequently weighed (g) to one decimal place using digital scales (Westlab Pty. Ltd., Ballarat, Victoria, AUS), and farm of origin noted (based on tag ID). Individual abalone were also sexed by lifting the mantle and observing the gonad colour, where pale beige and deep purple/green colourations were used to distinguish males and females, respectively (Heasman and Savva 2007). Sexing using this method could not be reliably performed for all of the smallest animals (10–20 g) due to a lack of gonad development, and subsequent analyses investigating the effect of sex excluded some of these individuals. A semi-quantitative estimate of physical condition of each animal was also recorded, based on visual inspection for abrasion of the epithelial layer of the pedal sole, based on the method by Ellis et al. (1993). A scale ranging from 0 to 4 was assigned to individuals, denoting immaculate, good, fair, poor and extremely poor condition, respectively. Behavioural data were also collected during the trial to identify individual animals where performance could have been compromised due to interactions with other individuals or with the nylon brush used in the experimental system. Animals maintained under constant temperature conditions were monitored in parallel with animals from the treatment groups as experimental controls.

Histological analyses were performed to assess the physiological consequences of thermal stress and to gain insights into the relationship between CT_{max} and gonad development. Upon animals reaching their thermal maxima, a cross section of gonad and digestive gland (one-third of the way along the conical appendage), pedal sole and side wall of the foot was excised from each animal using a sterile scalpel and fixed in 10% buffered formalin. Samples

were subsequently processed through dehydration across an increasing ethanol concentration series of 30–100%, cleared in Histolene® and impregnated with paraffin wax at 60 °C under vacuum (LEICA ASP 3005 automated tissue processor). Processed tissues were embedded in paraffin at 60 °C (LEICA EG1150H embedding station), then hand-sectioned to 4 µm (HM325 Microm microtome) onto glass slides. Slides were stained using standard haematoxylin and eosin (H&E) protocol and cover-slipped using D.P.X mounting agent. Each slide was analysed blind using a Zeiss Axiovert Universal Microscope and images captured using Ziess AxioCam HRc microimaging AxioVision digital capture system software. Male and female gonads were observed to confirm or determine sex, and gonad maturation was categorised against Gastropoda: Haliotidae gonad maturation stages

(Shin et al. 2020; Table 1). Digestive gland tubules were observed for evidence of atrophy and scored against a semi-quantitative digestive tubule atrophy scale modified from Weis et al. (1993; Table 2), and categorised against images of digestive gland metaplasia (Couch 1985), and juvenile green abalone digestive gland (Serviere-Zaragoza et al. 2016). The central pedal sole and side wall sections of the foot were examined for prevalence of histological alteration linked to potential loss of adhesion, including laceration injury, oedema, abscess, ulceration, epithelial erosion and cavitation of the pedal sole, lack of mucous cell secretion, vacuolation and necrosis of muscle fibres (Grenon & Walker 1978; Di et al. 2012; Hooper et al. 2014; Kang et al. 2020; Loehner and Moore 2020; Li et al. 2021).

Table 1 Gonad development stages in abalone modified from Shin et al. (2020)

Stage	Description—ovary development	Description—testicular development
1	Immature phase represented by primary oocytes very small in size proliferating along the germinal epithelium and trabeculae, strong basophilic staining	Inactive immature stage—loosely packed testis tissue comprising predominantly undeveloped germ cells along the germinal epithelium
2	Early growing maturation phase comprised of loosely packed small stalked tear drop shaped previtellogenic oocytes attached to trabeculae.	Early active stage—predominantly comprising spermatogonia with distinct nuclei and darkly stained nucleolus and slightly ovoid spermatocytes
3	Late growing maturation phase comprised of large elongate vitellogenic oocytes attached to trabeculae now extending into the lumen of the ovary.	Late active stage—increase in cell density comprising predominantly smaller rounded basophilic spermatids
4	Mature phase comprising densely packed large oocytes, hexagonal in shape with an apparent gelatinous coating, prominent nucleus, cytoplasm filled with yolk granules	Mature ripe stage—high cell density predominantly comprising slightly ellipsoid basophilic spermatozoa
5	Active spawning phase represented by loosely packed large, rounded/globular oocytes with thick gelatinous coating, present in the ovarian lumen	Spent stage—decreased cell density due to discharged spermatozoa, some undischarged spermatozoa remaining
6	Spent degenerative phase represented by collapsed trabeculae, oocytes of irregular shape and lack of nucleus, liquefaction necrosis of cells, strong eosinophilic staining	Degenerative stage—loosely packed tissue comprising degenerative necrosis of remaining spermatozoa

Table 2 Semi-quantitative scale for digestive tubule atrophy modified from Weis et al. (1993)

Score	Description
0	Normal wall thickness in most tubules, lumen nearly occluded, to slightly atrophied (representing 0-5% atrophy)
1	Most tubules average wall thickness significantly less than normal, but greater than one-half normal thickness (representing up to 25% atrophy)
2	Wall thickness averaging approximately one-half normal thickness (representing up to 50% atrophy)
3	Most tubules significantly less than one-half to one quarter normal thickness (representing up to 75% atrophy)
4	Wall thickness extremely thin, nearly all tubules affected (representing up to 95–100% atrophy)

Statistical analysis

Animals were removed from subsequent analyses if CT_{max} values could not be reliably recorded due to mortalities during acclimation, nylon brush preventing loss of adhesion, and animals ‘piggy-backing’ at CT_{max} endpoints. This resulted in the exclusion of 14% of animals from each trial. A test for significant effects were conducted using a mixed effects ANOVA to compare provenance, sex, body mass and condition as fixed factors and tank number as a random factor. Boxplots were generated for each of the acute and chronic trials using the *ggpubr* package in R (Kassambara 2020) to visualise the effect of provenance on abalone CT_{max} . Linear regressions were performed in R to investigate the relationships between abalone CT_{max} and wet weight, with Pearson’s correlation coefficients fitted to trendlines to measure the strength and significance of the linear relationship.

Male and female gonad development stages were combined to investigate the effect of maturity as estimates of gonad development, based on the metric provided by Shin et al. (2020), are relative to common sexual maturity stages of both sexes. A boxplot were generated using the *ggpubr* package in R (Kassambara 2020) to visualise the effect of gonad development stage on abalone CT_{max} , with significance testing performed using a mixed effects ANOVA with gonad development stage as a fixed factor and tank number as a random effect. Post-hoc testing was conducted using Tukey’s HSD test. A Wilcoxon non-parametric test was used to identify differences in semi-quantitative digestive gland tubule atrophy scores between controls and CT_{max} from experimental animals. A one-way ANOVA was used to test for significant differences between digestive gland tubule atrophy scores and animal size classes. Probit analysis was used to predict the effective CT_{max} temperature (ECT_{max}) at which a 10% (ECT_{max} 10), 25% (ECT_{max} 25) and 50% (ECT_{max} 50) reduction in digestive tubule wall thickness (atrophy) is predicted to occur. The lower the ET point estimate value, the higher the relative effect from temperature. Effect temperature estimate values were calculated by means of a logistic (sigmoidal) curve by minimising unweighted squared residuals sum (maximum likelihood) using log 10 transformed rates (adapted from Effective Concentration estimate calculation).

Results

Acute thermal stress trial

CT_{max} values were recorded for a total of 93 hybrid abalone exposed to acute thermal ramping conditions. The experiment lasted a total of 9 h, at which point the final animal reached its CT_{max} . The mean CT_{max} was 23.9 °C (range 19.4–28.3 °C) for SOM abalone and 24.5 °C (range 19.5–28.3 °C) for JTA abalone (Fig. 3). The mean CT_{max} across all experimental animals was 24.2 °C. A total of 49 control animals were monitored, none of which lost pedal adhesion during the trial, where the aquarium remained at 14 ± 1 °C.

Regression analyses indicated no significant effect of abalone wet weight on CT_{max} ($P > 0.05$; Fig. 2a). The mixed effect ANOVA revealed no significant effect of body mass, sex, provenance, condition or tank number on CT_{max} ($P > 0.05$; Table 3).

Chronic thermal stress trial

CT_{max} values were recorded for a total of 93 hybrid abalone exposed to chronic thermal ramping conditions. The experiment lasted a total of 180 h, at which point the final animal reached its CT_{max} . The mean CT_{max} was 26.1 °C (range 21.3–28.9 °C) for SOM abalone and 25.7 °C (range 21.3–28.9 °C) for JTA abalone (Fig. 3). The mean CT_{max} across all experimental animals was 25.9 °C. A total of 51 control animals were recorded, of which a total of six individuals lost pedal adhesion during the trial, occurring within 24 h of each other on the penultimate and final time points. The control aquarium remained at 14 ± 1 °C for the duration of the trial.

In contrast to the acute thermal ramping trials, regression analysis indicated a significant effect of abalone wet weight ($P = 0.018$; Fig. 2b) on CT_{max} measured during the chronic trials. Despite the significant effect, the Pearson correlation coefficient was weak ($R = -0.25$), with the regression indicating that significance is driven by the smallest and largest animals only (with high variability among intermediate size classes). However, the mixed model ANOVA revealed a significant effect of body mass on CT_{max} ($P = 0.0047$; Table 4). Contrary to our hypothesis, provenance did not have a significant effect on CT_{max} , nor did sex or condition ($P > 0.05$; Table 4). Interestingly, tank number as a random effect had

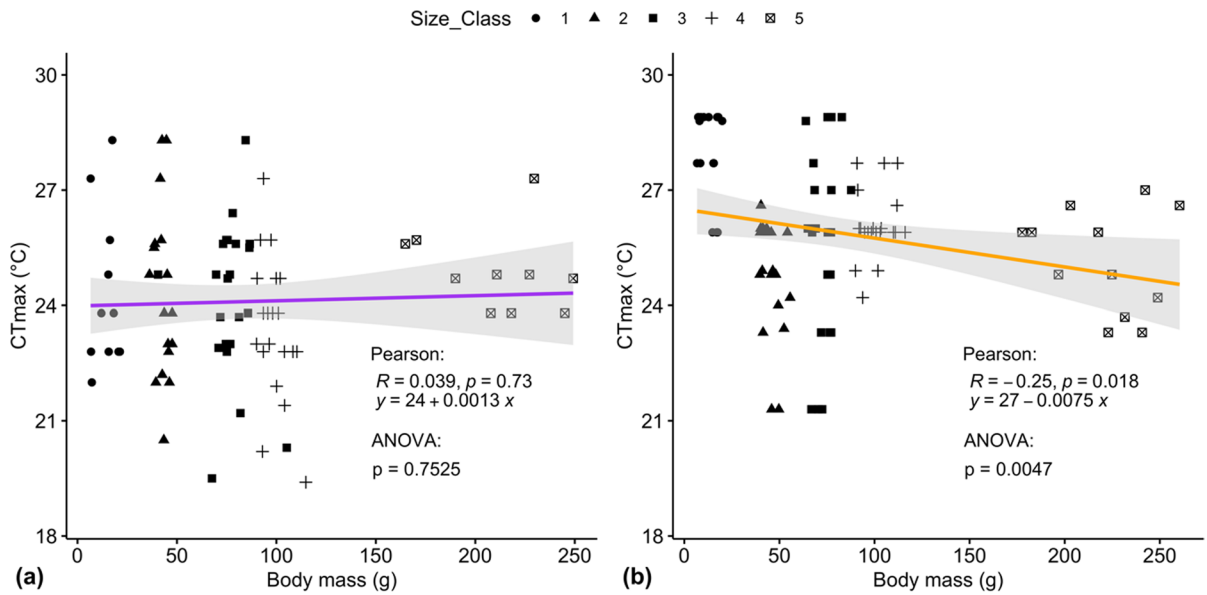


Fig. 2 Linear regressions comparing body mass and CT_{max} of abalone subjected to **a** acute thermal ramping (1 °C per hour; $n=81$) and **b** chronic thermal ramping (1 °C per 12 h; $n=92$).

Pearson’s correlation coefficient significance values and linear equations, and mixed model ANOVA significance values are depicted in the bottom right of each plot

Table 3 ANOVA results comparing the effect of animal body mass, provenance and sex as fixed effects, and tank as a random effect, on CT_{max} under acute thermal ramping conditions

Acute	Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr (>F)
Body mass	0.3746	0.3746	1	70.266	0.1002	0.7525
Provenance	1.2538	1.2538	1	72.984	0.3354	0.5643
Sex	8.3763	8.3763	1	72.395	2.2409	0.138
Condition	25.0177	6.2544	4	67.493	1.6732	0.1664
	npar	logLik	AIC	LRT	Df	Pr (> Chisq)
<None>	10	-167.28	354.56			
Tank	9	-167.28	352.56	6.28E-05	1	0.9937

a significant effect on CT_{max} ($P < 0.001$; Table 4), which appears to be driven by a disparity between the two systems (system 1=tanks 1 and 2, system 2=tanks 3 and 4; Figure S8). While the exact cause of this phenomenon is not known, it may be driven by minor differences in ramping between temperatures progressively impacting CT_{max} over time, resulting in a “lagging” effect (Figure S8).

Histological analyses

Tubule atrophy baseline condition was estimated as the mean pooled value across all control animals

(1.03 ± 0.46 SE), and suggested a mean tubule wall atrophy up to 25% digestive tissue loss in control animals. Analysis of animals subject to the acute temperature stress treatment revealed no change in digestive tubule atrophy relative to control animals. However, a moderate positive relationship between CT_{max} and digestive gland atrophy ($Rho = 0.6800, P < 0.0001$) was observed in animals subject to chronic thermal stress conditions. A significant increase of digestive gland tubule atrophy above control condition was observed in SOM abalone at CT_{max} 23 °C and above ($\chi^2 = 37.31, DF = 7, P < 0.0001$) and in JTA abalone at CT_{max} 25 °C and above ($\chi^2 = 25.00, DF = 7,$

Fig. 3 Boxplots comparing farm of origin and CT_{max} of abalone subjected to acute thermal ramping (purple; 1 °C per hour; $n=81$) and chronic thermal ramping (orange; 1 °C per 12 h; $n=92$). Mixed model ANOVA significance values for provenance effect on CT_{max} are depicted in the top right of the plot. Asterisks represent outliers and black dots represent the mean

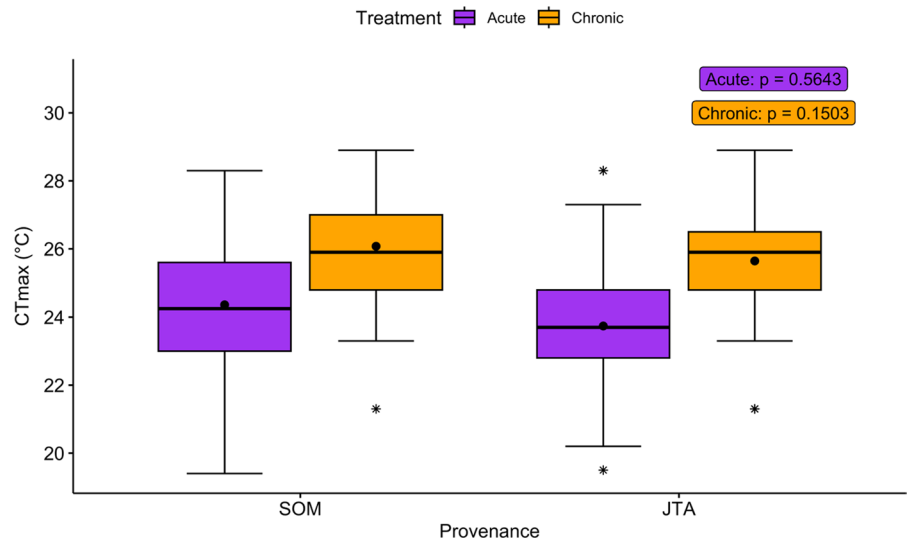


Table 4 ANOVA results comparing the effect of animal body mass, provenance and sex as fixed effects, and tank as a random effect, on CT_{max} under chronic thermal ramping conditions

Chronic	Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr (> F)
Body mass	20.9844	20.9844	1	81.348	8.451	0.0047
Provenance	5.2365	5.2365	1	81.433	2.1089	0.1503
Sex	2.2393	2.2393	1	81.723	0.9018	0.3451
Condition	12.0443	3.0111	4	81.507	1.2126	0.3118
	npar	logLik	AIC	LRT	Df	Pr (> Chisq)
<None>	10	-177.32	374.64			
Tank	9	-185.67	389.34	1.67E+01	1	4.36E-05

Significant p values are highlighted in bold

$P < 0.001$; Figure S2), however, these differences between animals from the two farms were not significant ($P > 0.05$). No correlation was identified between size class and atrophy index within each CT_{max} (Table S2). Probit analysis of the pooled digestive gland atrophy index data from the chronic thermal stress trial indicates abalone are predicted to exhibit a non-linear 10% reduction in tubule wall thickness at CT_{max} 21.50 °C, up to 25% reduction at CT_{max} 23.67 °C, and up to 50% reduction at CT_{max} 27.98 °C (Figure S3). Atrophy index values of 3–3.5 (indicating up to 75–87.5% digestive tissue reduction) were recorded in 35.7% of the pooled abalone across the CT_{max} range of 25–28 °C.

Analysis of animals subject to temperature stress treatments and control animals revealed no histological alteration in the pedal sole and side wall

of the foot (Figure S5). There was no evidence of laceration, haemorrhage or oedema, indicating the animals had not sustained a significant physical injury to the pedal sole during transfer to and between tanks. There was no cavitation or epithelial erosion of the pedal sole that would be indicative of ecdysis where extensive loss of epithelial cells would inhibit pedal sole adhesion to the substrate. Similarly, mucous secretions indicated mucous cells in the epidermal layer are active in the crucial adhesion area of the pedal sole. Further, there was no evidence of vacuolation or necrosis of muscle fibre bundles indicative of potential inhibition of pedal muscle contraction. These findings contradict the previous works of Park et al. (2015), however, energetic demands associated with gonad development and/or cardiovascular stress are possible influences

on loss of adhesion (Litaay and De Silva 2003; Lopez and Tyler 2006; Chen et al. 2020).

Histological gonad development assessments were not performed for animals from acute treatment trials given body mass had no significant effect on CT_{max} . In contrast, analyses indicated a significant effect of gonad development stage on CT_{max} in animals exposed to chronic thermal stress conditions ($P=0.04104$; Fig. 4; Table 5), however, Tukey’s HSD tests could not identify which group(s) were responsible for driving this effect ($P>0.05$), likely due to low replication. Early gonad development stages (1 and 2) were represented entirely by size class 1, with the exception of two individuals (size classes 2 and 4; Figure S7). Again, we detected a significant tank effect on CT_{max} ($P=0.002153$; Table 5).

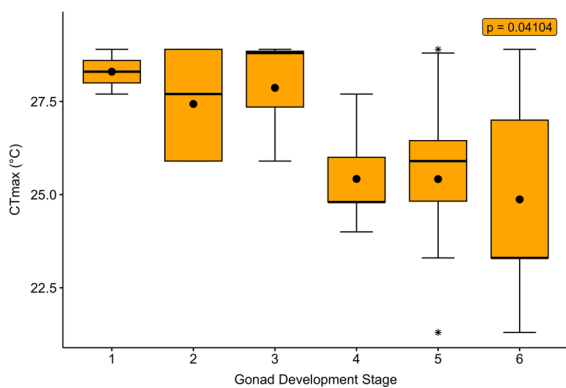


Fig. 4 Boxplots comparing gonad development stages of all abalone and CT_{max} of abalone subjected to chronic thermal ramping (1 °C per 12 h; $n=93$). One-way ANOVA significance values are depicted in the top right of the plot. Asterisks represent outliers and black dots represent the mean

Table 5 ANOVA results comparing the effect of gonad development stage as a fixed effect, and tank as a random effect, on CT_{max} under chronic thermal ramping conditions

Chronic	Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr (> F)
Gonad	36.354	7.2709	5	51.583	2.5169	0.04104
	npar	logLik	AIC	LRT	Df	Pr (> Chisq)
<None>	8	-114.04	244.07			
Tank	7	-118.74	251.49	9.4147	1	0.002153

Significant p values are highlighted in bold

Discussion

Worldwide, rising ocean temperatures pose a significant risk to many marine species supporting commercial fisheries and aquaculture (Brander 2010; Cochrane et al. 2009; Free et al. 2019), particularly thermally sensitive organisms such as abalone (Morash and Alter 2016). Predicting the future responses of commercial fisheries to ocean warming depends on understanding which life stages are most vulnerable (Kaustuv et al. 2001), the potential for evolutionary adaptive responses to changing thermal environments (Munday et al. 2013), and the availability of temperature tolerant genotypes which can be used to enhance resilience in wild fisheries and aquaculture through strategic interventions (Foo and Byrne 2016; Liu et al. 2022). This study aimed to address current knowledge gaps surrounding the vulnerability of Australian abalone to thermal stress by investigating the influence of body size and provenance on CT_{max} in farmed hybrid abalone (*H. rubra* × *H. laevigata*) under controlled acute and chronic thermal ramping conditions. These trials showed body mass-and gonad maturation of hybrid abalone had a significant effect on CT_{max} under chronic thermal ramping conditions, suggesting that larger, mature animals are most vulnerable at elevated temperatures. These findings are consistent with anecdotal evidence from farm settings in the region, and previous studies from other aquatic organisms (Daufresne et al. 2009; Messmer et al. 2017; Peck et al. 2013). The results of these trials support the notion that marine heatwaves and ongoing ocean warming may favour smaller, less fecund animals in farm and potentially natural settings. In contrast, provenance had no detectable effect on critical thermal limits despite our experimental animals coming from contrasting thermal environments. These findings are

inconsistent with those from similar trials (Yu et al. 2021b) and population genomic studies in other haliotids (De Wit and Palumbi 2013; Miller et al. 2019; Sandoval-Castillo et al. 2018; Yu et al. 2021a), which indicate adaptive genetic structure relating to temperature across haliotid distributions. However, our findings are inconclusive due to a number of potential limiting factors (discussed below), highlighting the need for further research, ideally using animals from natural populations. Future research of this kind will be key to informing adaptive management of abalone fisheries and understanding the possible effects of ocean warming on the future productivity of global fisheries.

The influence of body size on CT_{max}

Previous studies investigating the relationship between body size and CT_{max} in a range of aquatic ectotherms have provided valuable insights into intraspecific patterns of thermal sensitivity. Several studies on fishes have shown that juveniles and young adults often exhibit fitness advantages at elevated temperatures in contrast to earlier life stages or larger and more mature individuals (Clark et al. 2012; Daufresne et al. 2009; Di Santo and Lobel 2017). For example, studies on tropical clownfish (*Amphiprion melanopus*) and barramundi (*Lates calcarifer*) have found positive correlations between body mass and CT_{max} from larval to early juvenile developmental stages (Illing et al. 2020), whereas studies on coral trout (*Plectropomus leopardus*) have found inverse correlations between life stages spanning juveniles to late adulthood (Messmer et al. 2017). Increasing evidence suggests that these patterns also apply to invertebrates, with Peck et al. (2013) finding greater thermal tolerance in juvenile soft-shelled clams (*Laternula elliptica*), sea cucumbers (*Cucumaria georgiana*), sea urchins (*Sterechinus neumayeri*), and seastars (*Odonotaster validus*) than their mature counterparts. However, thermal stress studies of this nature on haliotids have been limited to either single life stages or a narrow range of size classes (Diaz et al. 2015; Gilroy and Edwards 1998; Hecht 1994; Searle et al. 2006) with limited statistical power for detecting allometric relationships (Nyboer et al. 2020). For the first time, this study demonstrated elevated thermotolerance in small (<20 g), reproductively immature farmed Australian

hybrid abalone under chronic thermal ramping conditions, suggesting that larger, mature animals may be more thermally sensitive.

Despite the influence of body size and maturation on CT_{max} under chronic thermal ramping, we found no such relationship under acute thermal ramping conditions. Contrasting patterns between controlled acute and chronic thermal ramping conditions have been shown in a range of aquatic taxa (Galbreath et al. 2004; Illing et al. 2020; Middlebrook et al. 2010). Higher overall CT_{max} values are seen in faster heating rates due, at least in part, to a lag between the environmental temperature and the internal temperature of the organism (reference). In contrast, a slower heating rate can allow some acclimation but also typically results in a lower CT_{max} , perhaps due to an accumulation of thermal stress (Illing et al. 2020; Kingsolver and Umbanhowar 2018). Faster rates can also overwhelm the organism, leading to increased physiological stress, ultimately masking the ecological relevance of the thermal maxima recorded, which may explain the lack of any observable differences in CT_{max} during the acute trial in this study (Christen et al. 2018; Ekstrom et al. 2017).

Nonetheless, findings here corroborate anecdotal evidence from both the abalone farms involved in this study, which observe higher summer mortalities in larger, mature individuals (H. Ebery, SOM and J. McIntyre, JTA, pers. comm., Feb 2021). While the drivers of the difference in CT_{max} observed across animal life stages remain uncertain, some previous studies propose that oxygen limitation may be responsible (Pörtner 2010; Pörtner and Knust 2007). Elevated temperature typically increases metabolic oxygen demand but decreases water oxygen availability, with larger animals having greater absolute oxygen demands and typically succumbing to hypoxia earlier than smaller conspecifics (Forster et al. 2012; Rubalcaba et al. 2020). Such observations have been recorded in abalone, with Vosloo et al. (2013) finding adult South African abalone (*H. midae*) to be more susceptible to the debilitating effects of hypoxia than juveniles. Increased susceptibility to hypoxia may be attributed to reductions in the diffusion surface area of the gills relative to body mass, leading to a progressive limitation in oxygen availability (Ragg and Taylor 2006). However, mounting evidence contradicts ‘oxygen limitation’ hypotheses (Clark et al. 2013b; Jutfelt et al. 2018; Lefevre et al. 2017;

Scheuffele et al. 2021) and as such the ideas should be interpreted with caution within the context of this study. Additionally, we found that maturity inferred from gonadal development stage also had a significant effect on CT_{max} . These findings are highly consistent with the literature pointing to the high energy demands of reproduction and the susceptability of more mature animals to environmental stress (Brokordt et al. 2015; Li et al. 2007; Sokolova et al. 2012). However, low levels of replication restricted the separation of males and females into their respective gonad development stages. While there was no apparent effect of sex on CT_{max} , the effect of gonadal development physiology specific to each sex may have an effect which was not observed here, possibly due to low replication. Future studies should therefore prioritise improved replication of gonad development stages across each sex to better investigate this.

The influence of provenance on CT_{max}

Several population genomic studies have demonstrated correlative patterns of adaptive genetic variation relating to temperature in a range of wild haliotids, including *H. rubra* and *H. laevisgata* (Miller et al. 2019; Sandoval-Castillo et al. 2018; Yu et al. 2021a). These findings have been further supported with experimental trials on farmed disk abalone (*Haliotis discus hannai*) that provided functional validation of adaptive genetic differences among farmed abalone stocks from contrasting thermal environments (Yu et al. 2021b). However, the present study found that provenance had no significant influence on CT_{max} . It is possible our findings are influenced by the mixed genetic backgrounds of the experimental animals, the strength of selection, heterosis driven by hybridisation, and the time needed to adapt to respective farm environments. Animals used in these trials are progeny of broodstock sourced from several thermally variable locations and reared in captivity across multiple generations (H. Ebery, SOM, pers. comm., Feb 2021; J. McIntyre, JTA, pers. comm., Feb 2021). Previous studies have shown that adaptation to culture environments can occur in as little as a single generation in fishes, crustaceans and molluscs (Araki et al. 2007; Araki and Schmid 2010; Christie et al. 2012). Additionally, Holland et al. (2022) recently demonstrated evidence of rapid selection in *H. rubra* following a single generation of exposure

to disease. Considering the potential for rapid evolutionary responses, it might be expected that multiple generations of captive rearing would be sufficient for local adaptation. Repeat trials, ideally using animals from natural populations spanning a greater thermal gradient, will help to confirm the presence of adaptive genetic differentiation relating to temperature in Australian haliotids.

Despite a lack of evidence for adaptive genetic differences among animals from JTA and SOM farms, farm observations indicate differences in thermal tolerance. Specifically, summer mortality at JTA is minimal at temperatures up to 25 °C, while moderate-high mortalities at SOM have been observed at temperatures approaching 21 °C (H. Ebery, SOM and J. McIntyre, JTA, pers. comm., Feb 2021). It is possible that these observations on farm could reflect plastic responses related to seasonal acclimation. JTA is located in Port Philip Bay and experiences considerable seasonal variation in SST (~7 °C difference between summer and winter averages), and greater exposure to heatwave events (Harris et al. 1996; Hobday and Lough 2011). In contrast, SOM is situated on the open coast where the upwelling of cold nutrient-rich waters from the continental shelf buffer summer SSTs and reduces the variability between seasons (~3 °C difference between seasonal averages; Kämpf et al. 2004; Nieblas et al. 2009). Therefore, the low mortality observed on-farm in animals from JTA may suggest that they are potentially accustomed to greater temperature fluctuations and acclimatise to the conditions throughout spring in the lead up to summer. Reciprocal transplant studies, involving the movement of animals between farms, would be beneficial for assessing the relative performance of genotypes under different environmental conditions, and the role of seasonal acclimation and plasticity in thermal stress response (Aitken and Bemmels 2016; Halbritter et al. 2018).

Future directions and implications for industry

Abalone fisheries in south-eastern Australia are facing numerous challenges, including disease, habitat modifications, and the potential decoupling of trophic interactions that support the region's fisheries (Gorfine et al. 2001; Holland et al. 2021; Hooper et al. 2007). Findings from this study indicate that ocean warming may compound these threats by

favouring and potentially selecting for smaller immature animals, possibly leading to reductions in harvestable biomass and disrupting population dynamics in wild-capture fisheries, and hindering production of larger animals of high value in farm settings (Audzijonyte et al. 2013; Baudron et al. 2014; van Rijn et al. 2017). Similar concerns have been raised for a range of fish and invertebrate species that also show allometrically determined maximum thermal limits under controlled experimental conditions (Clark et al. 2012, 2017; Daufresne et al. 2009; Messmer et al. 2017; Peck et al. 2013). These concerns have been reinforced by several studies which have demonstrated body size reductions in several wild fisheries due to ocean warming independent of size-selective fishing pressure (Daufresne et al. 2009; van Rijn et al. 2017; Wootton et al. 2021). Here, we also demonstrate that elevated temperatures can lead to significant reductions in digestive tubule thickness, potentially impacting nutrient uptake, aerobic metabolism and overall nutritional condition due to reduced numbers of digestive cells in the tubule wall (Garmendia et al. 2011; Kang et al. 2010). Reductions in nutrient uptake in conjunction with temperature stress are likely to impact growth (Vilchis et al. 2005) and potentially reduce harvestable biomass in both farm and wild settings. Nevertheless, we are cautious with our interpretations as these effects are unlikely to be spatially uniform due to the potential for genetically determined clinal variation among stocks across temperature gradients that could contribute to differences in thermal stress limits between wild and farm stocks from different thermal origins.

While our findings provide evidence of non-uniform warming threats to abalone of varying size and maturity, repeat trials using a greater number of animals aimed at testing for provenance, body size, sex and maturity effects on thermal stress responses in wild pure-bred *H. rubra* and *H. laevisgata* populations are needed to improve the translation of these findings to natural settings. Several studies have demonstrated interspecific hybrid abalone to exhibit heterosis relating to thermal tolerance (Tripp-Valdez et al. 2021; Xiao et al. 2022). Therefore it is possible that heterosis is potentially masking, and even underestimating, the actual risks of thermal stress to pure-bred wild species. Such studies will be essential for providing validation of allometrically determined differences in thermal limits in pure-bred wild species.

Similarly, these studies will provide more reliable assessments of heritable genetic variation relating to temperature across species distributions. Such information is needed for assessing the likelihood of standing genetic variation being available for adaptation to rising SSTs, and also for identifying ‘climate ready’ genotypes that could be used to enhance resilience of vulnerable wild stocks through targeted translocations (Hoffmann et al. 2021) and aquaculture through selective breeding programs (Li 2008).

Finally, our study highlights the importance of slow and ecologically realistic experimental heating regimes when testing for thermal tolerance limits in haliotids. Previous studies on haliotids have relied primarily on controlled heating rates of 1 °C per hour or faster (Gilroy and Edwards 1998; Hecht 1994; Searle et al. 2006), none of which have reported significant relationships between body size and CT_{max} . Experiments on other aquatic taxa have also demonstrated contrasting patterns of thermal tolerance between contrasting heating rates (Galbreath et al. 2004; Illing et al. 2020; Middlebrook et al. 2010). Briefly, consideration should be made regarding the effect of the experimental system used for future studies of this nature, as a significant tank effect was observed in the chronic experiment for both the multi factor and gonad interrogations. Despite the suitable water quality, differences were seen between systems. While we still saw a significant effect of body mass, it is recommended that future studies of this nature prioritise using larger, more uniform study systems to limit the effect of minor system differences that may impact the outcomes observed. Nevertheless, our comparative assessment of animal performances under both acute and chronic thermal ramping conditions adds to the literature utilising contrasting heating rates, highlighting the importance of slow temperature ramping for detecting allometric and ontogenetic effects on thermal stress responses, revealing patterns that would be otherwise masked under acute stress conditions.

Acknowledgements This project was funded by Deakin University’s Blue Sky Innovation Fund (2019) and the Holsworth Wildlife Research Endowment (Ecological Society of Australia, 2020). Timothy D. Clark was supported by an Australian Research Council Future Fellowship (FT180100154) funded by the Australian Government. We would like to thank Hamish Ebery and Mark Gervis from Southern Ocean Mariculture, and Carl Hitchings and Joshua McIntyre from Jade Tiger

Abalone for the provision of experimental animals. We would also like to thank Richard Zavalas, Zach Clark and Paul Tinkler for their technical assistance with animal husbandry, and Alex Shute for generating accurate temperature data from the target sites. Finally, we would like to thank Andrew Clarke and the Victorian Fisheries Authority for the provision of the translocation permit for the animals used in this study (Permit Number RP1445).

Author contributions This project was conceived by ADM, OJH, and TDC. Aquaria trials and associated data collection and analyses were performed by OJH, CS, ADM, TDC and NLCR. Histological sample processing and data analysis was led by JM and PC with assistance from OJH. Writing of the manuscript was led by OJH, CS, ADM, and TDC with assistance from all authors.

Funding Open Access funding enabled and organized by CAUL and its Member Institutions. This project was funded by Deakin University's Blue Sky Innovation Fund (2019) and the Holsworth Wildlife Research Endowment (Ecological Society of Australia, 2020). Timothy D. Clark was supported by an Australian Research Council Future Fellowship (FT180100154) funded by the Australian Government.

Data availability All data analysed in this paper are available at <https://doi.org/10.6084/m9.figshare.21714794.v1>.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Aitken SN, Bemmels JB (2016) Time to get moving: assisted gene flow of forest trees. *Evol Appl* 9(1):271–290. <https://doi.org/10.1111/eva.12293>
- Araki H, Schmid C (2010) Is hatchery stocking a help or harm? *Aquaculture* 308:S2–S11. <https://doi.org/10.1016/j.aquaculture.2010.05.036>
- Alter K, Andrewartha SJ, Morash AJ, Clark TD, Hellicar AD, León RI, Elliott NG (2017) Hybrid abalone are more robust to multi-stressor environments than pure parental species. *Aquaculture* 478:25–34. <https://doi.org/10.1016/j.aquaculture.2017.04.035>
- Araki H, Cooper B, Blouin MS (2007) Genetic effects of captive breeding cause a rapid, cumulative fitness decline in the wild. *Science* 318(5847):100–103. <https://doi.org/10.1126/science.1145621>
- Audzijonyte A, Kuparinen A, Gorton R, Fulton EA (2013) Ecological consequences of body size decline in harvested fish species: positive feedback loops in trophic interactions amplify human impact. *Biol Lett* 9(2):20121103. <https://doi.org/10.1098/rsbl.2012.1103>
- Barneche DR, Robertson DR, White CR, Marshall DJ (2018) Fish reproductive-energy output increases disproportionately with body size. *Science* 360(6389):642–645. <https://doi.org/10.1126/science.aao6868>
- Baudron AR, Needle CL, Rijnsdorp AD, Marshall T (2014) Warming temperatures and smaller body sizes: synchronous changes in growth of North Sea fishes. *Glob Change Biol* 20(4):1023–1031. <https://doi.org/10.1111/gcb.12514>
- Brander K (2010) Impacts of climate change on fisheries. *J Mar Syst* 79(3–4):389–402. <https://doi.org/10.1016/j.jmarsys.2008.12.015>
- Breitburg D, Levin LA, Oschlies A, Grégoire M, Chavez FP, Conley DJ, Zhang J et al (2018) Declining oxygen in the global ocean and coastal waters. *Science* 359(6371):eaam7240. <https://doi.org/10.1126/science.aam7240>
- Britz PJ, Hecht T, Knauer J (1996) Gastric evacuation time and digestive enzyme activity in abalone *Haliotis midae* fed a formulated diet. *S Afr J Mar Sci* 17(1):297–303. <https://doi.org/10.2989/025776196784158581>
- Brokordt K, Pérez H, Herrera C, Gallardo A (2015) Reproduction reduces HSP70 expression capacity in *Argopecten purpuratus* scallops subject to hypoxia and heat stress. *Aquat Biol* 23(3):265–274. <https://doi.org/10.3354/ab00626>
- Brown LD (1995) Genetic evidence for hybridisation between *Haliotis rubra* and *H. laevigata*. *Mar Biol* 123(1):89–93. <https://doi.org/10.1007/bf00350327>
- Bryndum-Buchholz A, Tittensor DP, Lotze HK (2021) The status of climate change adaptation in fisheries management: policy, legislation and implementation. *Fish Fish* 22(6):1248–1273. <https://doi.org/10.1111/faf.12586>
- Caputi N, Kangas M, Chandrapavan A, Hart A, Feng M, Marin M, Lestang Sd (2019) Factors affecting the recovery of invertebrate stocks from the 2011 western Australian Extreme Marine Heatwave. *Front Mar Sci* 6:484. <https://doi.org/10.3389/fmars.2019.00484>
- Carefoot TH, Qian P-Y, Taylor BE, West T, Osborne J (1993) Effect of Starvation on energy reserves and metabolism in the Northern abalone, *Haliotis kamtschatkana*. *Aquaculture* 118(3):315–325. [https://doi.org/10.1016/0044-8486\(93\)90466-C](https://doi.org/10.1016/0044-8486(93)90466-C)
- Champion C, Hobday AJ, Tracey SR, Pecl GT (2018) Rapid shifts in distribution and high-latitude persistence of oceanographic habitat revealed using citizen science data from a climate change hotspot. *Glob Change Biol* 24(11):5440–5453. <https://doi.org/10.1111/gcb.14398>

- Chen N, Shen YW, Yu F, Luo X, You WW, Ke CH (2020) A new indicator of hypoxia tolerance in abalone, developed based on heart rate fluctuations. *Aquaculture*. <https://doi.org/10.1016/j.aquaculture.2019.734903>
- Cheung WW, Lam VW, Sarmiento JL, Kearney K, Watson R, Zeller D, Pauly D (2010) Large-scale redistribution of maximum fisheries catch potential in the global ocean under climate change. *Glob Change Biol* 16(1):24–35
- Christen F, Desrosiers V, Dupont-Cyr BA, Vandenberg GW, Francois L, Tardif NR, Blier JC et al (2018) Thermal tolerance and thermal sensitivity of heart mitochondria: mitochondrial integrity and ROS production. *Free Radic Biol Med* 116:11–18. <https://doi.org/10.1016/j.freeradbiomed.2017.12.037>
- Christie MR, Marine ML, French RA, Blouin MS (2012) Genetic adaptation to captivity can occur in a single generation. *Proc Natl Acad Sci U S A* 109(1):238–242. <https://doi.org/10.1073/pnas.1111073109>
- Clark TD, Sandblom E, Cox GK, Hinch SG, Farrell AP (2008) Circulatory limits to oxygen supply during an acute temperature increase in the Chinook salmon (*Oncorhynchus tshawytscha*). *Am J Physiol Regul Integr Comp Physiol* 295:R1631–R1639. <https://doi.org/10.1152/ajpregu.90461.2008>
- Clark TD, Donaldson MR, Pieperhoff S, Drenner SM, Lotto A, Cooke SJ, Farrell AP et al (2012) Physiological benefits of being small in a changing world: responses of Coho Salmon (*Oncorhynchus kisutch*) to an acute thermal challenge and a simulated capture event. *PLoS ONE* 7(6):e39079. <https://doi.org/10.1371/journal.pone.0039079>
- Clark MS, Husmann G, Thorne MAS, Burns G, Truebano M, Peck LS, Philipp EER et al (2013a) Hypoxia impacts large adults first: consequences in a warming world. *Glob Change Biol* 19(7):2251–2263. <https://doi.org/10.1111/gcb.12197>
- Clark TD, Sandblom E, Jutfelt F (2013b) Aerobic scope measurements of fishes in an era of climate change: respirometry, relevance and recommendations. *J Exp Biol* 216(15):2771–2782. <https://doi.org/10.1242/jeb.084251>
- Clark TD, Roche DG, Binning SA, Speers-Roesch B, Sundin J (2017) Maximum thermal limits of coral reef damselfishes are size-dependent and resilient to near-future ocean acidification. *J Exp Biol* 220:3519–3526. <https://doi.org/10.1242/jeb.162529>
- Cochrane K, De Young C, Soto D, Bahri T (2009) Climate change implications for fisheries and aquaculture. *FAO Fish Aquac Tech Pap* 530:212
- Cook PA (2019) Worldwide abalone production statistics. *J Shellfish Res* 38(2):401–404
- Couch JA (1985) Prospective study of infectious and noninfectious diseases in oysters and fishes in three Gulf of Mexico estuaries. *Dis Aquat Organ* 1:59–82
- Dang VT, Speck P, Benkendorff K (2012) Influence of elevated temperatures on the immune response of abalone, *Haliotis rubra*. *Fish Shellfish Immunol* 32(5):732–740. <https://doi.org/10.1016/j.fsi.2012.01.022>
- Daufresne M, Lengfellner K, Sommer U (2009) Global warming benefits the small in aquatic ecosystems. *Proc Natl Acad Sci* 106(31):12788–12793. <https://doi.org/10.1073/pnas.0902080106>
- De Wit P, Palumbi SR (2013) Transcriptome-wide polymorphisms of red abalone (*Haliotis rufescens*) reveal patterns of gene flow and local adaptation. *Mol Ecol* 22:2884–2897. <https://doi.org/10.1111/mec.12081>
- Di G, Ni J, Zhang Z, You W, Wang B, Ka C (2012) Types and distribution of mucous cells of the abalone *Haliotis diversicolor*. *Afr J Biotechnol* 11(37):9127–9140. <https://doi.org/10.5897/AJB10.2066>
- Di Santo V, Lobel PS (2017) Body size and thermal tolerance in tropical gobies. *J Exp Mar Biol Ecol* 487:11–17. <https://doi.org/10.1016/j.jembe.2016.11.007>
- Díaz F, del Río-Portilla MA, Sierra E, Aguilar M, Re-Araujo AD (2000) Preferred temperature and critical thermal maxima of red abalone *Haliotis rufescens*. *J Therm Biol* 25(3):257–261. [https://doi.org/10.1016/s0306-4565\(99\)00032-7](https://doi.org/10.1016/s0306-4565(99)00032-7)
- Díaz F, Denisse Re A, Salas A, Galindo-Sanchez CE, Gonzalez MA, Sanchez A, Rosas C (2015) Behavioral thermoregulation and critical thermal limits of giant keyhole limpet *Megathura crenulata* (Sowerby 1825) (Mollusca; Vetigastropoda). *J Therm Biol* 54:133–138. <https://doi.org/10.1016/j.jtherbio.2013.05.007>
- Doney SC, Fabry VJ, Feely RA, Kleypas JA (2009) Ocean acidification: the other CO₂ problem. *Ann Rev Mar Sci* 1(1):169–192. <https://doi.org/10.1146/annurev.marine.010908.163834>
- Ekstrom A, Sandblom E, Blier PU, Cyr D, Brijs BA, Pichaud N (2017) Thermal sensitivity and phenotypic plasticity of cardiac mitochondrial metabolism in European perch, *Perca fluviatilis*. *J Exp Biol* 220(Pt 3):386–396. <https://doi.org/10.1242/jeb.150698>
- Eliason EJ, Clark TD, Hague MJ, Hanson LM, Gallagher ZS, Jeffries KM, Farrell AP et al (2011) Differences in thermal tolerance among Sockeye Salmon populations. *Science* 332(6025):109–112. <https://doi.org/10.1126/science.1199158>
- Ellis MS, Choi K-S, Wade TL, Powell EN, Jackson TJ, Lewis DH (1993) Sources of local variation in polynuclear aromatic hydrocarbon and pesticide body burden in oysters (*Crassostrea virginica*) from Galveston Bay, Texas. *Comp Biochem Physiol Part C Pharmacol Toxicol Endocrinol* 106(3):689–698. [https://doi.org/10.1016/0742-8413\(93\)90228-d](https://doi.org/10.1016/0742-8413(93)90228-d)
- Foo SA, Byrne M (2016) Acclimatization and adaptive capacity of marine species in a changing ocean. *Adv Mar Biol* 74:69–116
- Forster J, Hirst AG, Atkinson D (2012) Warming-induced reductions in body size are greater in aquatic than terrestrial species. *Proc Natl Acad Sci U S A* 109(47):19310–19314. <https://doi.org/10.1073/pnas.1210460109>
- Free CM, Thorson JT, Pinsky ML, Oken KL, Wiedenmann J, Jensen OP (2019) Impacts of historical warming on marine fisheries production. *Science* 363(6430):979–983. <https://doi.org/10.1126/science.aau1758>
- Frusher SD, Hobday AJ, Jennings SM, Creighton C, D’Silva D, Haward M, van Putten EI et al (2014) The short history of research in a marine climate change hotspot: from anecdote to adaptation in south-east Australia. *Rev Fish Biol Fish* 24(2):593–611

- Galbreath PF, Adams ND, Martin TH (2004) Influence of heating rate on measurement of time to thermal maximum in trout. *Aquaculture* 241(1–4):587–599
- Garmendia L, Soto M, Vicario U, Kim Y, Cajaraville MP, Marigómez I (2011) Application of a battery of biomarkers in mussel digestive gland to assess long-term effects of the prestige oil spill in Galicia and Bay of Biscay: tissue-level biomarkers and histopathology. *J Environ Monit* 13:915–932
- Gervais CR, Champion C, Pecl GT (2021a) Species on the move around the Australian coastline: a continental-scale review of climate-driven species redistribution in marine systems. *Glob Change Biol* 27(14):3200–3217. <https://doi.org/10.1111/gcb.15634>
- Gervais CR, Huveneres C, Rummer JL, Brown C (2021b) Population variation in the thermal response to climate change reveals differing sensitivity in a benthic shark. *Glob Change Biol* 27(1):108–120. <https://doi.org/10.1111/gcb.15422>
- Gilroy A, Edwards SJ (1998) Optimum temperature for growth of Australian abalone: preferred temperature and critical thermal maximum for blacklip abalone, *Haliotis rubra* (Leach), and greenlip abalone, *Haliotis laevigata* (Leach). *Aquac Res* 29:481–485. <https://doi.org/10.1046/j.1365-2109.1998.00241.x>
- Gorfine HK, Taylor BL, Walker TI (2001) Triggers and targets: what are we aiming for with abalone fisheries models in Australia? *J Shellfish Res* 20(2):803–812
- Grenon J-F, Walker G (1978) The histology and histochemistry of the pedal glandular system of two limpets, *Patella vulgata* and *Acmaea tessulata* (Gastropoda: Prosobranchia). *J Mar Biol Assoc U K* 58:803–816. <https://doi.org/10.1017/S0025315400056770>
- Halbritter AH, Fior S, Keller I, Billeter R, Edwards PJ, Holderegger R, Alexander JM et al (2018) Trait differentiation and adaptation of plants along elevation gradients. *J Evol Biol* 31(6):784–800. <https://doi.org/10.1111/jeb.13262>
- Harris G, Batley G, Fox D, Hall D, Jernakoff P, Molloy R, Skyring G et al (1996) Port Phillip Bay environmental study final report
- Hays GC (2017) Ocean currents and marine life. *Curr Biol* 27(11):R470–R473. <https://doi.org/10.1016/j.cub.2017.01.044>
- Heasman MP, Savva N (2007) Manual for intensive hatchery production of Abalone: theory and practice for year-round, high density seed production of Blacklip Abalone (*Haliotis rubra*). NSW Department of Primary Industries, Port Stephens Fisheries Centre
- Hecht T (1994) Behavioural thermoregulation of the abalone, *Haliotis midae*, and the implications for intensive culture. *Aquaculture* 126(1):171–181. [https://doi.org/10.1016/0044-8486\(94\)90258-5](https://doi.org/10.1016/0044-8486(94)90258-5)
- Hobday AJ, Lough JM (2011) Projected climate change in Australian marine and freshwater environments. *Mar Freshw Res* 62(9):1000–1014
- Hobday AJ, Pecl GT (2014) Identification of global marine hotspots: sentinels for change and vanguards for adaptation action. *Rev Fish Biol Fish* 24(2):415–425. <https://doi.org/10.1007/s11160-013-9326-6>
- Hoegh-Guldberg O, Bruno JF (2010) The impact of climate change on the world's marine ecosystems. *Science* 328:1523–1528. <https://doi.org/10.1126/science.1189930>
- Hoffmann AA, Miller AD, Weeks AR (2021) Genetic mixing for population management: from genetic rescue to provenancing. *Evol Appl* 14(3):634–652. <https://doi.org/10.1111/eva.13154>
- Holbrook NJ, Johnson JE (2014) Climate change impacts and adaptation of commercial marine fisheries in Australia: a review of the science. *Clim Change* 124(4):703–715. <https://doi.org/10.1007/s10584-014-1110-7>
- Holland OJ, Young MA, Sherman CDH, Tan H, Gorfine M, Matthews H, Miller AD (2021) Ocean warming threatens key trophic interactions supporting a commercial fishery in a climate change hotspot. *Glob Change Biol* 27(24):6498–6511. <https://doi.org/10.1111/gcb.15889>
- Holland OJ, Toomey M, Ahrens C, Hoffman AA, Croft LJ, Sherman CDH, Miller AD (2022) Whole genome resequencing reveals signatures of rapid selection in a virus affected commercial fishery. *Mol Ecol* 31(13):3658–3671. <https://doi.org/10.1111/mec.16499>
- Hooper C, Hardy-Smith P, Handlinger J (2007) Ganglioneuritis causing high mortalities in farmed Australian abalone (*Haliotis laevigata* and *Haliotis rubra*). *Aust Vet J* 85:188–193. <https://doi.org/10.1111/j.1751-0813.2007.00155.x>
- Hooper C, Day R, Slocombe R, Benkendorff K, Handlinger J (2011) Effect of movement stress on immune function in farmed Australian abalone (hybrid *Haliotis laevigata* and *Haliotis rubra*). *Aquaculture* 315(3–4):348–354. <https://doi.org/10.1016/j.aquaculture.2011.02.012>
- Hooper C, Day R, Slocombe R, Benkendorff K, Handlinger J, Goulias J (2014) Effects of severe heat stress on immune function, biochemistry and histopathology in farmed Australian abalone (hybrid *Haliotis laevigata* × *Haliotis rubra*). *Aquaculture* 432:26–37. <https://doi.org/10.1016/j.aquaculture.2014.03.032>
- Horne CR, Hirst AG, Atkinson D (2015) Temperature-size responses match latitudinal-size clines in arthropods, revealing critical differences between aquatic and terrestrial species. *Ecol Lett* 18(4):327–335
- Howells EJ, Beltran VH, Larsen NW, Bay LK, Willis BL, Van Oppen MJH (2012) Coral thermal tolerance shaped by local adaptation of photosymbionts. *Nat Clim Change* 2(2):116–120. <https://doi.org/10.1038/nclimate1330>
- Huang B, Thorne PW, Banzon VF, Boyer T, Chepurin G, Lawrimore JH, Zhang H-M et al (2017) Extended reconstructed sea surface temperature, version 5 (ERSSTv5): upgrades, validations, and intercomparisons. *J Clim* 30(20):8179–8205. <https://doi.org/10.1175/jcli-d-16-0836.1>
- Illing B, Downie AT, Beghin M, Rummer JL (2020) Critical thermal maxima of early life stages of three tropical fishes: effects of rearing temperature and experimental heating rate. *J Therm Biol* 90:102582. <https://doi.org/10.1016/j.jtherbio.2020.102582>
- IPCC (2021) Climate change 2021: the physical science basis. Contribution of working group I to the sixth assessment report of the intergovernmental panel on climate change. Retrieved from Cambridge UK

- Jeffery NW, Stanley RRE, Wringe BF, Guijarro-Sabaniel J, Bourret V, Bernatchez L, Bradbury IR et al (2017) Range-wide parallel climate-associated genomic clines in Atlantic salmon. *R Soc Open Sci* 4(11):171394. <https://doi.org/10.1098/rsos.171394>
- Johnson CR, Banks SC, Barrett NS, Cazassus F, Dunstan PK, Edgar GJ, Taw N et al (2011) Climate change cascades: shifts in oceanography, species' ranges and subtidal marine community dynamics in eastern Tasmania. *J Exp Mar Biol Ecol* 400:17–32. <https://doi.org/10.1016/j.jembe.2011.02.032>
- Jutfelt F, Norin T, Ern R, Overgaard J, Wang T, McKenzie DJ, Clark TD et al (2018) Oxygen- and capacity-limited thermal tolerance: blurring ecology and physiology. *J Exp Biol* 221(1):jeb169615. <https://doi.org/10.1242/jeb.169615>
- Kajtar JB, Holbrook NJ, Hernaman V (2021) A catalogue of marine heatwave metrics and trends for the Australian region. *J South Hemisphere Earth Syst Sci* 71(3):284. <https://doi.org/10.1071/es21014>
- Kämpf J, Doubell M, Griffin D, Matthews RL, Ward TM (2004) Evidence of a large seasonal coastal upwelling system along the southern shelf of Australia. *Geophys Res Lett*. <https://doi.org/10.1029/2003gl019221>
- Kang D, Yang H, Chu F, Choi KA (2010) Growth, reproductive condition, and digestive tubule atrophy of pacific oyster *Crassostrea gigas* in Gamakman Bay off the southern coast of Korea. *J Shellfish Res* 29(4):839–845
- Kang V, Lengerer B, Wattiez R, Flammang P (2020) Molecular insights into the powerful mucus-based adhesion of limpets (*Patella vulgata* L.). *Open Biol* 10:200019. <https://doi.org/10.1098/rsob.200019>
- Kassambara A (2020) Package 'ggpubr'. *R package version 0.1, 6*
- Kaustuv R, Jablonski D, Valentine JW (2001) Climate change, species range limits and body size in marine bivalves. *Ecol Lett* 4(4):366–370. <https://doi.org/10.1046/j.1461-0248.2001.00236.x>
- Kingsolver JG, Umbanhowar J (2018) The analysis and interpretation of critical temperatures. *J Exp Biol* 221(12):jeb167858. <https://doi.org/10.1242/jeb.167858>
- Klockmann M, Gunter F, Fischer K (2017) Heat resistance throughout ontogeny: body size constrains thermal tolerance. *Glob Change Biol* 23(2):686–696. <https://doi.org/10.1111/gcb.13407>
- Lefevre S, McKenzie DJ, Nilsson GE (2017) Models projecting the fate of fish populations under climate change need to be based on valid physiological mechanisms. *Glob Change Biol* 23:3449–3459. <https://doi.org/10.1111/gcb.13652>
- Leiva FP, Calosi P, Verberk W (2019) Scaling of thermal tolerance with body mass and genome size in ectotherms: a comparison between water- and air-breathers. *Philos Trans R Soc B* 374(1778):20190035. <https://doi.org/10.1098/rstb.2019.0035>
- Li X (2008) Abalone aquaculture subprogram: selective breeding of farmed abalone to enhance growth rates (II) (192156301X)
- Li Y, Qin JG, Abbott CA, Li X, Benkendorff K (2007) Synergistic impacts of heat shock and spawning on the physiology and immune health of *Crassostrea gigas*: an explanation for summer mortality in Pacific oysters. *Am J Physiol Regul Integr Comp Physiol* 293(6):R2353–R2362. <https://doi.org/10.1152/ajpregu.00463.2007>
- Li J, Ma C, Lui J, Dong Y, Lin J (2021) The co-effect of microstructures and mucus on the adhesion of abalone from a mechanical perspective. *Biosurf Biotribol* 7:180–186. <https://doi.org/10.1049/bsb2.12024>
- Ling SD (2008) Range expansion of a habitat-modifying species leads to loss of taxonomic diversity: a new and impoverished reef state. *Oecologia* 156:883–894
- Ling SD, Johnson CR, Ridgway K, Hobday AJ, Haddon M (2009) Climate-driven range extension of a sea urchin: inferring future trends by analysis of recent population dynamics. *Glob Change Biol* 15:719–731. <https://doi.org/10.1111/j.1365-2486.2008.01734.x>
- Litaay M, De Silva SS (2003) Spawning season, fecundity and proximate composition of the gonads of wild-caught blacklip abalone (*Haliotis rubra*) from Port Fairy waters, south eastern Australia. *Aquat Living Resour* 16(4):353–361. [https://doi.org/10.1016/S0990-7440\(03\)00067-6](https://doi.org/10.1016/S0990-7440(03)00067-6)
- Liu J, Peng W, Yu F, Shen Y, Yu W, Lu Y, Lin W, Zhou M, Huang Z, Luo X, You W, Ke C (2022) Genomic selection applications can improve the environmental performance of aquatics: a case study on the heat tolerance of abalone. *Evol Appl* 15(6):992–1001
- Loeher MM, Moore JD (2020) Foot injury survival in red abalone (*Haliotis rufescens*). *Aquaculture* 529:735734. <https://doi.org/10.1016/j.aquaculture.2020.735734>
- Lopez LM, Tyler P (2006) Energy budget of cultured female abalone *Haliotis tuberculata* (L.). *J Shellfish Res* 25(2):385–389. [https://doi.org/10.2983/0730-8000\(2006\)25\[385:Ebocfa\]2.0.Co;2](https://doi.org/10.2983/0730-8000(2006)25[385:Ebocfa]2.0.Co;2)
- Martino JC, Fowler AJ, Doubleday ZA, Grammer GL, Gillanders BM (2019) Using otolith chronologies to understand long-term trends and extrinsic drivers of growth in fisheries. *Ecosphere* 10(1):e02553. <https://doi.org/10.1002/ecs2.2553>
- Mayfield S, Mearns R, Gorfine HK, Peeters H, Burch P, Sharma S (2011) Survey estimates of fishable biomass following a mass mortality in an Australian molluscan fishery. *J Fish Dis* 34:287–302. <https://doi.org/10.1111/j.1365-2761.2011.01241.x>
- Mayfield S, Mundy C, Gorfine H, Hart A, Worthington D (2012) Fifty years of sustained production from the Australian abalone fisheries. *Rev Fish Sci* 20(4):220–250
- McCormick TB, Navas G, Buckley LM, Biggs C (2016) Effect of temperature, diet, light, and cultivation density on growth and survival of larval and juvenile white abalone *Haliotis sorenseni* (Bartsch, 1940). *J Shellfish Res* 35(4):981–992
- McLeay LJ, Doubell MJ, Linnane AJ (2019) Spatial and temporal variations in female size at maturity of a Southern Rock lobster (*Jasus edwardsii*) population: a likely response to climate change. *PLoS ONE* 14(11):e0225144. <https://doi.org/10.1371/journal.pone.0225144>
- Messmer V, Pratchett MS, Hoey AS, Tobin AJ, Coker DJ, Cooke SJ, Clark TD (2017) Global warming may disproportionately affect larger adults in a predatory coral reef fish. *Glob Change Biol* 23(6):2230–2240

- Middlebrook R, Anthony KRN, Hoegh-Guldberg O, Dove S (2010) Heating rate and symbiont productivity are key factors determining thermal stress in the reef-building coral *Acropora formosa*. *J Exp Biol* 213(7):1026–1034. <https://doi.org/10.1242/jeb.031633>
- Miller AD, Hoffmann AA, Tan MH, Young M, Ahrens C, Cocomazzo M, Sherman CDH et al (2019) Local and regional scale habitat heterogeneity contribute to genetic adaptation in a commercially important marine mollusc (*Haliotis rubra*) from southeastern Australia. *Mol Ecol* 28:3053–3072. <https://doi.org/10.1111/mec.15128>
- Miller AD, Coleman MA, Clark J, Cook R, Naga Z, Doblin MA, Bellgrove A et al (2020) Local thermal adaptation and limited gene flow constrain future climate responses of a marine ecosystem engineer. *Evol Appl* 13:918–934. <https://doi.org/10.1111/eva.12909>
- Morash AJ, Alter K (2016) Effects of environmental and farm stress on abalone physiology: perspectives for abalone aquaculture in the face of global climate change. *Rev Aquac* 8:342–368. <https://doi.org/10.1111/raq.12097>
- Munday PL, Warner RR, Monro K, Pandolfi JM, Marshall DJ (2013) Predicting evolutionary responses to climate change in the sea. *Ecol Lett* 16(12):1488–1500. <https://doi.org/10.1111/ele.12185>
- Newton JR, Smith-Keune C, Jerry DR (2010) Thermal tolerance varies in tropical and sub-tropical populations of barramundi (*Lates calcarifer*) consistent with local adaptation. *Aquaculture* 308:S128–S132. <https://doi.org/10.1016/j.aquaculture.2010.05.040>
- Nieblas A-E, Sloyan BM, Hobday AJ, Coleman R, Richardson AJ (2009) Variability of biological production in low wind-forced regional upwelling systems: a case study off southeastern Australia. *Limnol Oceanogr* 54(5):1548–1558. <https://doi.org/10.4319/lo.2009.54.5.1548>
- Nyboer EA, Chretien E, Chapman LJ (2020) Divergence in aerobic scope and thermal tolerance is related to local thermal regime in two populations of introduced Nile perch (*Lates niloticus*). *J Fish Biol* 97(1):231–245. <https://doi.org/10.1111/jfb.14355>
- Oliver ECJ, Benthuisen JA, Bindoff NL, Hobday AJ, Holbrook NJ, Mundy CN, Perkins-Kirkpatrick SE (2017) The unprecedented 2015/16 Tasman Sea Marine heatwave. *Nat Commun* 8:16101. <https://doi.org/10.1038/ncomm16101>
- Oliver ECJ, Lago V, Hobday AJ, Holbrook NJ, Ling SD, Mundy CN (2018) Marine heatwaves off eastern Tasmania: trends, interannual variability, and predictability. *Prog Oceanogr* 161:116–130. <https://doi.org/10.1016/j.pocan.2018.02.007>
- Park K, Lee JS, Kang JC, Kim JW, Kwak IS (2015) Cascading effects from survival to physiological activities, and gene expression of heat shock protein 90 on the abalone *Haliotis discus hannai* responding to continuous thermal stress. *Fish Shellfish Immunol* 42(2):233–240. <https://doi.org/10.1016/j.fsi.2014.10.036>
- Pearce AF, Feng M (2013) The rise and fall of the marine heat wave off Western Australia during the summer of 2010/2011. *J Mar Syst* 111–112:139–156. <https://doi.org/10.1016/J.JMARSYS.2012.10.009>
- Peck LS, Webb KE, Bailey DM (2004) Extreme sensitivity of biological function to temperature in Antarctic Marine species. *Funct Ecol* 18(5):625–630. <https://doi.org/10.1111/j.0269-8463.2004.00903.x>
- Peck LS, Clark MS, Morley SA, Massey A, Rossetti H (2009) Animal temperature limits and ecological relevance: effects of size, activity and rates of change. *Funct Ecol* 23(2):248–256. <https://doi.org/10.1111/j.1365-2435.2008.01537.x>
- Peck LS, Souster T, Clark MS (2013) Juveniles are more resistant to warming than adults in 4 species of Antarctic Marine invertebrates. *PLoS one* 8(6):e66033. <https://doi.org/10.1371/journal.pone.0066033>
- Pecl GT, Ward TM, Doubleday ZA, Clarke S, Day J, Dixon C, Stoklosa R et al (2014) Rapid assessment of fisheries species sensitivity to climate change. *Clim Change* 127(3–4):505–520. <https://doi.org/10.1007/s10584-014-1284-z>
- Pereira HM, Leadley PW, Proença V, Alkemade R, Scharlemann JPW, Fernandez-Manjarrés JF, Walpole M et al (2010) Scenarios for global biodiversity in the 21st century. *Science* 330(6010):1496–1501. <https://doi.org/10.1126/science.1196624>
- Pinsky ML, Eikeset AM, McCauley DJ, Payne JL, Sunday JM (2019) Greater vulnerability to warming of marine versus terrestrial ectotherms. *Nature* 569(7754):108–111. <https://doi.org/10.1038/s41586-019-1132-4>
- Pörtner HO (2010) Oxygen- and capacity-limitation of thermal tolerance: a matrix for integrating climate-related stressor effects in marine ecosystems. *J Exp Biol* 213(6):881–893. <https://doi.org/10.1242/jeb.037523>
- Pörtner HO, Knust R (2007) Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science* 315(5808):95–97. <https://doi.org/10.1126/science.1135471>
- Prince JD, Sellers TL, Ford WB, Talbot SR (1988) A method for ageing the abalone *Haliotis rubra* (Mollusca: Gastropoda). *Mar Freshw Res* 39:167–175
- Ragg NL, Taylor HH (2006) Oxygen uptake, diffusion limitation, and diffusing capacity of the bipectinate gills of the abalone, *Haliotis iris* (Mollusca: Prosobranchia). *Comp Biochem Physiol A Mol Integr Physiol* 143(3):299–306
- Raimondi P, Wilson C, Ambrose R, Engle J, Minchinton T (2002) Continued declines of black abalone along the coast of California: are mass mortalities related to El Niño events? *Mar Ecol Prog Ser* 242:143–152. <https://doi.org/10.3354/meps242143>
- Ramos JE, Pecl GT, Moltschanivskyj NA, Semmens JM, Souza CA, Strugnell JM (2018) Population genetic signatures of a climate change driven marine range extension. *Sci Rep* 8(1):9558. <https://doi.org/10.1038/s41598-018-27351-y>
- Rice JC, Garcia SM (2011) Fisheries, food security, climate change, and biodiversity: characteristics of the sector and perspectives on emerging issues. *ICES J Mar Sci* 68(6):1343–1353. <https://doi.org/10.1093/icesjms/fsr041>
- Roberts SD, Van Ruth PD, Wilkinson C, Bastianello SS, Bansemer MS (2019) Marine heatwave, harmful algae blooms and an extensive fish kill event during 2013 in South Australia. *Front Mar Sci* 6:610. <https://doi.org/10.3389/fmars.2019.00610>

- Robinson LM, Hobday AJ, Possingham HP, Richardson AJ (2015) Trailing edges projected to move faster than leading edges for large pelagic fish habitats under climate change. *Deep Sea Res Part II Top Stud Oceanogr* 113:225–234. <https://doi.org/10.1016/j.dsr2.2014.04.007>
- Rogers-Bennett L, Dondanville RF, Moore JD, Vilchis LI (2010) Response of red abalone reproduction to warm water, starvation, and disease stressors: implications of ocean warming. *J Shellfish Res* 29(3):599–611
- Rogers-Bennett L, Catton CA (2019) Marine heat wave and multiple stressors tip bull kelp forest to sea urchin barrens. *Sci Rep* 9(1):15050. <https://doi.org/10.1038/s41598-019-51114-y>
- Rubalcaba JG, Verberk W, Hendriks AJ, Saris B, Woods HA (2020) Oxygen limitation may affect the temperature and size dependence of metabolism in aquatic ectotherms. *Proc Natl Acad Sci U S A* 117(50):31963–31968. <https://doi.org/10.1073/pnas.2003292117>
- Sandoval-Castillo J, Robinson NA, Hart AM, Strain LWS, Beheregaray LB (2018) Seascape genomics reveals adaptive divergence in a connected and commercially important mollusc, the greenlip abalone (*Haliotis laevis*), along a longitudinal environmental gradient. *Mol Ecol* 27:1603–1620
- Scheuffele H, Jutfelt F, Clark TD (2021) Investigating the gill-oxygen limitation hypothesis in fishes: intraspecific scaling relationships of metabolic rate and gill surface area. *Conserv Physiol* 9(1):coab040. <https://doi.org/10.1093/conphys/coab040>
- Searle T, Roberts RD, Lokman PM (2006) Effects of temperature on growth of juvenile blackfoot abalone, *Haliotis iris* Gmelin. *Aquac Res* 37:1441–1449. <https://doi.org/10.1111/j.1365-2109.2006.01580.x>
- Seviere-Zaragoza E, Perez-Estrada CJ, Aldana Aranda D (2016) Status of the digestive gland and feed index in juvenile green abalone *Haliotis fulgens* fed rehydrated macroalgae. *Aquacult Nutr* 22(4):767–775
- Shepherd SA, Turner JA (1985) Studies on southern Australian abalone (genus *Haliotis*). VI. Habitat preference, abundance and predators of juveniles. *J Exp Mar Biol Ecol* 93(3):285–298
- Shin SR, Kim HJ, Lee DH, Kim H, Sohn YC, Kim JW, Lee JS (2020) Gonadal maturation and main spawning period of *Haliotis gigantea* (Gastropoda: Haliotidae). *Dev Reprod* 24(2):79–88. <https://doi.org/10.12717/dr.2020.24.2.79>
- Shipton TA, Britz PJ (2001) An assessment of the use of chromic oxide as a marker in protein digestibility studies with *Haliotis midae* L. *Aquaculture* 203(1–2):69–83. [https://doi.org/10.1016/s0044-8486\(01\)00604-4](https://doi.org/10.1016/s0044-8486(01)00604-4)
- Sokolova IM, Frederick M, Bagwe R, Lannig G, Sukhotin AA (2012) Energy homeostasis as an integrative tool for assessing limits of environmental stress tolerance in aquatic invertebrates. *Mar Environ Res* 79:1–15. <https://doi.org/10.1016/j.marenvres.2012.04.003>
- Stone DAJ, Bansemer MS, Lange B, Schaefer EN, Howarth GS, Harris JO (2014) Dietary intervention improves the survival of cultured greenlip abalone (*Haliotis laevis* Donovan) at high water temperature. *Aquaculture* 430:230–240. <https://doi.org/10.1016/j.aquaculture.2014.03.047>
- Sukhan ZP, Sharker M, Cho Y, Hossen S, Choi KS, Kho KH (2021) Thermal stress affects gonadal maturation by regulating GnRH, GnRH receptor, APGWamide, and serotonin receptor gene expression in Male Pacific Abalone, *Haliotis discus hannai* during breeding season. *Front Mar Sci* 8:664426
- Sumaila UR, Cheung WWL, Lam VWY, Pauly D, Herrick S (2011) Climate change impacts on the biophysics and economics of world fisheries. *Nat Clim Change* 1(9):449–456. <https://doi.org/10.1038/nclimate1301>
- Tripp-Valdez MA, Cicala F, Galindo-Sánchez CE et al (2021) Growth performance and transcriptomic response of warm-acclimated hybrid abalone *Haliotis rufescens* (♀) × *H. corrugata* (♂). *Mar Biotechnol* 23:62–76. <https://doi.org/10.1007/s10126-020-10002-7>
- Turko AJ, Leclair ATA, Mandrak NE, Drake DAR, Scott GR, Pitcher TE (2021) Choosing source populations for conservation reintroductions: lessons from variation in thermal tolerance among populations of the imperilled reidside dace. *Can J Fish Aquat Sci* 78(9):1347–1355. <https://doi.org/10.1139/cjfas-2020-0377>
- Tuynman H, Dylewski M (2022) Australian fisheries and aquaculture statistics 2021, ABARES, Canberra, December, CC BY 4.0. <https://doi.org/10.25814/amdt-x682>
- van Rijn I, Buba Y, Delong J, Kiflawi M, Belmaker J (2017) Large but uneven reduction in fish size across species in relation to changing sea temperatures. *Glob Change Biol* 23(9):3667–3674. <https://doi.org/10.1111/gcb.13688>
- Vergés A, Doropoulos C, Malcolm HA, Skye M, Garcia-Pizá M, Marzinelli EM, Steinberg PD et al (2016) Long-term empirical evidence of ocean warming leading to tropicalization of fish communities, increased herbivory, and loss of kelp. *Proc Natl Acad Sci U S A* 113:13791–13796. <https://doi.org/10.1073/pnas.1610725113>
- Vianna GMS, Zeller D, Pauly D (2020) Fisheries and policy implications for human nutrition. *Curr Environ Health Rep* 7(3):161–169. <https://doi.org/10.1007/s40572-020-00286-1>
- Vilchis LI, Tegner MJ, Moore JD, Friedman CS, Riser KL, Robbins TT, Dayton PK (2005) Ocean warming effects on growth, reproduction, and survivorship of Southern California abalone. *Ecol Appl* 15:469–480. <https://doi.org/10.1890/03-5326>
- Vosloo A, Laas A, Vosloo D (2013) Differential responses of juvenile and adult South African abalone (*Haliotis midae* Linnaeus) to low and high oxygen levels. *Comp Biochem Physiol A Mol Integr Physiol* 164(1):192–199. <https://doi.org/10.1016/j.cbpa.2012.09.002>
- Wade NM, Clark TD, Maynard BT, Atherton S, Wilkinson RJ, Smullen RP, Taylor RS (2019) Effects of an unprecedented summer heatwave on the growth performance, flesh colour and plasma biochemistry of marine cage-farmed Atlantic salmon (*Salmo salar*). *J Therm Biol* 80:64–74. <https://doi.org/10.1016/j.jtherbio.2018.12.021>
- Waldvogel AM, Feldmeyer B, Rolshausen G, Exposito-Alonso M, Rellstab C, Kofler R, Pfenninger M et al (2020) Evolutionary genomics can improve prediction of species' responses to climate change. *Evol Lett* 4(1):4–18. <https://doi.org/10.1002/evl3.154>

- Weis P, Weis JS, Couch J (1993) Histopathology and bioaccumulation in oysters *Crassostrea virginica* living on wood preserved with chromated copper arsenate. *Dis Aquat Organ* 17:41–46
- Wernberg T, Russell BD, Moore PJ, Ling SD, Smale DA, Campbell A, Connell SD et al (2011) Impacts of climate change in a global hotspot for temperate marine biodiversity and ocean warming. *J Exp Mar Biol Ecol* 400(1–2):7–16. <https://doi.org/10.1016/j.jembe.2011.02.021>
- Wootton HF, Audzijonyte A, Morrongiello J (2021) Multigenerational exposure to warming and fishing causes recruitment collapse, but size diversity and periodic cooling can aid recovery. *Proc Natl Acad Sci* 118(18):e2100300118. <https://doi.org/10.1073/pnas.2100300118>
- Worm B, Lotze HK (2021) Chapter 21: marine biodiversity and climate change. In: Letcher TM (ed) *Climate change*, 3rd edn. Elsevier, Amsterdam, pp 445–464
- Xiao Q, Gan Y, Yu F, Boamah GA, Shen Y, Wang Y, Huang Z, You W, Luo X, Ke C (2022) Study of hybrid and back-cross abalone populations uncovers trait separation and their thermal resistance capacity. *Aquac Res* 53:2619–2628. <https://doi.org/10.1111/are.15779>
- Young MA, Treml EA, Beher J, Fredle M, Gorfine H, Miller AD, Ierodiaconou D et al (2020) Using species distribution models to assess the long-term impacts of changing oceanographic conditions on abalone density in southeast Australia. *Ecography*. <https://doi.org/10.1111/ecog.05181>
- Yu F, Peng W, Tang B, Zhang Y, Wang Y, Gan Y, Ke C et al (2021a) A genome-wide association study of heat tolerance in Pacific abalone based on genome resequencing. *Aquaculture* 536:736436. <https://doi.org/10.1016/j.aquaculture.2021.736436>
- Yu F, Wu Y, Shen Y, Peng W, Liu J, Lin W, Ke C et al (2021b) Heat adhesion duration: a new high-throughput abalone thermal tolerance assessment method. *Aquaculture* 545:737226. <https://doi.org/10.1016/j.aquaculture.2021.737226>
- Yu F, Shen Y, Peng W, Chen N, Gan Y, Xiao Q, Liu J, Lu Y, Lin W, Han Z, Luo X (2023) Metabolic and transcriptional responses demonstrating enhanced thermal tolerance in domesticated abalone. *Sci Total Environ* 872:162060

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.