

Breeding Focus 2014 - Improving Resilience

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Breeding barramundi for resilience in the face of global climate change

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Abstract

Barramundi, *Lates calcarifer*, is an iconic and important tropical finfish species that is primarily farmed in open pond, raceway and sea cage facilities. In Australia, barramundi naturally occur in an area ranging from the Ashburton River, Western Australia (22° 30' S), across northern Australia, and as far south on the east coast as the Noosa River, central Queensland (26° 30' S). This area covers ~16 degrees of latitude and encompasses a wide range of environmental temperature regimes (water temperatures +5 °C warmer in the north of the species' distribution and -5 °C cooler in the south). Barramundi populations are also genetically structured, with 6 major genetic strains and up to 21 identifiable sub-populations evident. This genetic variability, coupled with differences in thermal exposure, is likely to be associated with temperature adaptation among populations. If properly defined and managed, this may represent a reservoir of adaptive genetic capacity within the species useful for aquaculture exploitation.

Climate modelling predicts that up to the year 2080 tropical Australia may experience temperature increases of around 5 °C. Given that current extreme summer temperature events place stress on farmed fish there is concern that future farming may be negatively impacted by climate change. Consequently, the whole organism and physiological tolerances of barramundi strains were characterised to identify the extent of genetic adaptive capacity for future breeding programs to exploit.

To establish whether barramundi strains exhibit adaptive differences in their upper thermal tolerances fish were subjected to a series of experiments where they were exposed to elevated water temperatures. The ability of strains to cope with thermal stress was then evaluated in a variety of ways including swimming barramundi in flumes and establishing time and water speed when the fish fatigues (critical swimming speeds (U_{crit})) and time to loss of swimming equilibrium, hypoxia tolerance, basal metabolic rate, through to whole transcriptome and gene pathway profiling. Climate modelling was also conducted to predict the impact future climate may have on aquaculture productivity and suitable farming environments.

Experiments provide evidence of local adaptation to temperature among barramundi strains, with barramundi from far northern Australian populations exhibiting the capability to withstand and swim at hotter temperatures for more sustained periods. Transcriptome analyses also show differences in the way barramundi from populations with different thermal profile backgrounds regulate genes in response to thermal stress and highlight the strong underlying genetic basis to thermal tolerance. This raises the possibility of identifying specific thermal tolerance marker genes in this species, if the barramundi aquaculture industry wanted to include thermal tolerance as a trait in their breeding objective in future improvement programs. Barramundi from all populations were shown to be tolerant of temperature-induced low oxygen conditions (hypoxic events) and only exhibited slight population-level differences in their energetic metabolism in response to temperature. Finally, climate modelling predicts that barramundi farming in northern Australia may actually benefit from warmer climate, resulting in increased growth rates and productivity, and an increase in suitable farming sites with thermal profiles suitable for barramundi aquaculture.

Introduction

Predicted changes in climate

Tropical Australia is a region characterised by complex climate patterns, including monsoonal intra-year variability in rainfall and evaporation rate, mid-latitude seasonal oscillations, intra-annual fluctuations in the Madden Julian Oscillation, as well as longer global climate impacts such as the Interdecadal Pacific and El Niño Southern Oscillation Indices (Balston, 2007; Balston, 2009a, b). Predicted climate change up to 2100 is expected to introduce an additional layer of stochastic variability onto this already complex climate pattern through average annual temperature increases and more frequent and intense extreme rainfall events (i.e. -5% - 15% in the wet tropics; Balston, 2009 b). As a consequence, tropical aquatic environments will be impacted through changes in water temperature, freshwater flow regimes, and salinity levels driven by changes to evaporation, precipitation, saltwater incursions, and nutrient pulses.

Despite sustained growth of the Australian aquaculture industry, the implications of climate change for tropical farmed species have been given minimal consideration. Average global temperature has risen by 0.6 °C over the past century, and there are predictions that global temperature increases of between 1.4 and 5.0 °C from the year 2000 levels can be expected by the year 2080. Similar to possible impacts on wild populations, increases in temperature can be expected to exercise strong physiological, reproductive and growth influences over aquaculture species, while changes in rainfall and evaporation patterns may affect the suitability of locations where species can be farmed (De Silva, 2009). Temperature increases, for example, may be beneficial for aquaculture by enabling diversification to novel species in areas where previously they could not be farmed and through improved performance where growth is currently temperature limited (Troadec, 2000; McCarthy *et al.*, 1999). There may also be negative impacts associated with exceeding a species' upper temperature physiological comfort zone, or indirectly by leading to frequent hypoxic events. For the aquaculture industry to be resilient

into the future it is essential for farmers to understand the physiological limits of farmed species, and to identify adaptive capacity within populations that can be targeted through selective breeding to produce fish that are better suited to likely future environmental regimes.

Barramundi aquaculture and threats of climate change

Barramundi (*Lates calcarifer*) is an iconic, catadromous (breeds in marine conditions, conducts part of its lifecycle in freshwater), fish species that supports wild catch, aquaculture, and recreational fisheries throughout northern Australia. Barramundi is an important aquaculture species across the monsoonal tropical north, where the majority of farmed production is conducted in earthen ponds, concrete raceways, or sea cages. Accordingly, due to the exposure of barramundi production systems to the local climate any changes in climatic and environmental variables that induce additional stress on farmed fish have the potential to impact on this industry and limit its future growth.

In Australia, barramundi naturally occur across 16 degrees of latitude, roughly corresponding to north of the Tropic of Capricorn, and across this distribution exhibit significant population genetic structuring (Shaklee and Salini, 1985; Salini and Shaklee, 1988; Chenoweth *et al.*, 1998; Doupé *et al.*, 1999; Keenan, 1994; Marshall, 2005). Barramundi is considered an eurythermal species (i.e. can tolerate temperature fluctuations), yet until recently very little was known about how the species tolerates the broad range of water temperatures (16 to 36 °C) it encounters across its extensive geographic range, or indeed whether the various genetic strains exhibit differences in adaptation to local environmental stressors such as high water temperature and/or hypoxia. If variation in responses to these stressors are present, defining and identifying genetic variability within and among barramundi populations could provide new breeding options for the barramundi industry to respond to climate change. This review summarises the current knowledge regarding thermal and hypoxia tolerance in Australian barramundi and suggests how the variability present can be exploited by the aquaculture industry to breed fish that are more resilient to predicted climatic conditions.

Adaptive capacity of Australian barramundi to climate change

Genetic structure of barramundi populations

Genetic differentiation among Australian barramundi has been extensively examined using different types of genetic markers, including allozymes, microsatellites, and mitochondrial DNA (mtDNA). Initial studies identified 8 to 16 discernible populations that fall within three broader genetic stocks; a reduced genetic diversity eastern Queensland stock, a northern to northwestern genetic stock, and a central stock exhibiting relatively higher genetic diversity within the Gulf of Carpentaria. Genetic differences among populations within these major stocks conformed to expectations under an isolation-by-distance model of gene flow, whereby increasing genetic differentiation was observed with increasing geographic separation between populations (Salini and Shaklee, 1988; Shaklee *et al.*, 1993; Keenan, 1994). Of prominence also was

the significant effect that the Torres Strait barrier which existed in recent glacial maxima had on shaping genetic structure of Australian populations, where a clear and major genetic break exists between populations east and west of Cape York. This pattern of both small-scale and regional genetic differentiation was later confirmed by studies based on mtDNA that sampled discrete parts of the barramundi's distribution (Chenoweth *et al.*, 1998; Doupé *et al.*, 1999; Marshall, 2005). There were, however, inconsistencies between mtDNA and allozyme studies in the number of genetic populations identified, particularly in the poorly sampled Western Australian part of the distribution.

In an attempt to bring some consistency to the assessment of *L. calcarifer* stock structure in Australia, we recently initiated a large-scale microsatellite analysis utilizing 16 microsatellite loci covering the species' distribution from Western Australia across the north and down to the southern extremities in eastern Australia (Jerry *et al.*, 2013). This study identified a total of 21 discernible subpopulations among the 43 locations sampled, with modest divergence present among populations as indicated by a $F_{ST} = 0.079$ (i.e. ~ 8% of genetic variation in this species in Australia is defined by genetic differences among collections) (Jerry *et al.*, 2013). An analysis of the current dataset using Bayesian clustering of individual multilocus genotypes supported Chenoweth *et al.*'s (1998) mtDNA data and Keenan's (1994) earlier allozyme study by highlighting the influence of the Torres Strait as an important historical biogeographic barrier (Fig 1). High membership coefficients to alternative genetic clusters are found in individuals sampled either side of this region and a clear pattern of admixture within the Gulf of Carpentaria itself is present. This indicates contemporary barramundi gene flow across the Torres Strait, since this biogeographic barrier to migration reopened (Level 1, Fig. 1). Further geographical substructure within regions either side of the Torres Strait, including between the most south-western and more northern or north-western samples, is also evident. This supports the existence of six major genetic management stocks of barramundi throughout Australia (Level 2 and 3, Fig. 1). From the perspective of aquaculture, these population genetic studies highlight the large amount of genetic diversity present within Australian barramundi stocks and the possible accumulation of local adaptive capacity within each of these stocks to the varying environments the species is exposed to across its distribution.

Thermal tolerance

Across their 16 degrees of latitude barramundi are exposed to different thermal regimes (i.e. annual temperatures range from 23.2 – 32.0 °C in Darwin, Northern Territory, to 18.5 – 27.7 °C in Gladstone, central Queensland (Bureau of Meteorology 2011). Studies that have examined thermal tolerance in Australian *L. calcarifer* using various molecular and phenotype indicators show that this thermal gradient underpins adaptive variability in temperature tolerance in barramundi and that this variability is correlated with latitude. For example, Newton *et al.* (2010), and later Jerry *et al.* (2013), used an assay based on establishing the ratio between live and dead caudal fin cells and loss of swimming equilibrium (LOSE) to test when fish were exposed to a heat stress to show that lower latitude (i.e. northern) populations exhibit more tolerance to warm water conditions than those from southern populations (Fig. 2). Thermally induced dif

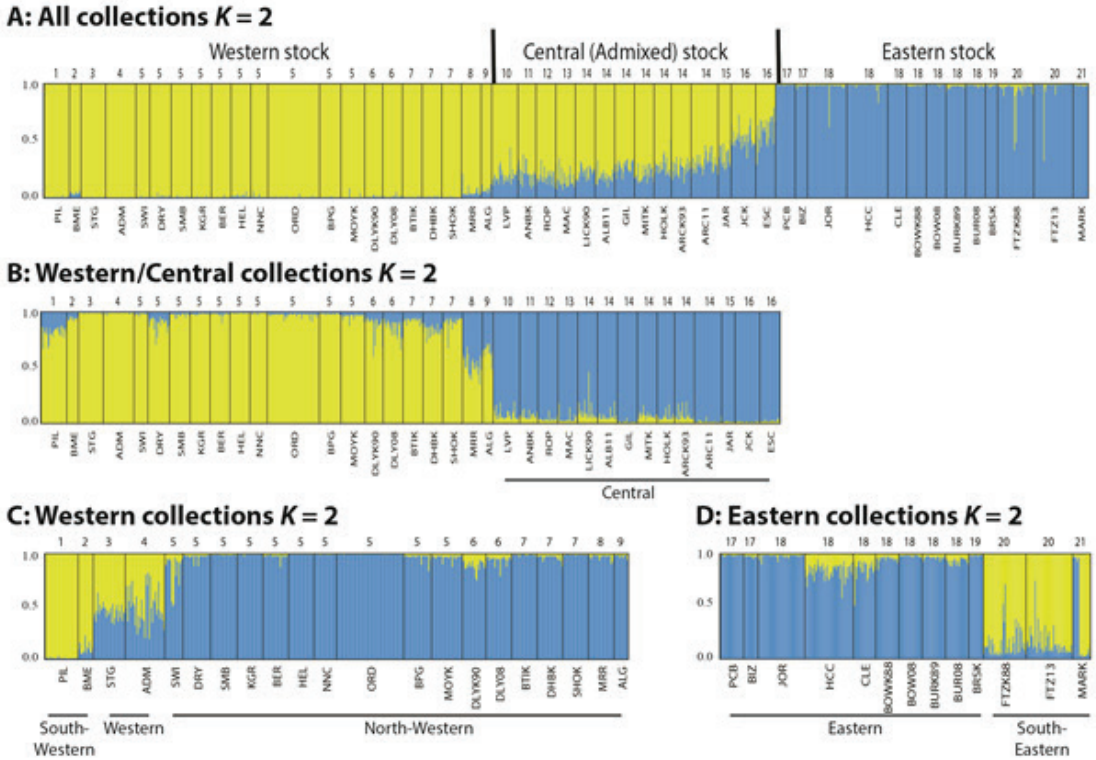


Figure 1. Co-ancestry plots for 1273 individual barramundi sampled from 48 wild collections. Collection codes are given on the x-axis while subpopulation codes are given above each collection. The y-axis shows the average membership coefficients (q -values) for each sampled fish indicating level of co-ancestry within two distinct ancestral clusters ($K = 2$) represented by blue and yellow respectively. The analysis was conducted in a hierarchical fashion and major stock groups are labelled in A, C and D and are indicated by solid lines along the x-axis joining the included collection codes in C and D. Population codes are as follows; PIL Pilbara, BME Broome, STG St George Basin, ADM Admiralty Gulf, SWI Swift Bay, DRY Drysdale R, SMB Salmon Bay, KGR King George, BER Berkley R, HEL Helby R, NNC Nulla Nulla Ck, ORD Ord R, BPG Bonaparte Gulf, Moyyk Moyle R, DLYK90 Daly R (1990 collection), DLY08 (2008 Collection), BTK Bathurst Island, DHBK Darwin Harbour, SHOK Shoal Bay, MRR Mary R, ALG Alligator R, LVP Liverpool R, ANBK Arnhem Bay, ROP Roper R, MAC McArthur R, LICK Leichardt R, ALB11 Albert R, GIL Gilbert R, MITK Mitchell R, HOLK Holroys R, ARCK93 Archer R (1993 collection), ARC11 Archer R (2011 collection), JAR Jardine R, JCK Jacky Jacky Ck, ESC Escape R, PCB Princess Charlotte Bay, BIZ Bizant R, JOR Johnstone R, HCC Hinchinbrook, CLE Cleveland Bay, BOWK88 Bowling Green Bay (1988 collection), BOW08 Bowling Green Bay (2008 collection), BURK89 Burdekin R (1989 collection), BURK08 Burdekin R (2008 collection), BRSSK Broad Sound, FTZ88 Fitzroy R (1988 collection), FTZ13 Fitzroy R (2013 collection), MARK Mary R

ferences are also evident between populations in locomotor phenotypes (i.e. critical swimming speeds or U_{crit}) (Edmunds *et al.*, 2009), lactate dehydrogenase gene expression pattern (ability to rapidly breakdown accumulation of lactic acid after a period of oxygen deficit in tissues) (Edmunds *et al.*, 2009) and transcriptome regulation (Newton *et al.*, 2013). For example, when *L. calcarifer* from northern (low latitude) and southern (high latitude) populations were swum under native (30 °C and 25 °C) and non-native (20 °C and 35 °C) temperatures, distinct differences in the swimming performance of individuals were observed. More specifically, under cold-stress conditions (20 °C), fish from cooler latitudes exhibited significantly faster swimming speeds ($32.10 \pm 0.33 \text{ cm}\cdot\text{s}^{-1}$) than their northern counterparts ($28.58 \pm 0.64 \text{ cm}\cdot\text{s}^{-1}$), while under heat-stress (35 °C) northern fish from warmer latitudes performed significantly better ($51.63 \pm 2.1 \text{ cm}\cdot\text{s}^{-1}$) than their southern counterparts ($44.18 \pm 3.11 \text{ cm}\cdot\text{s}^{-1}$) (Fig. 3).

As final evidence of adaptive genetic differences in Australian barramundi to temperature, when fish from northern (Darwin) and southern (Gladstone) populations were reared for 3.5 months under 22 °C or 36 °C genome-scale differences in gene expression patterns were evident, with fish from the Darwin population showing a massive reorganisation and up-regulation of genes compared to that seen both when reared at 22 °C and when compared to the southern population (Newton *et al.*, 2013). Genes that were observed to differ were those largely involved in the regulation of peptidase activity, microtubule based processes and cell structural processes, as well as cell metabolism, membrane and cytoplasm activity (Newton *et al.*, 2013).

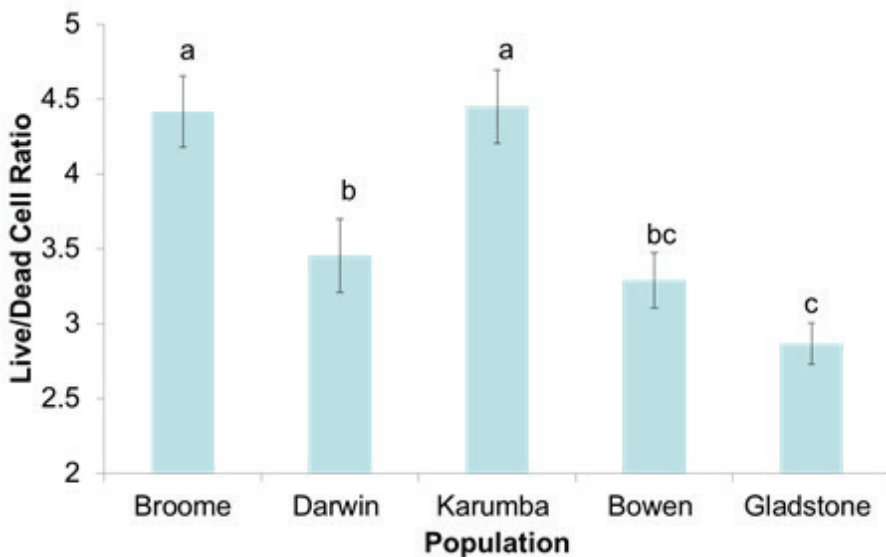


Figure 2. Ratio of mean dissociated live to dead caudal fin cells from five populations of barramundi when subjected to heat stress at 43 °C. Different letters above bars denote populations that were significantly different at $P < 0.05$. Error bars are standard errors of the mean. (After Jerry *et al.*, 2013)

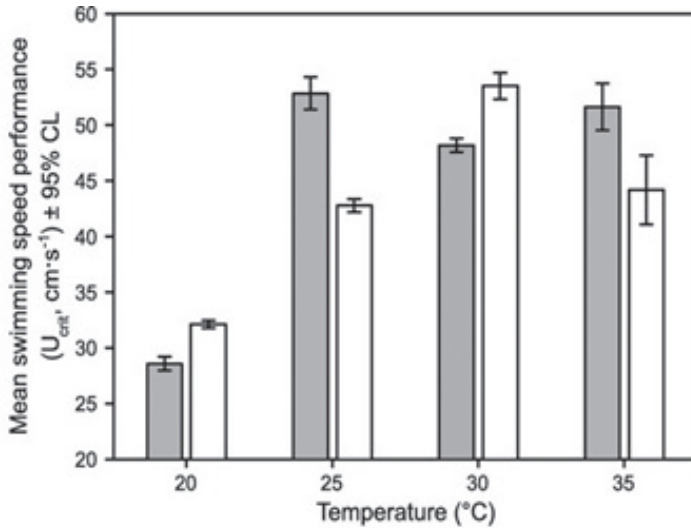


Figure 3. Mean critical swimming speed performance (U_{crit}) of *Lates calcarifer* from northern (shaded bars) and southern (open bars) Australian populations exposed to four thermal treatments during early growth ($n = 8$ individuals per bar). Note that northern (low latitude) fish exhibit a significantly slower U_{crit} at 20 °C and a relatively greater increase in U_{crit} from 20 °C to 25 °C than southern (high latitude) fish. U_{crit} values are mass-adjusted means ($n = 8$) with 95% confidence limits (CL) calculated from a general linear mixed model (GLM) analysis (Edmunds et al., 2010)

Physiological testing

If average temperatures are set to rise by up to 5 °C by 2080, along with an increased occurrence of more intense episodic heatwave events, there will also be an increased risk of hypoxia in poorly-aerated aquaculture systems leading to mass mortality. This is because the oxygen carrying ability of water is dependent on temperature; the warmer the water the less oxygen it can carry at saturation.

Whilst fish have some capacity to respond to low oxygen by increasing gill ventilation rates and/or numbers of red blood cells, acute or long-term exposure to hypoxic conditions can have effects on immune competence, growth and reproduction (Vaquer-Sunyer and Duarte, 2008). Although there is a point of oxygen saturation below which fish cannot recover, above this point there is evidence that the physiological response to hypoxia can be modulated by the frequency and severity of hypoxic events. It is even possible, if events are frequent, that natural selection might lead to local adaptation in hypoxia tolerance among fish populations (Farrell and Richards, 2009). Because northern populations of barramundi are exposed to warmer water temperatures on average and possibly hypoxic events, intra-specific variability in hypoxia tolerance may exist in this species, which if identified, could be selected to produce hypoxia tolerant strains for farming.

To test for intra-specific variability in hypoxia tolerance in Australian barramundi, Collins *et al.* (2013) subjected fish from five genetically distinct populations to hypoxic conditions. They exposed fish that had been maintained at two temperatures (26 °C and 36 °C) to decreasing oxygen saturation levels until the critical oxygen saturation level ($[O_2]_{crit}$) was reached ($15.44 \pm 3.20\%$ and $21.07 \pm 3.92\%$ (means \pm SD) at 26 and 36 °C, respectively) (Fig. 4). Interestingly, no mean differences between the $[O_2]_{crit}$ among populations were found. However, when they measured resting metabolic oxygen demands at 36 °C, modest differences in consumption rates were found between barramundi from Gladstone (high latitude) and Broome (low latitude). Despite this small difference, however, it does appear that hypoxia tolerance in Australian barramundi is relatively conserved and is a trait that will not be easy to improve through selection.

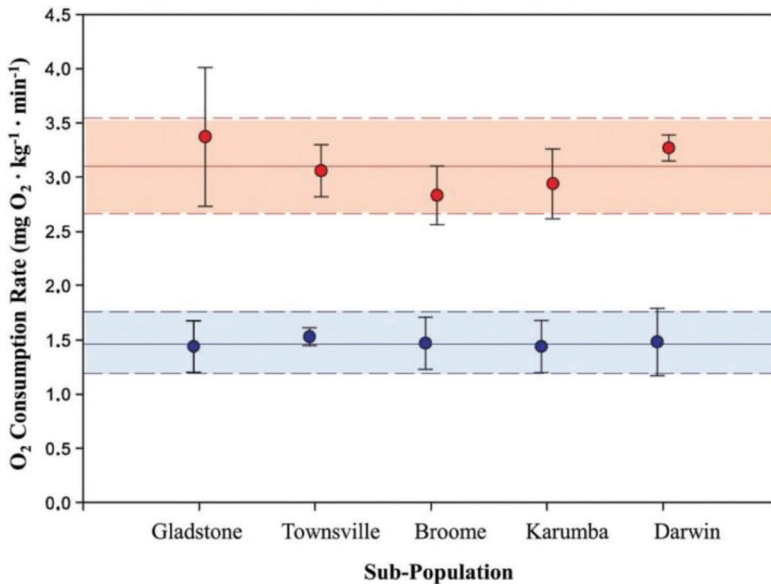


Figure 4. Resting oxygen consumption rates (in milligrams of O_2 per kilogram per minute; means \pm SD) for five barramundi sub-populations at 26°C (blue; $n = 48$) and 36°C (red; $n = 59$). Oxygen consumption rates were calculated from the average slope of the decline in chamber $[O_2]$ across a 15 min period during the ‘closed’ cycle of intermittent flow-through respirometry, and measured every 45 min. The continuous and dashed horizontal lines represent the mean and standard deviation for all populations at each temperature. (After Collins *et al.*, 2013)

Modelling

Temperature is perhaps the most important factor influencing growth in fish (Huey and Stevenson, 1979). Increases in temperature cause increased metabolism and feeding (Brett and Groves, 1979; Jobling, 1994), and energy that is not spent on metabolic processes promotes enhanced growth in warmer temperatures (Katersky and Carter, 2007). Every species exists within a thermal tolerance range, and growth is maximised at an optimal temperature (Huey

and Stevenson, 1979). Barramundi have a wide thermal tolerance of 15 – 40 °C and several studies have found that maximum growth efficiency occurs between 27 – 36 °C (Katersky and Carter, 2005; Glencross, 2008). Outside these temperatures growth, and thus productivity, rapidly declines. As there is large variability in current thermal regimes where barramundi are farmed, we can expect that some areas are more productive than others purely because of temperature. Importantly, climate change is expected to lead to temperature increases of up to 5 °C and this may influence where barramundi can be productively farmed.

Jerry *et al.* (2013) examined the implications of increasing global temperatures on pond-based barramundi aquaculture. In this study the growth function determined by Bermudes *et al.* (2010) that describes weight gain by barramundi as a function of fish weight and water temperature was used, along with current geographic temperature data, to determine thermal suitability and productivity of barramundi farming across Australia. They then used the Representative Concentration Pathways (RCP) 8.5 emissions scenario of 18 global climate models (GCMS) to predict future temperature profiles across Australia in the years 2030, 2050 and 2080. This modelling showed that currently 38.2% of continental Australia is thermally suitable for pond-based aquaculture of barramundi (Fig. 5). Within this suitable area, weight gain per fish per year (Jan-Dec) ranges between 296 - 2989 g, with the most productive areas being in the north. Twenty-seven percent of Australia could theoretically currently produce fish between 1500 - 2500 g within one year.

When growth is predicted under future climate scenarios models showed that a) there will be a significant southward expansion of regions suitable for farming barramundi; and b) areas currently suitable will see increased weight gain and productivity in the future (Fig. 5). The total thermally suitable area for pond-based barramundi aquaculture increases from 38% currently, to 47.5% by 2030; 54.5% by 2050; and 66% by 2080. This represents an expansion of thermally suitable area of 173% over the current thermally suitable area by 2080. Modelling also indicated that barramundi will grow faster in the future due to higher annual temperatures (and smaller periods of the year with winter temperatures at the lower end of the temperature-induced growth curve). In 2030, barramundi grown within current suitable areas will potentially add an additional 238 - 484 g per year to their growth. By 2080, the average and maximum weight gain per year will increase to 354 and 1000 g more than current growth, respectively. Areas not currently suitable for barramundi aquaculture may support fish that grow up to 1754.7 g by 2030, and up to 1936.2 g by 2080.

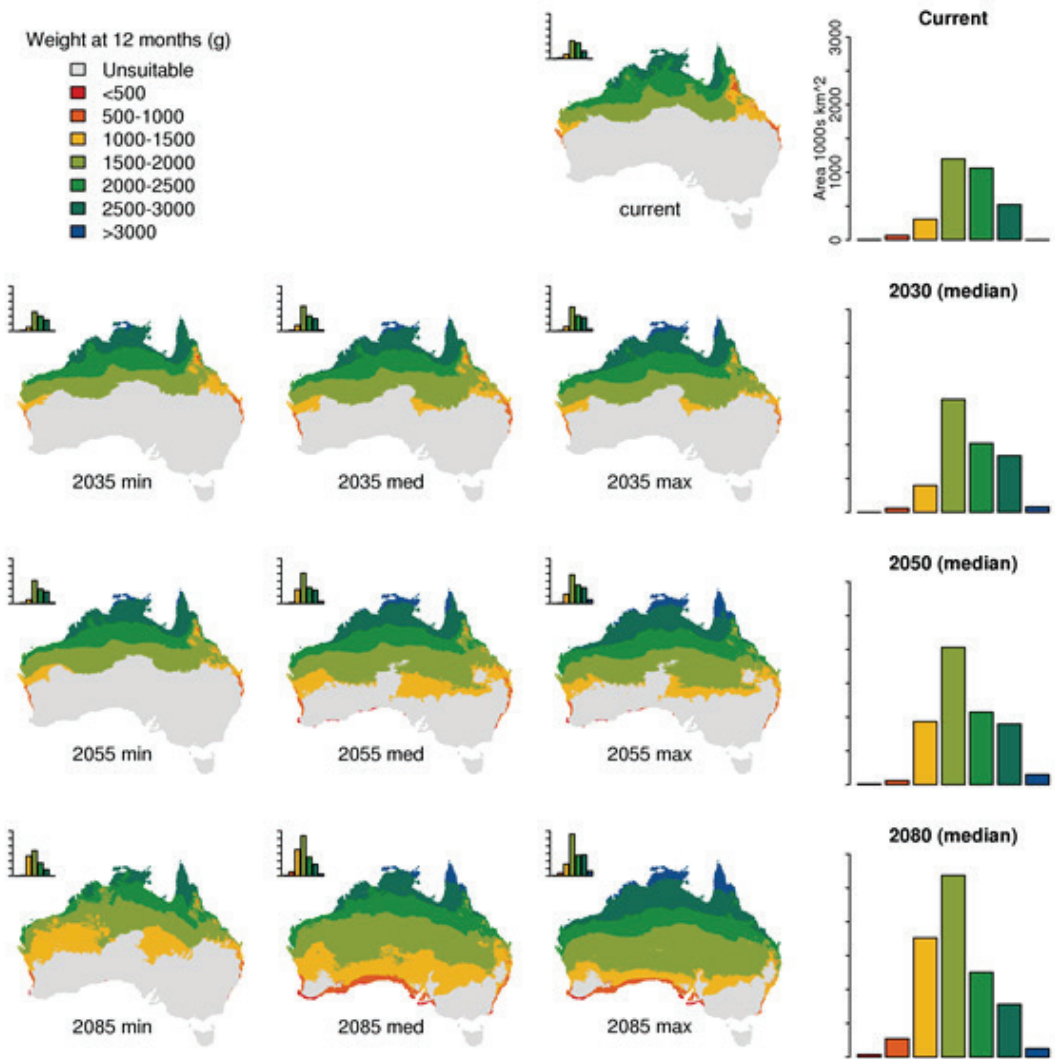


Figure 5. Current and future suitability (estimated as gain in grams per day for one year) for barramundi aquaculture. Where monthly mean temperature during the coldest month reached 15 °C these areas were considered unsuitable and are marked in grey. Future scenarios show weighted mean of 30 runs of 8 GCMS. Area within each growth category shown on bar plots in 1000s km²

Breeding for resilience in the face of climate change

Accumulating research indicates that Australian barramundi exhibit genetically determined differences in thermal tolerance across the species' latitudinal range. Given that environmental thermal profiles are expected to rise over the coming decades, this variability in thermal tolerance represents an important repository for barramundi farmers to target and may help the farmers to select the best genetic stocks for their region as an adaptation strategy to changing climate. In particular, farmers may want to consider rearing barramundi which are not derived from current local stocks, but that demonstrate better performance under the environmental temperatures they may be exposed to in the future. This would mean that farmers in the south of the barramundi's current distribution could rear fish from those originating from more northern stocks which show higher tolerance to warm waters. Similarly, as thermal profiles become more suitable for barramundi farming below the Tropic of Capricorn, farmers would want to rear barramundi from the most southern stocks which exhibit a wider tolerance of cooler water temperatures.

In addition to selecting population-level genetic differences in temperature tolerance, studies in Nile tilapia (*Oreochromis niloticus*), stickleback (*Gasterosteus aculeatus*), red drum (*Sciaenops ocellatus*) and killifish (*Heterandria formosa*) have highlighted additive genetic variability for temperature tolerance in fish (Charo-Karisa *et al.*, 2005; Ma *et al.*, 2007; Barrett *et al.*, 2010; Doyle *et al.*, 2011). For example, the heritability of heat tolerance in killifish is between 0.19 - 0.46 (Doyle *et al.*, 2011). Whilst similar heritability estimates have not been obtained for barramundi it is conceivable that if heritabilities for temperature tolerance are similar to other species, individuals or families with increased thermal tolerances can be identified. Selection for this trait in barramundi breeding programs could lead to the development of more thermally tolerant strains which would provide future resilience against climate induced temperature changes into the future.

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