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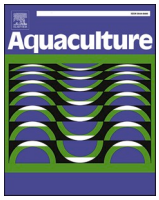

# Enhanced survival and growth in the selectively bred *Chrysophrys auratus* (Australasian snapper, tāmure)

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ABSTRACT

We report results from a comparison of a wild ($F_1$) and a selectively bred elite ($F_3$) strain of *Chrysophrys auratus* (Australasian snapper, tāmure), a species that has been selected for enhanced growth using genomics-assisted breeding selection. Populations ($n$ = 100) of each strain were cultivated in replicated tanks over 39 days and fed for 8 h/day at two feeding frequencies (hourly and bihourly). Survival, feed intake, weight gain and feed conversion ratio (FCR) were measured as the fish grew from approximately 5 to 15 g at a mean temperature of 18.6 °C. The selectively bred strain exhibited significantly improved performance over the wild strain in all measured traits. The $F_3$ strain exhibited almost 100% survival, compared with 85% survival in the wild strain. The weight gain of the selected strain was 28–30% higher and FCR improved by 33–73%. In addition, intra-cohort variation was considerably lower for the $F_3$ strain, and these fish were less sensitive to the effects of feed frequency. Feed intake was not substantially different between strains, and breeding gains in this species seem to be underpinned by substantially improved feed conversion. The results of this study indicate that the genomics-assisted selective breeding of *C. auratus* has significant potential to address production cost and efficiency concerns hindering the development of farming of this species in Australasia.

## 1. Introduction

Selective breeding programmes for aquaculture are a relatively recent endeavour compared with the long history of terrestrial plant and animal breeding programmes (Gjedrem and Robinson, 2014; Gjedrem et al., 2012). However, with the increasing global need for food, the number of new aquaculture breeding programmes has risen considerably over the last decade (Bostock et al., 2010; Garlock et al., 2020; Valenza-Troubat et al., 2021). Growth improvement is a key target for many selective breeding programmes because growth can be easily quantified, often shows high heritability, and improvement in growth rate has a significant and direct impact on commercial returns (Gjedrem, 2005; Vandeputte et al., 2019).

The high heritability of many growth traits means that gains of 10–20% can be made with every generation of selective breeding, although that varies with species and the strength of selection applied (Gjedrem and Robinson, 2014; Houston et al., 2020; Valenza-Troubat et al., 2022). For example in Atlantic salmon (Salmonidae: *Salmon salar*), selection for faster growth over 40 years (i.e. ten generations) has led to more than a doubling of growth (Houston and Macqueen, 2019). Similarly, in the red seabream (Sparidae: *Chrysophrys/Pagrus major*) selective breeding over the last 60 years (i.e. around twenty generations) has resulted in a doubling of growth, and this species is now one of the most cultured species in Japan (Murata et al., 1996; Ogata et al., 2002). Likewise, selective breeding programmes on the gilthead seabream (Sparidae: *Sparus aurata*) over the last 20–30 years have resulted in significant growth improvements as well as in other key production traits, such as reduced deformities, and these have all contributed to this species becoming a key aquaculture species for the Mediterranean region (Boudry et al., 2021).

In this paper we report the aquaculture performance gains resulting from a breeding programme for Australasian snapper (indigenous Māori name tāmure), *Chrysophrys auratus* (formerly known as *Pagrus auratus*), a widely distributed species found in Aotearoa/New Zealand, Australia and parts of South East Asia (Chiba et al., 2009). While this marine finfish species is hardy and a good candidate for aquaculture given that

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what is known about the other members of the Sparidae farmed in the northern hemisphere (Basurco et al., 2011; Teles et al., 2011), the growth rate of *C. auratus* is often cited as a limiting factor to aquaculture development (Booth et al., 2007; Fielder et al., 2001; Pham and Fotedar, 2017). A selective breeding programme for *C. auratus* was started by the New Zealand Institute for Plant and Food Research Limited (PFR) in the port city of Nelson in the early 2000s (Baesjou and Wellenreuther, 2021). The breeding selection has evolved over time, and is currently based on mass spawning and subsequent pedigree assignment of offspring to select the fastest growing fish while minimising inbreeding using advanced genomic selection tools (Ashton et al., 2019a; Ashton et al., 2019b; Catanach et al., 2019; Montanari et al., 2022).

To evaluate gains achieved in the $F_3$ generation, an experiment was conducted to grow $F_1$ offspring from wild broodstock alongside the selectively improved $F_3$ strain of *C. auratus* and compare production performance (growth, mortality and feed conversion) under two feeding frequencies. To our knowledge, this species is not currently farmed anywhere in the world, and only a modest body of published aquaculture performance information is available, and this is solely for wild-type strains (Booth et al., 2007; Booth et al., 2004; Doolan et al., 2007; Fielder et al., 2001). Quantification of growth gains has traditionally been conducted by comparing realised growth over different generations or strains (Carlberg et al., 2018; Murata et al., 1996), but such comparisons are complicated by year to year variation in rearing parameters such as stocking and husbandry, diet quality and environmental conditions. Another way to quantify generational growth gains is to compare, in parallel, offspring derived from wild broodstock with offspring from a selected broodstock strain (Glover et al., 2009; Neely et al., 2008; Ogata et al., 2002; Thodesen et al., 1999), and this was the approach taken in the current study.

## 2. Materials and methods

### 2.1. Experimental strains, spawning and larval rearing

All broodstock and offspring used in this study were maintained at the PFR Maitai Finfish Facility located in Nelson, which is a land-based, pump-ashore, single pass system contained within multiple steel-walled tunnel houses with polyethylene covers. The selectively bred strain was represented by progenies of a third filial generation ($F_3$) and was produced following genomic selection for increased weight of the $F_2$ broodstock. The wild strain was represented by progenies of a first generation ($F_1$) produced from wild broodstock captured from Tasman Bay (located in the north of the South Island of Aotearoa/New Zealand).

Each broodstock was maintained in a 13,000-L circular plastic tank and supplied with ambient temperature seawater from the Nelson Harbour. Spawning was allowed to occur naturally (i.e. no hormonal, photoperiod or temperature manipulation) with an unknown number of males and females contributing to the group spawning events typical of this species. Eggs from the selected $F_3$ and wild type $F_1$ *C. auratus* were collected each morning (08:00 h) over 5 days for the $F_3$ strain and 3 days for the $F_1$ wild strain in the same reproduction cycle in December 2018 and kept in 4.4-$m^3$ circular larval rearing tanks. The purpose for collecting eggs over multiple days was to maximize the parental contributions from the snapper broodstock. The age of the fish was expressed as days post hatch (DPH), with day 0 set at the first day on which hatched larvae were observed (22 December 2018 for both strains).

Eggs were incubated according to a PFR protocol that was broadly based on the Japanese red sea bream method. Eggs were incubated in the larval rearing tank under semi-static conditions, with gentle aeration, and temperature maintained between 22 and 24 °C. Hatching occurred around days 4–5 post spawn, and at first feeding (2–4 days post hatch) tanks were supplied with algal paste (RotiGreen Nanno from Reed Mariculture, California, USA) and enriched rotifers (*Brachionus plicatilis* (L-strain, Selco S.Presso Enrichment, INVE Aquaculture, Nonthaburi, Thailand) to a maintain a target concentration of 15 rotifers $mL^{-1}$. Enriched AF *Artemia* were fed from 13 DPH to 21 DPH, and then SEPArt *Artemia* (INVE Aquaculture) enriched with Selco Spresso were supplied from 16 DPH and rotifer addition finished by 21 DPH. Levels of water exchange were progressively increased from influent 4 L $min^{-1}$ at 10 DPH to 42 L $min^{-1}$ by 57 DPH and dry diets were introduced at 25 DPH, with the last day of *Artemia* addition 35 DPH.

Each strain of juvenile fish (approximately 10,000 individuals) had water temperature gradually reduced from 62 DPH to ambient water conditions (20–22 °C) and progressively moved through increasing pellet sizes (O.range hatchery feeds, INVE Aquaculture, followed by increasing sizes of extruded pelletised marine diets from Skretting and Ridley, Australia). A minimal degree of in-tank hand grading was periodically undertaken to remove very small individuals from both cohorts to reduce cannibalism and foster homogenous growth. Both strains were graded through a bar grader twice ($F_3$ at 59 DPH and $F_1$ at 61 DPH, and then both at 81 DPH). The main experiment commenced at 90 DPH (22 March 2019).

### 2.2. Experimental setup for strain comparison

The strain comparison experiment was undertaken using an array of 800-L polyethylene tanks with conical bases. Ambient condition seawater was supplied at 15–20 L $min^{-1}$. A small airlift within the tank provided directional water circulation to promote uniform swimming behaviour and concentrated uneaten food towards the centre drain. Uneaten food was collected on a mesh screen at the outflow. The tanks had opaque lids to reduce visual disturbance from above and were kept under ambient photoperiod (approximately 11 h light, 13 h dark).

Water quality was monitored regularly throughout all experiments. Temperature, pH and dissolved oxygen were measured twice a day in each tank, at 08:15 and 15:45 h, with a YSI 1020 PRO multimeter (Yellow Springs Instruments, Ohio, USA). Oxygen values were above the recommended minimum oxygen supply of 5 mg $L^{-1}$ for warm water finfish species and pH was within the normal variation of incoming seawater for the site (7.0–8.2). Nitrate, nitrite and ammonia were monitored once a week using an aquarist drip-test kit (API Aquarium Pharmaceutics), none of which registered significant values in terms of water quality, which is to be expected of a lightly stocked tank in a flow-through aquaculture system.

The diet used in the current trial was from an extruded pellet produced by Ridley Australia (Pelagica 3 mm, 50% protein, 18% fat, gross energy 22.8 MJ $kg^{-1}$, digestible energy 19.8 MJ $kg^{-1}$).

### 2.3. Pilot trial to establish feeding regimes

To evaluate whether feeding and digestive efficiency attributes changed during selective breeding, we compared the performance of both strains fed to satiation at two feeding frequencies. Prior to the main experiment a pilot trial was undertaken to gauge the maximum daily feed intake. Two tanks were stocked with 150 juveniles from the $F_3$ strain (mean individual weight 6.1 g) and over the following two days these were hand-fed manually four times a day (08:30, 10:30, 12:30, 14:30 h) to measure the quantity of food ingested. This trial also allowed the experimenter (J Schleyken) an opportunity to observe feeding behaviour, to optimise the feed-out technique and collection of uneaten pellets. It took approximately 2 min of hand-feeding to satiate the fish; after this time most pellets went eaten. Uneaten pellets from such a feeding event were concentrated in the outflow sieve within 5 min and could be collected throughout the day and stored in a freezer for later quantification. It was decided that the two feeding regimes for the main experiment should have the same daily start and end times, allow for maximum voluntary intake in any one feeding event, and differ only in the frequency of food administered (*hourly*: one feeding per 1 h; versus *bihourly*: one feeding per 2 h).

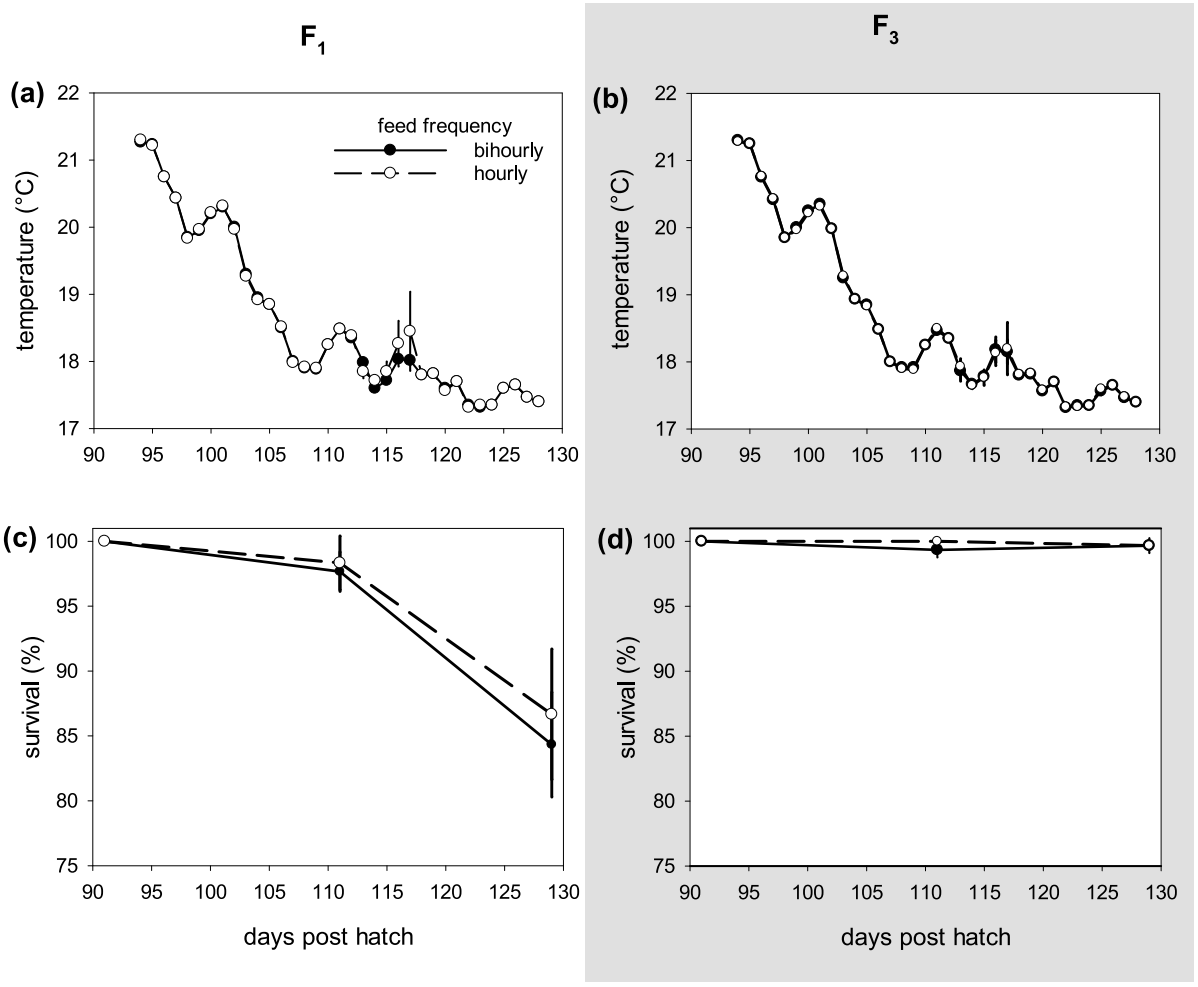


**Fig. 1.** Variation in rearing water temperature (a & b) and survival (c & d) of $F_1$ and $F_3$ generation Australasian snapper fed at hourly and bihourly frequencies. Data given as mean ± SD of replicate tanks ($n = 3$). Legend given in (a).

### 2.4. Main experiment

For the main experiment two factors were tested (strain, *$F_1$* versus *$F_3$*, and feeding frequency, *hourly* versus *bihourly*) with 3 replicate tanks for each combination (12 tanks in total). The endpoint of the experiment was set to be at least a doubling of body weight (which was estimated to take 6 weeks) with an inventory of each tank at the beginning, middle and end. To initiate the trial (22 March 2019) the bulk rearing tanks of each strain were lightly anaesthetised (isoeugenol 5 ppm, AQUI-S, Lower Hutt, New Zealand) and groups of individuals haphazardly captured in dip nets. Fish were then taken from the dip nets, imaged for individual identification (described below), weighed to the nearest 0.1 g (model HL-400, A&D Weighing, Adelaide, Australia) and added into the experimental tanks until 100 individuals per tank had been stocked (stocking density 0.7 kg $m^{-3}$). Fish were maintained on the pre-experiment feeding schedule for 96 h for all the juveniles, to adapt to the new tank environment and check there was no significant post-transfer and handling mortality. During this phase each tank was supplied a total of 20 g of feed per day (3–4% of tank biomass, spread over three feeding events per day) until 25 March 2019.

The following day the experimental feeding regimes started, with timings as follows: *hourly* from 08:30 to 15:30 (eight feeding events) and *bihourly* at 08:30, 10:30, 12:30, 14:30 h. Daily pellet quantities were pre-apportioned and were estimated to be in excess of that which the fish could consume. For a single event the experimenter would open the lid to a tank, add small portions of pellets from the daily allowance over approximately two minutes until the fish stopped eating and then move on to the next tank. The appearance of pellets in the outflow sieve and waning of feeding behaviours indicated that food was not being consumed. The tank array was fed within 20–25 min (depending on intake quantities). Uneaten pellets were collected from the outflow and frozen for later quantitation of intake. To determine the exact quantity of the surplus feed, uneaten samples were dried in a drying oven at 60 °C for 75 h and weighed. The dry weight was measured and converted back to an original pellet weight using an experimentally determined conversion factor.

To estimate survival, each tank was monitored daily for mortalities and moribund fish. Fish that died during the experimental period were counted but not replaced. Since most of the carcasses were damaged by cannibalism, weights and lengths of the dead fish could not be measured.

### 2.5. Fish phenotype measurements

Fish were measured and inventoried at three time points during the trial: beginning (22 March 2019, 91 DPH, 5–7 g body weight); mid (11 April 2019, 111 DPH, 7–11 g); and end (29 April 2019, 129 DPH, 11–15 g). On the measurement days, the fish were anaesthetised in the trial tanks (AQUI-S 5 ppm) before being more deeply sedated in a separate tank (AQUI-S 10 ppm for 5 min) for measurement of individual weight (to 0.1 g accuracy, scale type HL-400, A&D Weighing, Adelaide, Australia) and placed inside a custom-built imaging box with lighting, a

**Table 1**
Summary statistics of main experimental metrics of $F_1$ versus $F_3$ tāmure/Australasian snapper. Data given as replicate mean ± standard deviation.

| Strain | | $F_1$ | $F_1$ | $F_3$ | $F_3$ | MANOVA | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Feed frequency | | Hourly | Bihourly | Hourly | Bihourly | Time/age | | Strain | | Feed frequency | |
| Replicate tanks x ind. per tank | | 3 × 100 | 3 × 100 | 3 × 100 | 3 × 100 | P | $\eta_p^2$ | P | $\eta_p^2$ | P | $\eta_p^2$ |
| Days post hatch | | | | | | | | | | | |
| Survival (% from start date) | 91–111 | 98.3 ± 2.1 $^{B}$ | 97.7 ± 1.5$^{B}$ | 100.0 ± 0.0$^{A}$ | 99.3 ± 0.6 $^{B}$ | <0.001 | 0.86 | <0.001 | 0.86 | 0.246 | 0.08 |
| | 112–129 | 86.7 ± 5.0$^{C}$ | 84.3 ± 4.0$^{C}$ | 99.7 ± 0.6 $^{B}$ | 99.7 ± 0.6 $^{B}$ | | | | | | |
| Fork length (mm) | 91 | 59 ± 4$^{G}$ | 61 ± 3$^{G}$ | 65 ± 3$^{F}$ | 65 ± 3$^{F}$ | <0.001 | 0.56 | <0.001 | 0.98 | 0.316 | 0.10 |
| | 111 | 67 ± 8$^{E}$ | 67 ± 5$^{E}$ | 77 ± 5$^{C}$ | 79 ± 5$^{B}$ | | | | | | |
| | 129 | 75 ± 10$^{D}$ | 75 ± 6$^{D}$ | 85 ± 6$^{A}$ | 85 ± 6$^{A}$ | | | | | | |
| Body weight (g) | 91 | 5.1 ± 0.2$^{F}$ | 5.3 ± 0.1$^{F}$ | 6.3 ± 0.1$^{E}$ | 6.6 ± 0.1$^{DE}$ | <0.001 | 0.56 | <0.001 | 0.99 | 0.398 | 0.08 |
| | 111 | 7.1 ± 0.3$^{CD}$ | 7.3 ± 0.3$^{C}$ | 11.0 ± 0.2$^{B}$ | 10.8 ± 0.2$^{B}$ | | | | | | |
| | 129 | 10.6 ± 0.2$^{B}$ | 10.8 ± 0.5$^{B}$ | 15.2 ± 0.6$^{A}$ | 15.0 ± 0.3$^{A}$ | | | | | | |
| Condition factor | 91 | 2.46 ± 0.93$^{ABCDEF}$ | 2.36 ± 0.30$^{BDEF}$ | 2.31 ± 0.31$^{FG}$ | 2.42 ± 0.24$^{ABCDE}$ | <0.001 | 0.04 | 0.541 | <0.01 | 0.790 | <0.01 |
| | 111 | 2.25 ± 0.42$^{GH}$ | 2.35 ± 0.39$^{EF}$ | 2.40 ± 0.47$^{CDE}$ | 2.14 ± 0.16$^{H}$ | | | | | | |
| | 129 | 2.40 ± 0.62$^{ABCDEF}$ | 2.51 ± 0.89$^{AC}$ | 2.47 ± 0.47$^{AB}$ | 2.46 ± 0.70$^{ABCD}$ | | | | | | |
| CV weight (%) | 91 | 21.4 ± 1.1$^{B}$ | 22.6 ± 0.6$^{B}$ | 15.8 ± 0.5$^{D}$ | 16.2 ± 0.6$^{CD}$ | <0.001 | 0.93 | <0.001 | 0.97 | 0.109 | 0.22 |
| | 111 | 37.4 ± 2.6$^{A}$ | 38.7 ± 2.5$^{A}$ | 19.9 ± 2.6$^{BC}$ | 21.0 ± 1.8$^{B}$ | | | | | | |
| | 129 | 36.6 ± 2.9$^{A}$ | 38.4 ± 3.8$^{A}$ | 19.0 ± 1.4$^{BCD}$ | 20.2 ± 2.0$^{B}$ | | | | | | |
| Tank biomass increase (g per period) | 91–111 | 190.1 ± 1.5$^{C}$ | 185.5 ± 37.6$^{C}$ | 469.3 ± 24.9 $^{A}$ | 407.1 ± 7.4$^{AB}$ | 0.981 | <0.01 | <0.001 | 0.96 | 0.253 | 0.14 |
| | 112–129 | 218.0 ± 43.9$^{C}$ | 194.8 ± 44.2$^{C}$ | 410.7 ± 34.4$^{B}$ | 427.7 ± 22.8$^{AB}$ | | | | | | |
| Specific Growth Rate (% weight gain per day) | 91–111 | 1.67 ± 0.10$^{D}$ | 1.61 ± 0.19$^{D}$ | 2.78 ± 0.13 $^{A}$ | 2.43 ± 0.02$^{B}$ | 0.018 | 0.26 | <0.001 | 0.66 | 0.058 | 0.18 |
| | 112–129 | 2.21 ± 0.24$^{BC}$ | 2.15 ± 0.07$^{C}$ | 1.78 ± 0.09$^{D}$ | 1.85 ± 0.06$^{D}$ | | | | | | |
| Tank feed consumption (g per period) | 91–111 | 316.8 ± 22.8$^{DE}$ | 249.9 ± 35.9$^{E}$ | 421.9 ± 21.6 $^{AB}$ | 405.8 ± 9.6$^{BC}$ | <0.001 | 0.67 | <0.001 | 0.91 | 0.107 | 0.25 |
| | 112–129 | 340.2 ± 53.1$^{CD}$ | 294.1 ± 25.0$^{DE}$ | 459.9 ± 31.2$^{AB}$ | 464.7 ± 41.3$^{A}$ | | | | | | |
| Daily feed consumption (% body weight day$^{-1}$) | 91–111 | 2.24 ± 0.29 | 2.75 ± 0.29 | 2.67 ± 0.10 | 2.55 ± 0.04 | <0.001 | 0.96 | 0.491 | 0.06 | 0.162 | 0.20 |
| | 112–129 | 2.46 ± 0.37 | 2.93 ± 0.34 | 2.83 ± 0.10 | 2.71 ± 0.04 | | | | | | |
| Feed Conversion Ratio | 91–111 | 1.31 ± 0.18$^{BC}$ | 1.78 ± 0.54$^{C}$ | 0.90 ± 0.05$^{A}$ | 1.00 ± 0.04$^{AB}$ | 0.042 | 0.34 | <0.001 | 0.78 | 0.085 | 0.27 |
| | 112–129 | 1.37 ± 0.15 $^{BCE}$ | 1.83 ± 0.59$^{C}$ | 1.13 ± 0.14 $^{AB}$ | 1.09 ± 0.13 $^{AB}$ | | | | | | |

scale bar and digital camera (Panasonic Lumix DMC-GH4 SLR with H-X025 lens). The left side of each fish was imaged (with the scale displayed weight contained within the image) and the fish was then transferred back to the experimental tank. The images were later analysed with the Plant & Food Research Morphometrics™ software https://www.plantandfood.co.nz/page/morphometric-software-home/, which is able to derive fish fork length (to nearest mm) from images.

### 2.6. Calculation of performance characteristics and comparisons

Survival rate (% survival from start of trial) was determined as the number of survivors at each measurement interval divided by the initial stocking numbers. Specific Growth Rate (SGR, % body weight gain day$^{-1}$) was calculated using the formula SGR = $(\exp^{g} - 1) \times 100$, where $g = (\ln W_{T1} - \ln W_{T0})/T_1 - T_0$, $W$ = mean individual weight, and $T$ = time (days). Feed intake was computed as a daily intake relative to body weight (% body weight ingested day$^{-1}$), with daily body weight estimated via interpolation using SGR. The biological feed conversion ratio (BFCR) was calculated as the mass of feed consumed per measurement interval divided by the biomass increase. The coefficient of variation for weight ($CV_W$, %) was used to evaluate population size distribution, and fish condition evaluated via Fulton's condition factor $K = 100$ x $(W/L^3)$, where $L$ = fork length (cm).

### 2.7. Statistical analyses

Statistical analyses of all data collected over the course of the experiment were carried out in R (R Core Team, 2012). The data were analysed using a linear mixed-effects modelling approach to take account of dependence. Assumptions of normality were evaluated prior to conducting statistical tests. While the high sample size for the individual fish morphometric data made them suitable for parametric testing, the replicates could not be tested for normal distribution or homogeneity of variance owing to the low number of degrees of freedom. Results were analysed and reported using a three-factor model (*time/age*, *strain, feed frequency*) without consideration of interactions between factors (for simplicity). Differences between group means were evaluated using MANOVA and reported as $P$ values, while effect size (partial eta-squared, $\eta_p^2$) was used to estimate the relative importance of experimental factors in structuring the data. Post hoc testing was undertaken to identify significantly different group differences.

## 3. Results

### 3.1. Survival and weight gain during the experiment

The water temperature decreased during the course of the experiment, from 21.3 °C to 18.4 °C over the first 20 days of the trial, followed by a lower rate of decrease in the final 18 days (18.4 °C to 17.4 °C, Fig. 1a & b). The mean temperature over the trial was 18.6 °C ± 1.2 °C

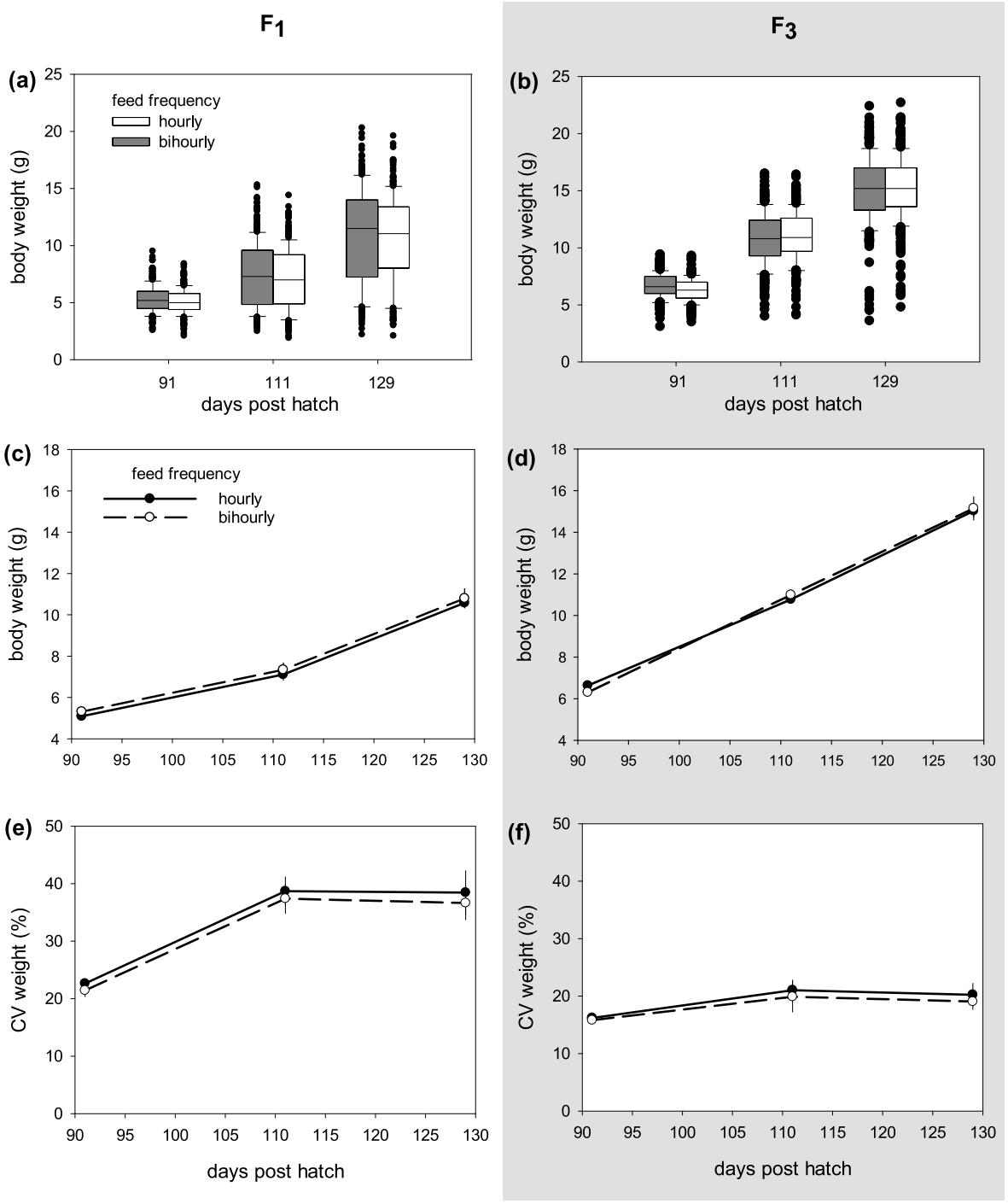


**Fig. 2.** Variation in body weight of $F_1$ and $F_3$ generation tāmure/Australasian snapper fed at *hourly* and *bihourly* frequencies. (a and b) box and whisker plots of all individuals (median, lower and upper quartile, 10th and 90th percentile); (c and d) mean body weight and (e and f) the coefficient of variation of body weight. Data in (c–f) presented as mean ± SD of replicate tanks ($n = 3$), legend given in (c).

(mean ± SD) for all treatments. Survival differed significantly and markedly between strains ($P < 0.001$, $\eta_p^2 = 0.98$, Table 1), with almost all $F_3$ fish surviving (<1% mortality) compared with 85–87% survival for the $F_1$ strain at completion of the 38-day trial (Fig. 1c & d). Despite being age matched, the $F_3$ strain were 16–23% larger than the $F_1$ strain at the start of the growth experiment (Table 1). The $F_3$ strain continued to exhibit superior weight gain throughout the trial, finishing with a 28–30% higher mean individual weight than the $F_1$ strain (Table 1, Fig. 2a–d). The variance in body weight per replicate tank was consistently lower for the $F_3$ strain throughout the trial ($CV_{weight}$ 16–21% for $F_3$ versus 21–39% for $F_1$, Fig. 2e & f). Inspection of the population distribution indicated a similar total range of body weights present at each sampling point; however, the $F_3$ strain tended to have more individuals clustered around the median over time, while the $F_1$ strain exhibited increasing kurtosis, with the lower 10% of the population barely changing in weight during the trial (Fig. 2a & b). The mean condition factor ranged from 2.25 to 2.51, but showed no correlation with age, strain or feed frequency (Table 1).

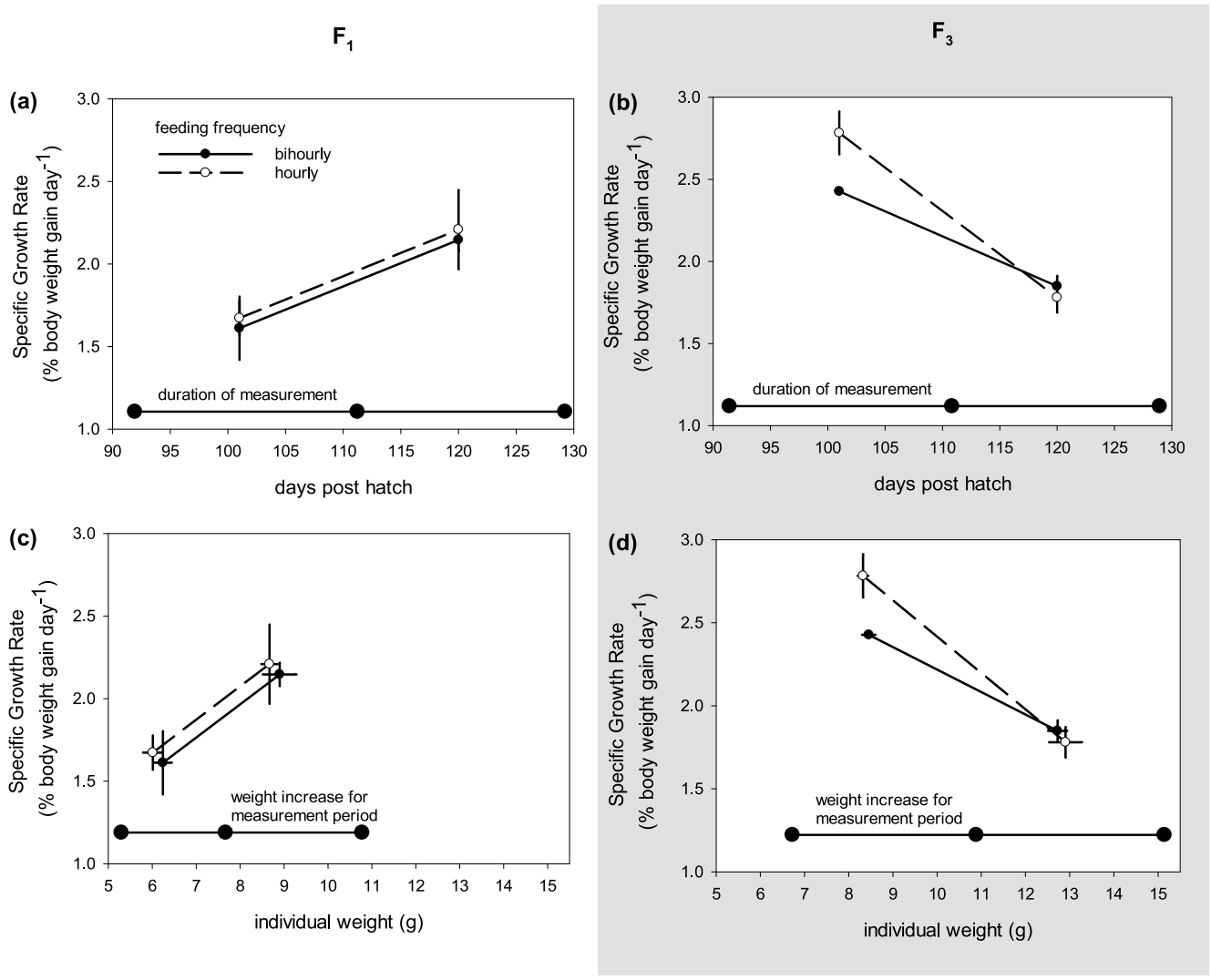


**Fig. 3.** Specific Growth Rate (SGR) of $F_1$ and $F_3$ generation tāmure/Australasian snapper fed at *hourly* and *bihourly* frequencies. (a and b) SGR versus time and; (c and d) SGR versus geometric mean individual weight. Data presented as mean ± SD of replicate tanks ($n$ = 3), legend given in (a).

### 3.2. Changes in SGR and FCR

While fish age significantly affected SGR ($P < 0.05$, $\eta_p^2 = 0.26$), strain had an even more pronounced effect ($P < 0.001$, $\eta_p^2 = 0.66$, Table 1). The $F_1$ strain exhibited an increasing SGR over time, while the $F_3$ strain exhibited the opposite (Fig. 3a & b). To account for ontogenetic differences in growth rate, SGR was plotted against geometric mean body size for the two measurement intervals. The geometric mean body size of $F_1$ fish in the second measurement interval (8.7–8.9 g) was comparable to that of $F_3$ strain fish in the first measurement interval (8.3–8.4 g), and at these sizes the growth rate of the $F_3$ strain was markedly higher than the $F_1$ (2.43–2.78 versus 2.15–2.21% day$^{-1}$, Fig. 3c & d).

The FCR values recorded over the two measurement intervals differed significantly between strains ($P < 0.001$, $\eta_p^2 = 0.78$), with the $F_3$ strain exhibiting superior feed conversion and lower variance ($F_3$ FCR range 0.90–1.13 versus $F_1$ FCR range 1.31–1.83, Table 1, Fig. 4a & b). Fish age also had a significant effect on FCR ($P < 0.05$, $\eta_p^2 = 0.34$), which increased over time, while feed frequency had no effect (Table 1). The mean ± SD FCR over the full 39-day trial were 1.80 ± 0.54 and 1.33 ± 0.04 for F1 *bihourly* and *hourly* (respectively), and 1.04 ± 0.06 and 1.00 ± 0.09 for F3 *bihourly* and *hourly* (respectively). These correspond to a 73% genetic improvement for *bihourly* feeding and a 33% improvement for *hourly* feeding.

Mean daily feed intake for the two measurement periods ranged from 2.24 to 2.93% body weight day$^{-1}$ (Table 1), with the trial mean similar for both strains, at 2.3% body weight day$^{-1}$. The main driver of variation in daily feed intake was time/age ($P < 0.001$, $\eta_p^2 = 0.96$) rather than strain or feed frequency ($P > 0.10$, Table 1). There was a sizable increase in feed intake for all treatments from days 103 to 108 (Fig. 4c & d), which occurred three days after a short spike in water temperature (Fig. 1a & b). After this time feeding returned to similar rates as those observed at the beginning of the trial. For both strains, the quantity of feed consumed on any given day was strongly correlated ($r^2 > 0.71$) for *hourly* and *bihourly* feed frequency treatments (Fig. 4e & f). There was evidence the $F_1$ strain were more sensitive to the effects of feed frequency, as feed intake was generally higher for *bihourly* than for *hourly* feeding for any given day (relative position of linear regression and 95% CI shown in Fig. 4e & f above the y = x reference line). As observed with all other traits measured in this experiment, the between-replicate variation in feed intake was much lower for the $F_3$ strain than for the $F_1$ strain (Table 1 and Fig. 4e & f).

## 4. Discussion

Here we report, from a comparison aquaculture performance, the results of attributes of $F_3$ versus wild-type juveniles of *C. auratus*, as well

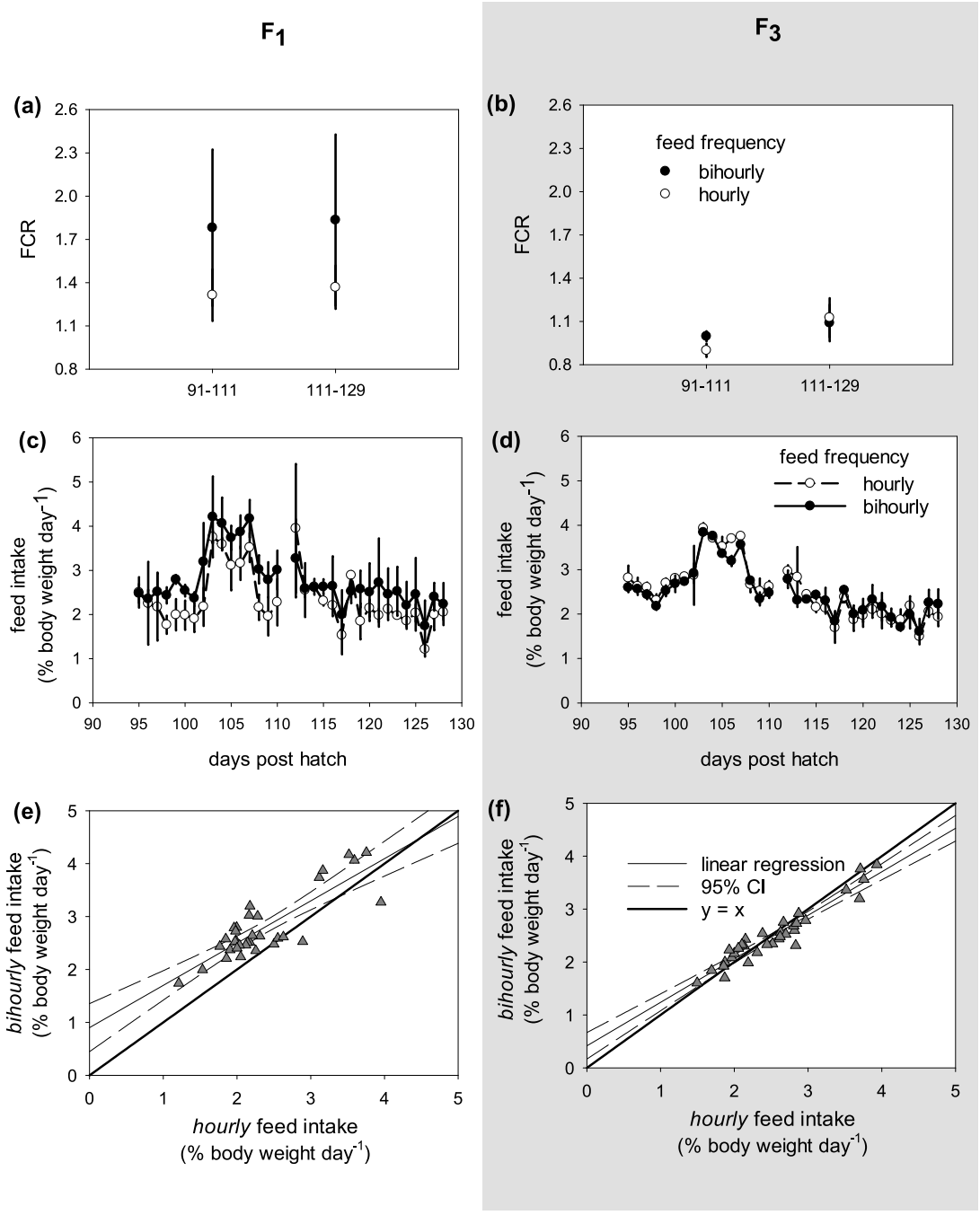


**Fig. 4.** Comparison of feeding and feed conversion of $F_1$ and $F_3$ generation tāmure/Australasian snapper fed at *hourly* and *bihourly* frequencies. (a and b) Feed Conversion Ratio for the two measurement periods and; (c and d) daily feed intake over time, and; (e and f) correlation of day-specific intake for *hourly* versus *bihourly* feeding ($F_1$ $r^2 = 0.71$, $F_3$ $r^2 = 0.91$). Data presented as mean ± SD of replicate tanks ($n = 3$), legends given in (b, d and f).

as the impact of feeding frequency, an important co-variate to understand when seeking to evaluate unconstrained growth. We found that the selectively bred *C. auratus* significantly outperformed the wild strain in all traits critical to aquaculture that we measured, including survival, growth and feed conversion. Survival rate was effectively fully improved in the $F_3$ strain (99.7% survival over 39 days versus 84–87% for $F_1$), while weight gain was 28–30% higher, and FCR improved by 33–73%. In addition, intra-cohort variation was considerably lower for the $F_3$ strain, and these fish were less sensitive to the effects of feed frequency.

The rates of improvement per generation observed in the current study align with figures reported for other species. The per-generation gains observed for *C. auratus* were approximately 10% for body weight and 5% for survival. In a review of selective breeding in aquaculture, Gjedrem and Robinson (2014) reported that average rates of improvement per generation were 13% for body weight and 6% for survival. A comparison of wild versus $F_5$ generation Atlantic salmon by Thodesen et al. (1999) recorded a 5% improvement in feed conversion efficiency per generation. In the current study FCR improved by between 11 and 24% per generation for *C. auratus,* depending on the feeding frequency tested.

Direct comparison of performance data from the present study with other studies of *C. auratus* is difficult given the relatively narrow size range evaluated (5–15 g body weight) and the general paucity of information about aquaculture of this species. The best comparison is with

the study by Booth et al. (2008), who measured performance of $F_1$ *C. auratus* over 42 days at 24 °C from approximately 5–20 g under different feeding regimes. The optimal feeding regimes reported by Booth et al. (2008) included >4 feedings per day. The current study used 4 and 8 feedings per day and occurred over 39 days at a mean temperature of 19 °C. The FCR of the $F_3$ strain were superior to the values reported by Booth et al. (2008) (<1.13 versus 1.29–1.42), and considering the substantial temperature difference between the studies, the weight gain potential demonstrated by $F_3$ *C. auratus* looks to be significantly improved against the $F_1$ tested in the present study as well as the $F_1$ studied by Booth et al. (2008).

The feeding frequencies tested in this study had no observable effects on growth rate or survival, which is consistent with results from previous studies of cultured juvenile *C. auratus* (Booth et al., 2008; Tucker et al., 2006) and juveniles of the related *S. aurata* (Goldan et al., 1998). Daily feed intake was variable and probably influenced by the changing water temperatures over the course of the trial; however, the replicate tanks tended to follow a common pattern day-to-day, with no observable differences between strains. While the feed intake of $F_3$ *C. auratus* did not vary with feed frequency, there was evidence that daily feed intake in the $F_1$ strain was consistently higher when fed bihourly versus hourly (four versus eight meals per day). The physiological reasons underpinning this observation in the $F_1$ are unclear, but from a breeding and production perspective, the reduced sensitivity of feed intake by selectively bred *C. auratus* to different feed-out rates is highly desirable, as is the much reduced intra-individual variability in feed intake that was observed between the $F_3$ strain replicate tanks. The lack of variation in feed intake between $F_1$ versus $F_3$ strains of *C. auratus* contrasts with the findings reported for the closely related *P. major* in Japan, where an $F_4$ strain had higher feed intake than a wild-type red sea bream (Ogata et al., 2002).

While the current study was relatively short, we were able to observe substantial improvements in all aquaculture performance attributes studied for selectively bred *C. auratus*, including elevated survival and weight gain, more efficient feed conversion and reduced variation between individuals. The additional growth performance exhibited by $F_3$ strains was not related to elevated feed intake, but rather more efficient nutrient conversion. The causes underlying the improved feed conversion efficiency with breeding are not particularly well understood, and could be related to numerous behavioural and physiological factors (de Verdal et al., 2018).

The improvements that we recorded in the selected strain in feed conversion ratio are likely to have resulted from domestication selection (Teletchea, 2015). This process can be powerful in changing the composition and performance of individuals by exerting strong selection pressure to only retain individuals that carry traits that makes them well equipped to thrive and survive in a new artificial environment. In addition to domestication selection, our strain was also exposed to genomic selection for improved growth, and this has likely added additional selection pressure on individuals and favoured those that not only survived well in the new environment, but only retained those that were also able to grow better than average (e.g. Baesjou and Wellenreuther, 2021; Wellenreuther et al., 2019). Together, domestication selection in concert with genomics-informed selective breeding for improved growth have resulted in an elite snapper strain with an improved feed conversion ability, and subsequent faster growth and survival rates, which makes this strain a promising candidate for future aquaculture ventures.

Taken together the data provided in this study and more generally what is known about the suitability of sparid species for aquaculture farming globally, there is significant scope for selective breeding to even further improve key production traits commonly cited as limiting factors to the development of *C. auratus* aquaculture in Australasia, namely growth rate and feed conversion.

## CRediT authorship contribution statement

**Damian Moran:** Data curation, Formal analysis, Visualization, Writing – original draft, Writing – review & editing. **Jonathan Schleyken:** Data curation, Formal analysis, Methodology, Visualization. **Christina Flammensbeck:** Data curation, Methodology. **Warren Fantham:** Methodology, Resources. **David Ashton:** Data curation, Software. **Maren Wellenreuther:** Conceptualization, Funding acquisition, Project administration, Supervision, Writing – original draft, Writing – review & editing.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data will be made available on request.

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