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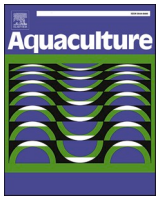

Generational breeding gains in a new species for aquaculture, the Australasian snapper (*Chrysophrys auratus*)

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ABSTRACT

Selective breeding for improved trait performance is a promising approach for developing new species for food production. Globally, a shortage of livestock species presents a significant bottleneck, and this is particularly pronounced for the aquaculture sector. In New Zealand, the Australasian snapper (*Chrysophrys auratus*) is a potential candidate for aquaculture, and a breeding programme was started in 2004. Here we assess the performance of the most recent F_4 cohort in terms of growth and survival against 1) previous generations and 2) unselected offspring from wild broodstock over the first 6 months. First, we detected generational gains over the entirety of the breeding programme in growth, averaging 11.4% for length and 81.1% for weight over 3 years, and detected a strong seasonal Specific Growth Rate (SGR) increase during summer and a general decrease of growth with age. Second, when growing the F_4 and F_1 cohort side by side, we found a consistent pattern of superior performance, less growth heterogeneity, and a higher condition factor within the F_4 population. Notably, these data revealed breeding gains of 4.9% in survival, 10.5% in length and 41.4% in weight for F_4 snapper over the first 6 months from hatching. Together these results indicate that domestication gains and genetic improvement can strengthen the potential of snapper as a candidate to diversify and grow aquaculture in New Zealand.

1. Introduction

Human population growth has increased demand for food products, which is expected to double in coming decades (FAO, 2018). Until recently, this demand has been mostly met by expanding the global agricultural area and by intensifying monoculture of a few terrestrial species. This has changed recently, however, and now aquaculture is the fastest-growing farmed food sector. Continued growth of aquaculture production is expected to come from the addition of new species and continued genetic improvement of species production traits via selective breeding programmes (Gentry et al., 2017; Garlock et al., 2020). Selective breeding programmes have in the last decade gained effectiveness due to advances and cost savings in genome sequencing technologies and downstream bioinformatic pipelines. This has allowed an increasing number of breeding programmes to apply genomic insights across all stages of the domestication process to optimise selective breeding decisions and to accelerate gains (Gjedrem et al., 2012; Gjedrem and Robinson, 2014).

The aim of selective breeding programmes is to select and breed superior animals so that resulting offspring will perform more efficiently under future production circumstances. During the last 40 years, it has been shown that well-planned breeding programmes can yield high rates of improvement for aquatic species, often yielding a 10% improvement rate or more per generation. The main reasons for the large genetic gains observed for aquatic species are their relatively high fertility and the natural existence of broad genetic variation for many economically important traits, which facilitates the application of high selection intensities during the selection process. The genomics revolution has provided refined methods to inform the breeding approach (Bernatchez et al., 2017), and an increasing number of genomics-informed breeding programmes have emerged (e.g. Valenza-Troubat et al., 2021). Genomics-informed technologies have the power to overcome many of the shortcomings of traditional breeding methods while controlling for inbreeding, and this can result in accelerated genetic gains and higher

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prediction accuracies than traditional pedigree-based methods (Boudry et al., 2021; Song et al., 2023; Yáñez et al., 2023).

Despite these recent advancements, breeding programmes continue to be a long-term investment that require significant resourcing in terms of staff hours and infrastructure. Further, the establishment and the continued maintenance of genetic diversity requires careful management and the development of protocols that control reproduction. In addition, parallel investments into methods that allow the development of techniques that can help to preserve genetic material, such as milt cryopreservation, are often needed to ensure the long-term viability of breeding programmes (Wylie et al., 2023). Trait selection also needs to consider potential trade-offs with other traits and needs to ensure that the overall resilience to stressors of the elite lines is maintained. In New Zealand, only one finfish species is commercially farmed, and this is Chinook salmon (*Oncorhynchus tshawytscha*), also referred to as King salmon (Symonds et al., 2019). This species has been introduced from North America and requires cool water for optimal growth (ideally <14 °C degrees year-round), and this can only be found around the South Island of New Zealand, not the North Island. With sea surface temperature rising in recent years, the availability of water space for New Zealand's only finfish aquaculture species has become even more restricted (Richter and Kolmes, 2005), and there is consequently a growing interest in the development of new species for aquaculture.

The Australasian snapper *Chrysophrys auratus*, known as tāmure by the indigenous Māori people of New Zealand, is a marine teleost of the family Sparidae, which can be found in the coastal waters of Australia, including Tasmania, and New Zealand. Snapper are of significant commercial, recreational, ecological and cultural importance, and a breeding programme was started in New Zealand in 2004 (Baesjou and Wellenreuther, 2021). Genomic-informed selective breeding was

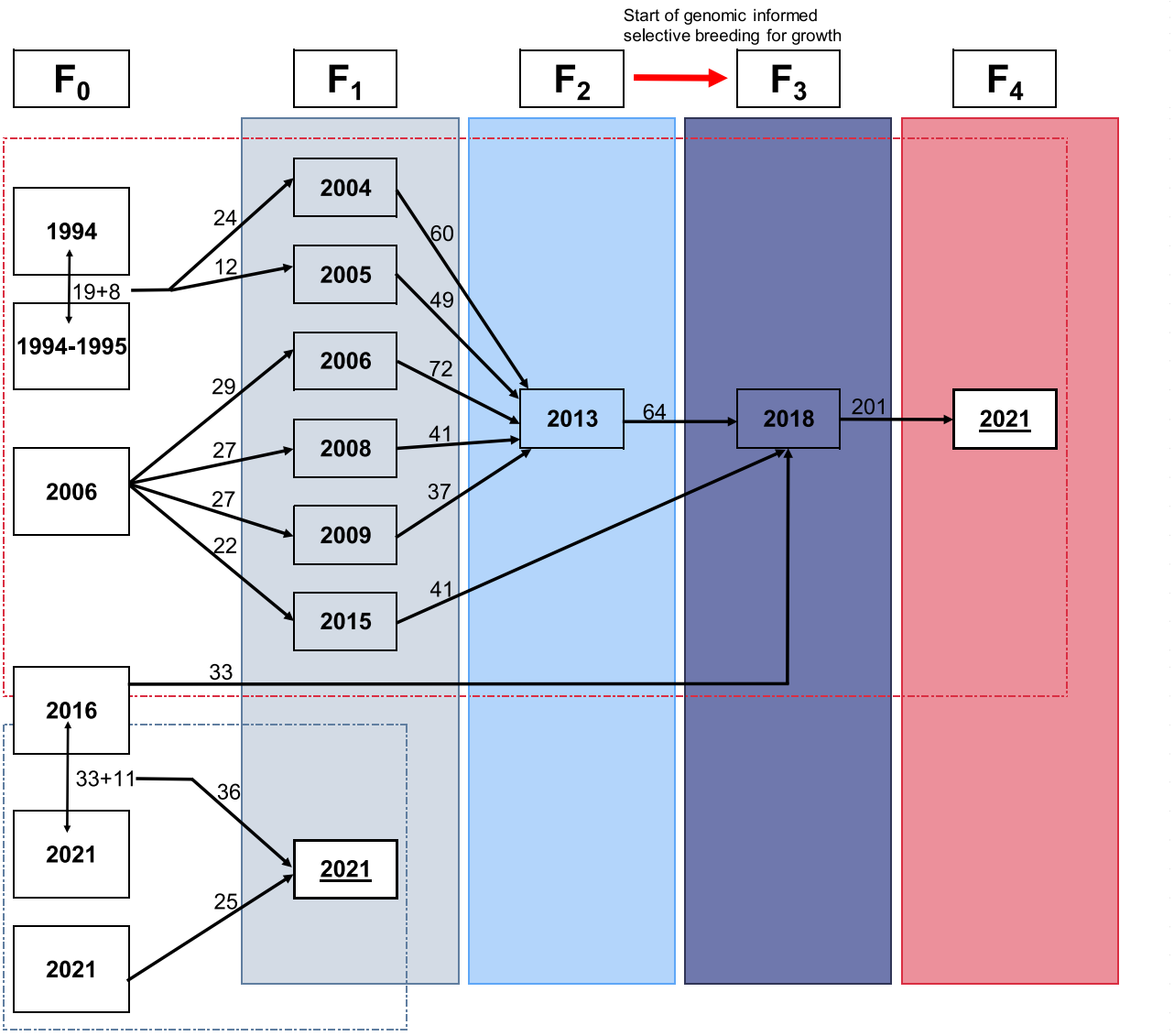

Fig. 1. Genealogy chart showing the history of Australasian snapper (*Chrysophrys auratus*) ●F_4 and ●F_1 cohorts used for this experiment. There are now four generations of snapper at The New Zealand Institute for Plant and Food Research Limited; these are indicated at the top of the figure and have been coded by colour. Six F_0 populations have been collected since 1994, with capture date indicated within the boxes below the generation. Some of these populations have since been combined, indicated by a double arrow between F_0 populations. The first offspring were generated in 2004, with incubation date indicated within the boxes below the generation. The parental links between generations are shown using a single arrow between the parent(s) and offspring with the number on the arrow representing the total number of broodstock present at the time of spawning. Those populations in relation to the ●F_4 cohort are displayed in a red dotted box, while those relating to the ●F_1 cohort used in this experiment are displayed in a grey dotted box. The red arrow linking ●F_2 to ●F_3 indicates the point in time when genomic-informed selective breeding for fast growth was introduced into the breeding programme. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

introduced to the programme in 2016 when selecting broodstock to produce the first F_3 population (Fig. 1) (Ashton et al., 2019a; Ashton et al., 2019; Wellenreuther et al., 2019). The key economic trait that is being selected for is growth, to yield an elite strain with superior growth qualities; something that has been achieved for its sister species the red sea bream, *Pagrus major*, and the gilthead sea bream *Sparus auratus* (Murata et al., 1996; Janssen et al., 2017).

In this study, we assess the performance of the most recent F_4 cohort in terms of growth and survival against 1) previous generations and 2) unselected offspring from wild broodstock over the first 6 months. This was first done by assessing the improvements in larviculture methods and generational breeding gains from F_1–F_4 snapper produced from 2005 to 2021. Second, we focused on assessing average growth and survival of F_4 and F_1 cohorts for the first 3 months in the hatchery. Finally, we used a controlled and replicated experiment to assess individual growth and survival of F_4 and F_1 cohorts between months 3 and 6. We discuss these findings in light of snapper as a potential candidate for aquaculture in New Zealand and take into account the expanding aquaculture space for this species owing to the rising sea temperatures.

2. Materials and methods

2.1. Historical overview of snapper production and breeding history

The breeding programme started with a New Zealand government funded research project in 1994 and involved the construction of a small aquaculture facility in Nelson which received a collection of wild snapper from the Marlborough Sounds and Tasman Bay (Te Tauihu region, South Island of New Zealand). The original F_0 broodstock from 1994 consisted of 24 snapper at the time they generated the first F_1 population in 2004 (Fig. 1). In 2005, a second F_1 population was generated from the same broodstock; however, six individuals of a separate F_1 generation were supplied from Moana Pacific and were added to the broodstock population prior to spawning, totalling 12 broodstock at this time. Subsequent F_1 populations were generated in 2006, 2008, 2009, and 2015 from F_0 broodstock collected from Tasman Bay in 2006. A total of 300 snapper from the F_1 populations, excluding those generated in 2015, went on to generate the first F_2 population in 2013. Up until then, no specific broodstock selection was implemented, meaning that for the generation of F_1 and F_2, the snapper lines were exposed only to domestication selection.

In 2016, genomics-informed selection was introduced into the breeding programme (see Ashton et al., 2019b; Ashton et al., 2019; Baesjou and Wellenreuther, 2021) with the aim of selecting the F_2 broodstock for enhanced growth. The selection of broodstock was based on genomically derived breeding values for length and weight traits, while taking co-ancestry between individuals into account. This led to a total of 138 individuals being selected to generate the first F_3 population in 2018 (33 individuals from the 2016 Tasman Bay F_0 population, 41 individuals from the 2015 F_1 population, and 64 individuals from the F_2 population), together with measurement of key breeding gains (Moran et al., 2023). The F_4 generation were produced in 2021 using a genomic selection approach (described below).

Together with genetic improvements, the larviculture and husbandry has evolved over the 17 years. The improvements in the larviculture and husbandry were based on research exchanges with Kindai University in Japan with the goals to transfer knowledge from the red sea bream breeding programme (*Pagrus major*) to the Australasian snapper (its sister species). Until then and prior to 2017 larval production of snapper was done using high density culture (up to 300 ind L^{-1}) at ambient summer water temperatures (ranging from 18 to 21 °C). Moreover, our larvae used to be supplied with live algae and enriched rotifers up to approximately 30 days post hatch (DPH), and enriched *Artemia salina* were supplied once larvae reach a notochord length of 5–7 mm (approximately 19–25 DPH) until they were weaned onto an extruded micro diet at 40 to 60 DPH. Following reciprocal visits with Japanese scientists, larviculture methods changed in 2017 to become more aligned with those of the Japanese red sea bream industry, where larvae are cultured at lower densities (< 20 ind L^{-1}), and in-tank heat exchangers are used to maintain temperature between 22 and 23 °C (discussed further below). The use of live algae was replaced with a concentrated algal paste and improvements have been made in the culture of rotifers and *Artemia*. In addition, automatic belt feeders have been introduced to continue delivering feed outside of working hours and allowing weaning to occur earlier. The rearing environments have also changed over time as the research hatchery moved to a new site and sea pen trials were undertaken. These changes were implemented and refined over time, and have not been assessed in isolation to quantify the impact of individual factors on fish performance.

2.2. Evaluation of breeding and production improvements over time

Changes in the growth performance over time were evaluated in two ways. Firstly, by comparison of historic data of cohort weight gain, specific growth rate (SGR), and thermal growth coefficient for F_1 to F_4 generation fish, and secondly, a controlled test of breeding gains alone by direct comparison of a F_1 versus F_4 populations reared concurrently under the same conditions (discussed next section). To analyse historic data, length and weight measurements from nine cohorts were compiled representing F_1 to F_4 generation fish. This data included 6 different F_1 cohorts, and 1 each of F_2, F_3, and F_4 cohorts. For seven cohorts' data were available for at least 3 years. Data filtering included knowing the sample was representative of the population and having at least 10 observations of length or weight at a given time point. Mean length and weight were plotted over time together with the water temperature. Generational differences in length and weight gain were plotted at the 6-month and 3-year time scales and tabulated as comparisons at similar time points. Growth data for F_4 snapper were only available for the first 6 months. The weight gain was converted to SGR (% weight gain day^{-1}) for each growth increment via computation of *G* (Crane et al., 2020), resulting in 75 discrete measurements. The relative importance of fish size, temperature and genetic origin in structuring the growth data was investigated via a Generalised Linear Modelling (GLM) approach.

2.3. Broodstock selection and generation of F_4 and F_1 cohorts for the controlled performance experiment

In October 2021, 201 individuals from the F_3 population were selected for broodstock based on genomically derived breeding values for improved growth, while accounting for co-ancestry. In short, genomic selection was applied to generate breeding values for individuals based on length by applying the Van Randen methodology (VanRaden, 2008) using a GBLUP in standalone Asreml 4.2, and population ID was fitted as the only fixed effect, i.e. the model was length ~ population_batch_ID + individual, where the individual was fitted as a random effect linked to the SNP derived genomic relatedness matrix. This model was run while applying a constraint on co-ancestry for all breeding candidates between 0.01 and 0.1. The resulting broodstock were split over four 5000 L tanks for spawning a F_4 cohort. In parallel, 61 F_0 wild and mature individuals from Marlborough and Tasman Bay were selected as wild broodstock, split over two 13,000 L tanks, and spawned to produce a F_1 cohort to use in comparison against the F_4 cohort. As it was the first time for the F_3 broodstock to reproduce (they were all 3 years of age), a proportion of the broodstock (~80%) were hormone treated with an intramuscular injection of human chorionic gonadotropin (Chorulon®, Intervet), at target dose of 600 IU kg^{-1} body weight, to facilitate spawning synchronisation and ensure a high contribution among individuals. The F_0 broodstock was caught from the wild, and was on average older than the F_3 broodstock, and thus received no hormone treatment owing to their vast breeding experience, and were left to spawn naturally. Egg collection began on 4 November 2021 and continued over a 5-day window. Approximately 134,604 eggs

were incubated to generate the F_4 cohort, and 115,240 eggs for the F_1 cohort. Eggs were incubated in one 5000 L tank per cohort. This resulted in approximately 21,374 F4 larvae, and 27,113 F1 larvae at the end of incubation.

2.4. Larviculture and rearing conditions of F_4 and F_1 cohorts

Snapper larvae were cultured based on the protocols reported by Moran et al. (2023). Prior to spawning, water conditions were kept as similar as possible between the broodstock populations. Once spawning commenced, the eggs were incubated at the ambient temperature of 16 °C to match that of the broodstock tank, and then slowly heated to 22 °C over the 10 days following hatching via an in-tank heat exchanger. The temperature was maintained at 22 °C until 59 DPH, at which point the ambient water exceeded 20°°C. The water supply remained at the ambient incoming temperature for the remainder of this study. Aeration during incubation was initially minimal and designed to gently circulate water within the tank, and increased over time as the larvae grew. Oxygen was added through a ceramic diffuser from 9 DPH onwards to maintain a dissolved oxygen concentration above 6.5 mg L^{-1}. pH was maintained between 7.5 and 8.0 via water exchange and aeration. Water quality parameters were measured twice daily using a YSI Pro1020 Dissolved Oxygen and pH Meter. Flow rate at incubation was ~3 L min^{-1}, and this was increased to approximately 6 L min-1 when the larvae were able to swim in a weak current (18 DPH) and in subsequent weeks, increased as required.

Larvae were initially fed rotifers (*Brachionus plicatitis*, L-strain) enriched with Selco® S.presso liquid live food enrichment by INVE Aquaculture from 4 to 37 DPH to maintain a target concentration of 15 ind mL^{-1}. In addition, Roti Green Nano® from Reed Mariculture was added to the tanks. *Artemia salina*, also enriched using Selco® S.presso, was feed from 24 to 49 DPH. The co-feeding periods were wider than those typically used for single spawn cohorts to allow for larvae of different ages to ween. From 26 DPH, a mixture of inert diets (NRD from INVE aquaculture and GEMMA Diamond from Skretting) was introduced in small amounts by hand and gradually increased over time to replace live feed. Feed size was increased gradually over time as the larvae grew and a mixture of feed sizes were presented to support the transition of larvae of different ages. Automatic belt feeders were installed on each tank at 36 DPH as the amount of live feed was reduced. The belt feeders were set with a measured amount of feed based on intake from the previous day appetite, water quality, and the length of daylight. Food was added to the tank over a 12-h period.

Growth was assessed regularly from 41 DPH, with sub-samples of 100 fish measured for length (fork length) and weight in most weeks. Density reduction of both F_4 and F_1 cohorts was required three times during the first 3 months (41, 69, and 75 DPH) to maintain a density below 12 kg m^{-3} within the tanks and between cohorts. Density reduction was done randomly, to ensure non-graded populations were maintained throughout the larval rearing period. Waste from each cohort was vacuumed into a sieve daily and inspected for mortalities. Total mortality data were collated for each of the first 3 months and percentage survival of each cohort calculated from the known population counts at the time of density reductions. At 3 months post hatching, both F_4 and F_1 cohorts were graded for deformities, with 7.7% and 5.6% of the cohorts being removed, respectively. After this, 225 individuals from each cohort were randomly allocated into tanks for a controlled growth experiment (see below).

2.5. F_4 vs F_1 controlled performance experiment

A controlled and replicated performance experiment was established to compare both growth and survival between the F_4 and F_1 cohorts over a 12-week period from 3 months post hatching onwards (9 February 2022–4 May 2022). Three replicate tanks (800 L) were stocked with either: a mixed cohort ($n = 25$ $F_4 + 25$ F_1 *ind* per tank); a single F_4 cohort ($n = 50$); or a single F_1 cohort ($n = 50$).

Growth data were collected at the beginning and end (3 and 6 months post hatching) of the experiment via a measurement of weight (g) and automated fork length (mm) calculation from images (Fig. 2). Images were captured of the left side of each individual, using a Panasonic Lumix DMC-GH4 camera, set within a custom-built light box following workflows similar to those outlined by Tuckey et al. (2022).In addition, individual identity data were extracted from each fish image using a biometric identification (bio-ID) model. These models use machine learning methods to detect the unique pattern of spots visible on the side of each snapper image, before applying pattern matching methods to identify pairs of images. These models allow consecutive sets of observations of the same individual, at different time points, to be linked giving personalised individual growth data within the population.

Five micron filtered, and UV-treated water was supplied to each tank at 8.5–12 L min^{-1}. Pure oxygen was injected into the header tank via a ceramic diffuser. Temperature and oxygen were measured twice daily using the YSI ProSolo Digital Water Quality Meter. Experimental tanks were cleaned every 3 days and purged twice daily for 30 s. All snapper were fed a mixture of Skretting Nutra RC 1.2 mm, 1.8 mm and 2.3 mm pellets to satiation. To assess mortality, all replicate tanks were inspected twice daily, and any mortalities recorded.

On completion of the experiment, growth data and images were again collected. In addition, all snapper were counted to assess any additional mortalities that may have gone unrecorded. The images were processed through the bio-ID model and used to calculate individual length and weight gains, along with individual survival over the course of the experiment.

Statistical analyses of growth and survival performance data were carried out in R (V4.1.2) (R Core Team, 2021) and using the tidyverse package (Wickham et al., 2019). To ensure that statistical tests were robust, the mean gains in length (mm) and weight (g) for each population were compared using a full linear mixed model with tank treatment (mixed or single cohort) as a random effect with the lmer function from the lme4 package (Bates et al., 2015). Plots were produced in R (v4.1.2) using tidyverse, ggpp (Aphalo, 2022), and RainCloudPlots (Allen et al., 2019).

3. Results

3.1. Generational breeding gains: domestication gains

Historical growth comparisons of nine cohorts (F_1 through to F_4 generation produced between 2005 and 2021), showed a general trend towards improving performance in terms of both length and weight gain (Fig. 3 A–D, Fig. 4 A–D). When compared to the F_1 generation, weight gain was improved in the F_2 generation at 6 and 12 months of age, after which point length data were collected (Table 1 and Supplementary Table 1). The 2–4% improvement of F_2 over F_1 performance was evident until data collection ceased at around 3 years (Supplementary Table 2).

3.2. Generational breeding gains: domestication plus genetic improvement gains

Comparisons of F_3 against F_2 populations displayed improvements at 6 months, with a 18.6% and 52.1% improvement in length and weight, respectively. At 1 year, improvements continued to be observed with 15.7% and 74.5% gains for length and weight, respectively. At 2 years, the data showed a 14.2% improvement in length, with no data being available for weight (Supplementary Table 2). No comparisons could be made at 3 years as there were no data for the F_2 cohort. Finally, a comparison of F_4 against F_3 at 6 months of age showed a 28.4% and 122.7% gain in length and weight, respectively (Table 2 and Supplementary Table 2). Over the duration of the breeding programme, F_1 to F_3, we observe an overall gain in length of 4.1% and 18.7% at 6 months

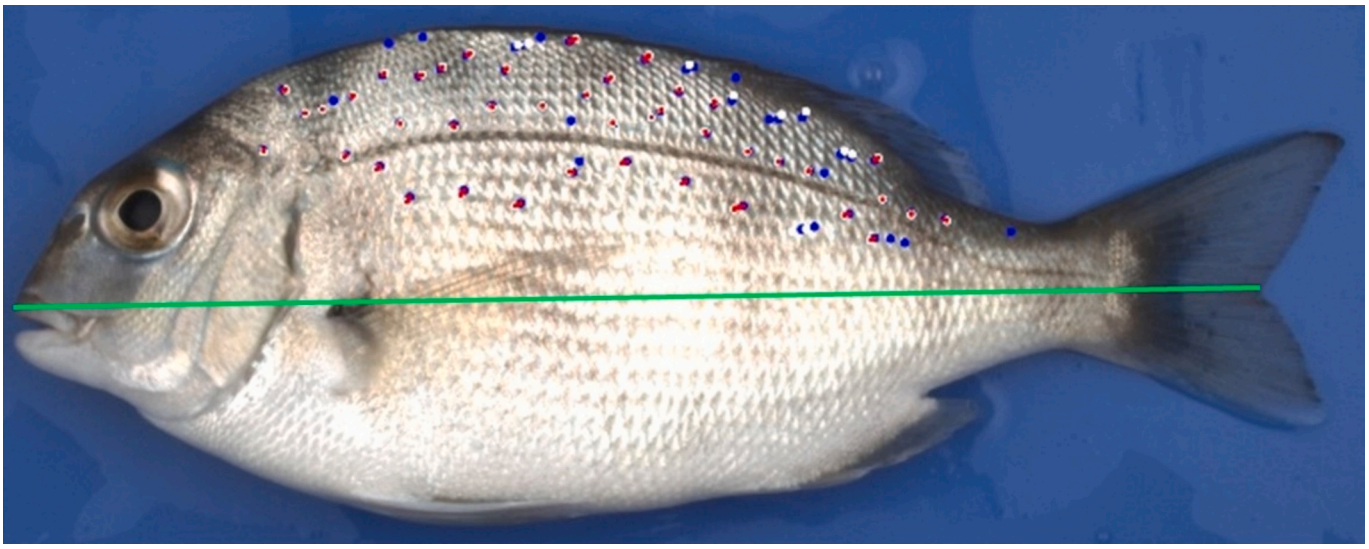

Fig. 2. Output image from the Australasian snapper (*Chrysophrys auratus*) biometric identification pipeline showing the spot detection from an image taken at the beginning of the performance experiment (white) and an image taken on completion of the performance experiment (blue). Red spots indicate matching spots, allowing the successful re-identification of the snapper. In addition, the morphometric benchtop pipeline has been overlaid to show the length output. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

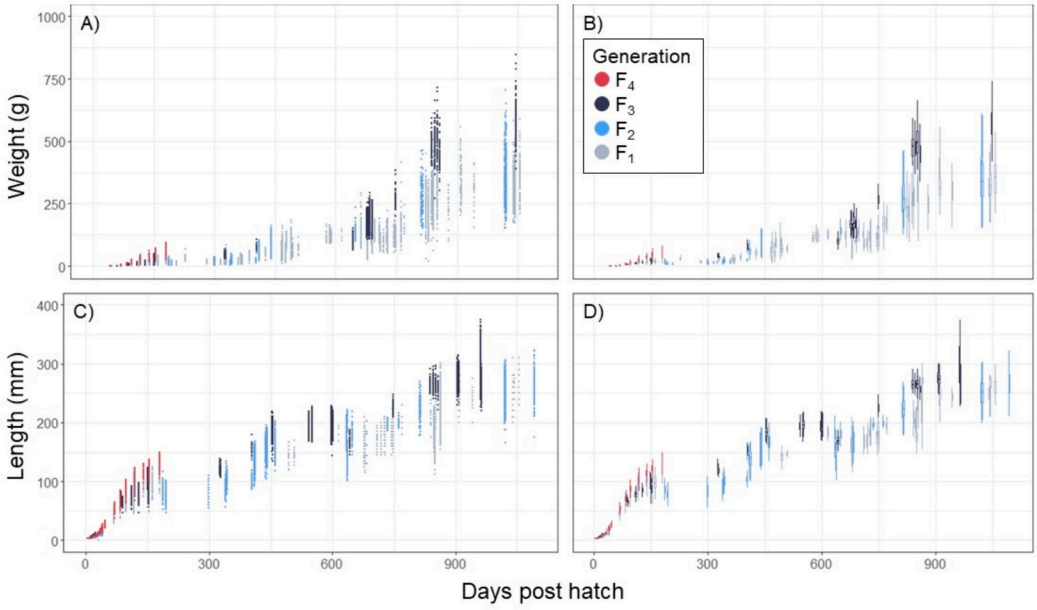

Fig. 3. A–D. Growth of Australasian snapper (*Chrysophrys auratus*) generations ●F_1 through to ●F_4 over the first 3 years post hatching with size (either length or weight) up the y-axis and days post hatch along the x-axis. Panels A and B show the weight distributions as a scatter plot and boxplot, respectively, while panels C and D show the distributions for length. Generations have been coded by colour, with ●F_1 as grey, ●F_2 as light blue, ●F_3 as dark blue, and ●F_4 as red. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and 2 years of age, respectively, with no data available to show breeding gains in length at 1 or 3 years. More pronounced breeding gains are displayed in weight with gains of 58.9%, 77.7%, 122.2%, and 65.7% at 6 months, 1, 2, and 3 years of age, respectively.

Data on weight gain from the nine cohorts were plotted alongside the water temperature to visualise growth trends, and growth-temperature dependencies (Fig. 5). Growth trends showed a significant seasonal pattern, with the majority of the weight gain occurring in months >15 °C (rising to a maximum between 20 and 23 °C in summer). In line with this, it was evident that little to no weight gain was occurring during the winter months (where water temperatures were ~ 9–12 °C), and in some cases there was minor weight loss recorded. Generational growth improvements over time were again evident for weight indicating both domestication gains, and genetic gains for the last two generations. For example, in 2022 the F_3 cohort took a little under 2.9 years (1046 days) to reach 572 g, whereas the first F_1 cohort spawned in 2005 took 2.4 years (879 days) years to reach 236 g. Additionally, a later generated F_1 cohort from 2010 took 2.9 years (1055 days) to reach 356 g, showing a slightly faster growth rate when compared to the F_1 cohort generated in 2005, while still slower growth than F_3 snapper. These improvements in F_1 cohorts are likely due to gains in hatchery and husbandry improvements over time.

Conversion of weight gain increments to SGR showed a strong trend of decreasing growth rate with age across generations, particularly when

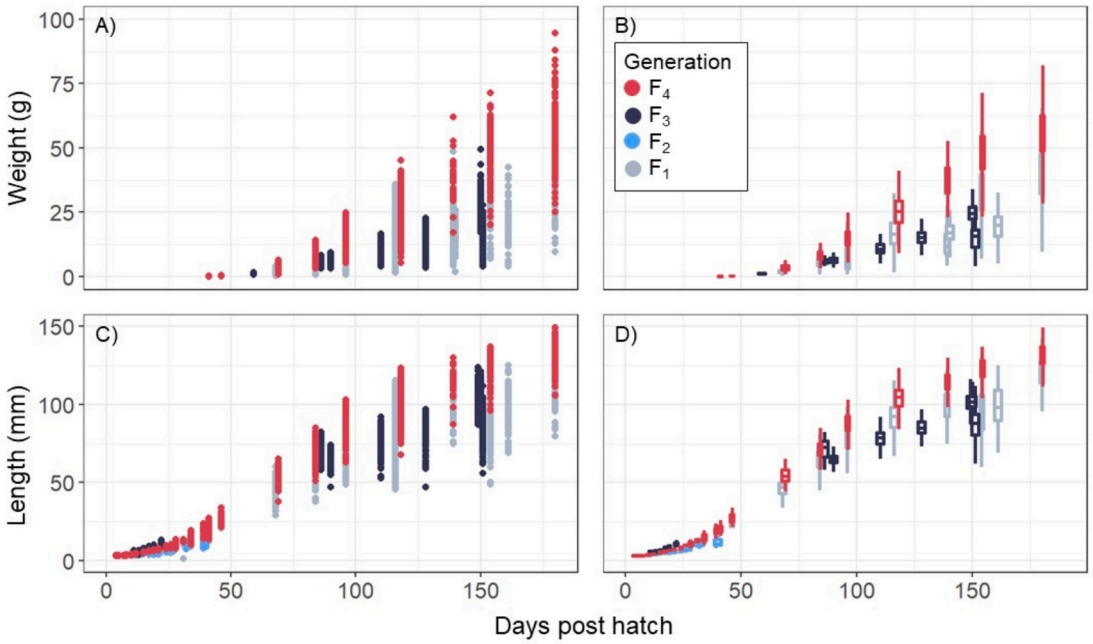

Fig. 4. A–D. Growth of Australasian snapper (*Chrysophrys auratus*) generations ●F_1 through to ●F_4 over the first 6 months post hatching with size (either length or weight) up the y-axis and days post hatch along the x-axis. Panels A and B show the weight distributions as a scatter plot and boxplot, respectively, while panels C and D show the distributions for length. Generations have been coded by colour, with ●F_1 as grey, ● F_2 as light blue, ●F_3 as dark blue, and ●F_4 as red. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Growth summary statistics for length (mm) and weight (g) for the first 3 years post hatching of Australasian snapper (*Chrysophrys auratus*) generations ●F_1, ●F_2, ●F_3, and ●F_4. The table shows snapper generations, the year cohorts were generated, the number of parents used to produce each cohort, the average length (mm, mean ± SE), the average weight (g, mean ± SE), for 6 months and years 1, 2, and 3 post hatching. The 2021 F_1 cohort has been highlighted grey to indicate that it is a separate cohort only used in direct comparison with the F_4 cohort.

			Length (mm)				Weight (g)			
Generation	Cohort	N of Parents	6 months	Year 1	Year 2	Year 3	6 months	Year 1	Year 2	Year 3
●F_1	2004	24							65.9 ± 3.0	
	2005	12				248 ± 3		14.8 ± 0.3	128.0 ± 1.7	337.5 ± 8.8
	2006	29			181 ± 2		8.8 ± 0.2	28.2 ± 0.8	120.4 ± 2.8	295.9 ± 6.9
	2008	27	98 ± 1			264 ± 3	20.4 ± 0.7	31.4 ± 0.4	125.8 ± 1.3	326.9 ± 3.3
	2009	27			198 ± 4	270 ± 2	18.2 ± 0.3	17.9 ± 0.8	172.5 ± 11.2	445.4 ± 12.5
	2015	22								
	2021	61	119 ± 1				39.5 ± 0.8			
●F_2	2013	259	86 ± 1	102 ± 1	197 ± 12	265 ± 2	16.5 ± 0.5	23.5 ± 0.6		
●F_3	2018	127	102 ± 0	118 ± 1	225 ± 1		25.1 ± 0.1	41.0 ± 1.0	272.2 ± 4.6	572.2 ± 5.8
●F_4	2021	201	131 ± 1				55.9 ± 0.8			

Table 2
Length (mm, mean ± SE), weight (g, mean ± SE) and population survival (%) for Australasian snapper (*Chrysophrys auratus*) ●F_4 and ●F_1 cohorts. Data are displayed at 1-, 2-, and 3-months post hatching with generational breeding gains calculated for length, weight, and survival at each month of age.

	●F4			●F1			Generational breeding gains		
Age (month)	1	2	3	1	2	3	1	2	3
Length (mm) ± SE	15 ± 0	54 ± 0	88 ± 0	14 ± 0	46 ± 1	79 ± 1	7.1%	17.4%	11.4%
Weight (g) ± SE		3.4 ± 0.1	15.0 ± 0.3		2.0 ± 0.1	9.9 ± 0.3		70.0%	51.5%
Survival %	93.7%	95.7%	99.9%	93.3%	91.9%	98.9%	0.5%	4.1%	1.0%

examining snapper that were less than ~25 g (Supplementary Fig. 1). For the subsequent analysis, data below 25 g were removed to focus on sizes more relevant to the on-growing phase of an aquaculture farming operation (due to this, 7338 data points were removed from a total data set of 14,971). The resulting dataset was used to generate a linear model incorporating SGR, weight and temperature as follows (SGR (% weight gain day^{-1}) = −2.679 * weight (g) +6.226 * temperature (°C) -1.131).

The model had a modest predictive value (adjusted $R^2 = 0.49$) and is graphically presented in Fig. 6A. The model predicts zero growth at 10.8 °C for a 100 g fish, and at 14.3 °C for a 500 g fish. Second, a generalised linear model was used to evaluate the relative importance of weight, temperature and generation in determining SGR (represented graphically in Fig. 6B and GLM results given in Supplementary Table 3). Temperature had a highly significant effect ($P < 0.001$) on variation in SGR, as did fish weight ($P < 0.05$, Supplementary Table 3). Compared to these factors there was no detectable effect of generation on the SGR

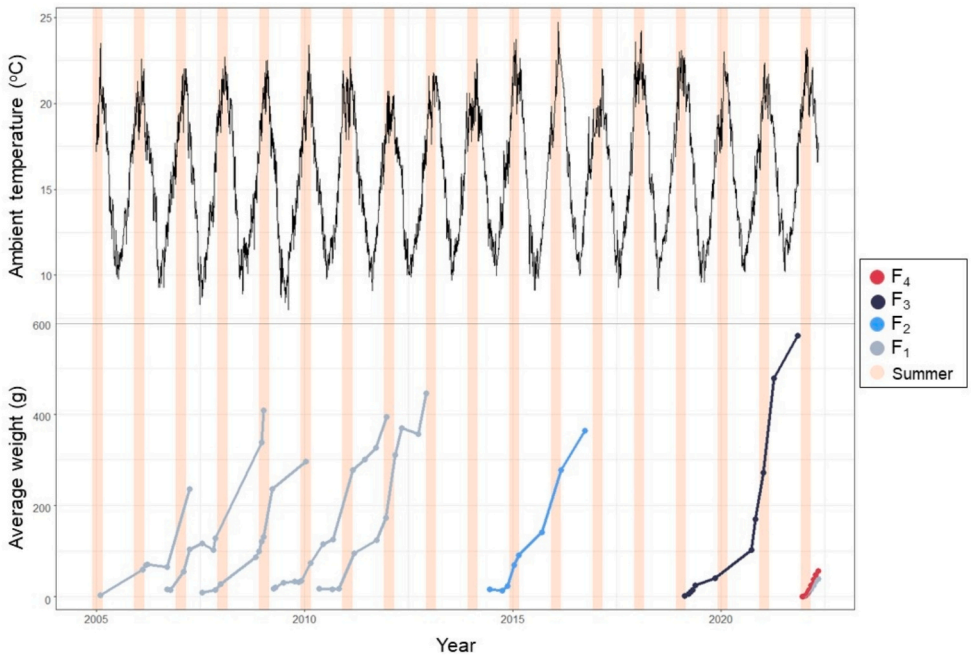

Fig. 5. Australasian snapper (*Chrysophrys auratus*) growth against ambient temperature from 2005 to 2021. The top half of the figure displays ambient water temperatures (y-axis) snapper were exposed to over time (x-axis). The lower half of the figure shows average growth curves for weight (y-axis) of 9 different cohorts of snapper of varying generations over time (x-axis). Generations have been coded by colour, with ●F_1 as grey, ● F_2 as light blue, ●F_3 as dark blue, and ●F_4 as red. In addition, New Zealand summer months have been highlighted in orange across the figure. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

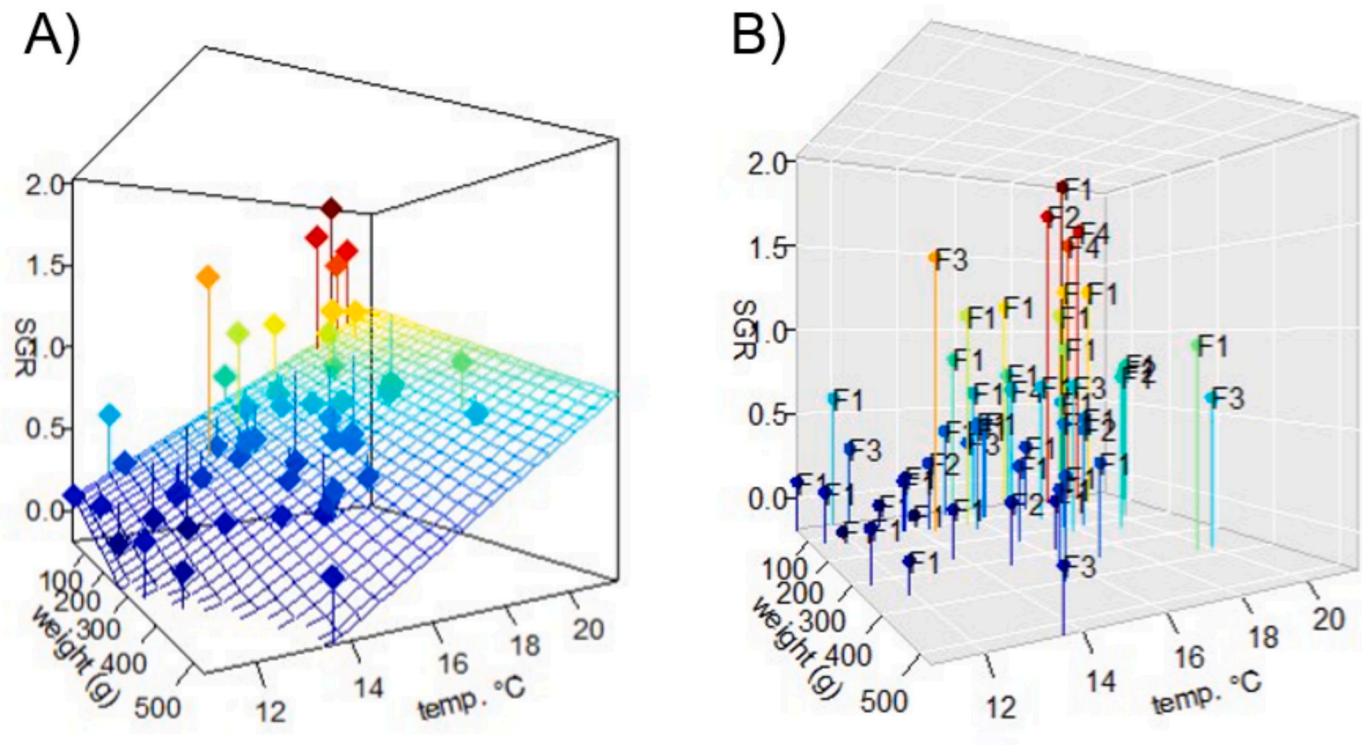

Fig. 6. A-B. Panel A displays Specific Growth Rate (SGR) of Australasian snapper (*Chrysophrys auratus*) against weight (g) and water temperature (°C) together with a linear model, as discussed Results. Panel B displays SGR against weight (g) and water temperature (°C) in addition to generations.

data set, however, there was evidence that the impact of breeding was becoming more important as the *P* value used to detect differences between F_1 (the reference generation) versus other generations was becoming more significant over time ($P = 0.99$ for F_2, 0.24 for F_3 and 0.15 for F_4, Supplementary Table 3). These findings reflect the challenge of detecting breeding gains over different generations across nearly 20 years of evolving husbandry methods and variable environmental conditions. This provides the rationale for a direct test of breeding gains by

comparing generations concurrently under standardised conditions.

3.3. Length, weight and survival of F_4 and F_1 cohorts during juvenile culture

Growth of the F_4 cohort over the first 3 months post hatching showed improvements in both length and weight compared to the F_1 cohort. Length measurements taken at the end of months 1, 2, and 3 showed a 7.1%, 17.0% and 11.4% breeding improvement, respectively (Table 2). Improvements were more pronounced for weight, showing a 70.0%, 51.5% increase at months 2 and 3, respectively. No weight measurements were recorded for the first month owing to the small size of the larvae (Table 2). Survival data from 14 DPH to 3 months demonstrated a total breeding gain of 4.8% from 14.4% mortality in the F_1 cohort to 10.3% in the F_4 cohort. Breaking these survival data down, there is a 0.5% breeding gain from 14 DPH to 1 month, 4.1% gain from 1 to 2 months, and a 1.0% gain from 2 to 3 months (Table 2).

3.4. F_4 vs F_1 controlled performance experiment

As discussed above, both length and weight of F_4 cohort were already significantly different to the F_1 cohort at 3 months post hatching ($P < 0.005$), therefore weight and length gain were compared over the performance evaluation period (3 months post hatch) rather than absolute length or weight.

Statistical testing, using tank treatment as a random effect, showed the F_4 cohort had significantly greater breeding gains over the F_1 cohort (Table 3), with 8.6% improvement from 40 mm to 44 mm length gained between months 3 and 6. ($P < 0.005$). Breeding gains were both significant and more pronounced with a 39.2% improvement from 29.6 g to 41.2 g weight gained between months 3 and 6 ($P < 0.005$). Condition factor (K) at the beginning of the experiment (3 months) was 2.17 for the F_4 cohort and 1.99 for the F_1 cohort, and already showed significant differences between cohorts ($P < 0.005$). On completion of the experiment (6 months), K had increased to 2.45 and 2.26 for F_4 and F_1 cohorts, respectively, but remained significantly ($P < 0.005$) higher in F_4 fish (Table 3). The coefficient of variation (CV) for weight remained lower for the F_4 cohort throughout the experiment ranging from 26.1 to 22.0% compared to 34.8–31.5% for F_1 (Table 3). The same trend was observed in CV for length (Table 3). The SGR calculated over the duration of the experiment and showed that the F_4 cohort have a higher SGR of 2.47 than the 2.16 of the F_1 cohort (Table 3).

Survival data between months 3 and 6 was calculated on completion of the experiment and displayed further breeding gains of 7.2% from 7.6% mortality in the F_1 cohort reduced to 0.9% in the F_4 cohort.

4. Discussion

Aquaculture, the farming of aquatic animals and seaweeds, is now the fastest growing food production sector in the world. Owing to the continuous growth of the human population, this trend will likely continue, and will require in-parallel improvements in the efficiency and sustainability of animal production systems. The application of genetic improvement has for decades been one of the most efficient tools to increase the biological performance of terrestrial animal production systems (Goddard and Hayes, 2009). However, while aquaculture breeding programmes lag behind terrestrial selective breeding practices (Gjedrem, 2012), several new breeding initiatives have started to diversify the available species pool for aquaculture (Yáñez et al., 2022). Such enhanced species diversity adds resilience to the aquaculture sector, for instance, in case of a disease outbreak, and increases the space utilisation that is possible, particularly if new species have different niche requirements to existing species. In New Zealand, no finfish species are farmed around the coast of the North Island and the only commercial aquaculture finfish species is Chinook salmon (*Oncorhynchus tshawytscha*). This species requires cold water to thrive (ideally <14 °C degrees year-round) (Symonds et al., 2019), and can consequently be grown only around the South Island. In recent years, increasing sea surface temperatures and periodic heatwaves have meant that some of the farming locations in the top of the South Island have become unsuitable for salmon (Broekhuizen et al., 2021). In fact, heatwaves in recent years have caused significant diseases, mortalities, and farm closures in the top of the South Island (Chiswell and Sutton, 2020). Developing a new species that can be grown in warmer waters and be farmed around the North Island, and around the top of the South Island is thus a pressing need for New Zealand to better utilise the marine food-growing capacity.

The breeding programme of the Australasian snapper (*Chrysophrys auratus*) in New Zealand started in 2004, with the goal of evaluating the potential of this species for aquaculture. The broodstock were obtained from the Marlborough Sounds and Tasman Bay, and the first two generations were generated using simple domestication selection. Following this, genetic screening of the population was added to reconstruct the full pedigree, as well as selection for improved growth performance, and the subsequent two generations were derived using genomics-informed selection for growth. During this time, significant genomic resources were developed to aid the efficient selection of superior breeders, including a genome (Catanach et al., 2019), linkage map (Ashton et al., 2019), regions in the genome corresponding to growth (Ashton et al., 2019a; Ashton et al., 2019; Ruigrok et al., 2022; Sandoval et al., 2022), transcriptome (Wellenreuther et al., 2019) and an understanding of the genomic changes occurring during breeding (Baesjou and Wellenreuther, 2021).

Generational comparisons were carried out in this study to quantify performance gains over the entirety of the breeding programme. It should be stated, however, that the data were not originally collected to carry out this comparison and therefore the dataset contains a certain degree of error. For example, the growth data were not always collected from tanks that had an even density across years and, given that our land-based facility uses ambient water, the differences in annual temperature profiles may have added additional noise to the data set. In addition, changes and improvements made to culture methods also created variation in growth of snapper batches over the years, which can be seen within the various F_1 batches. For these reasons, our

Table 3
Mean length (mm) and corresponding coefficient of variation (CV), mean weight (g) and CV, and condition factor (K) of Australasian snapper (*Chrysophrys auratus*) at the beginning (month 3) and end (month 6) of the controlled performance trial. In addition, Specific Growth Rate (SGR) was calculated from 2 to 3 months and then 2 to 6 months post hatching. Data is displayed per cohort (●F_4 or ●F_1) for both mixed cohort and single cohort treatments.

Generation	●F4						●F1					
Treatment	Mixed cohort		Single cohort		All replicates		Mixed cohort		Single cohort		All replicates	
Age (months)	**3**	**6**	**3**	**6**	**3**	**6**	**3**	**6**	**3**	**6**	**3**	**6**
Mean length (mm)	88	132	88	131	88	131	79	119	79	119	79	119
CV length	8.8%	7.7%	7.6%	5.7%	8.0%	6.4%	9.6%	11.6%	11.0%	10.0%	10.6%	10.6%
Mean weight (g)	14.98	56.94	15.15	55.91	15.10	56.26	10.21	40.73	10.22	39.29	10.22	39.78
CV weight	26.3%	23.0%	25.9%	21.4%	26.1%	22.0%	32.8%	33.6%	35.7%	30.2%	34.8%	31.5%
K	2.17	2.44	2.17	2.45	2.17	2.45	1.98	2.26	1.99	2.26	1.99	2.26
SGR (% weight gain/day) from 2 months	4.90	2.48	4.94	2.46	4.93	2.47	3.61	2.18	3.61	2.15	3.61	2.16

generational gain estimates should be taken with some degree of caution, as they by necessity represent measures that are impacted by multiple factors that have changed over time, including the change from domestication selection (first and second generation) and selective breeding for enhanced growth (third and fourth generation). Moreover, changes in culture methods not only improved growth of the snapper but made improvements in survivability of snapper between egg to weaned larvae. Survival has improved from <5% to survival ranging between 20% to 40% since these changes were implemented. The growth data across generations showed some up and downs, likely in part because of these aforementioned factors, but overall, there was a clear trend towards enhanced growth gains over the generations. This was particularly pronounced when comparing the F_3 with previous generations' growth profiles; and these growth gains stretched from the early stages of development all the way to when the snapper matured, which is around 3–4 years old. The same trend could be observed when looking at the generational comparisons of the F_4 cohorts, however, in this case the comparisons could only be carried out for the first 6 months.

When assessing the total growth gains that have been made in this selective breeding programme, it is important to note that the first two generations (F_1 and F_2) were obtained only through domestication selection. In other words, no selective pressure on improved growth or any other economically important traits was exerted during these early generations (Baesjou and Wellenreuther, 2021). The only selective pressure was survival in a new artificial environment, as only snapper that were able to mature in the land-based facility and under the rearing conditions were able to form the next generation of broodstock. Then in 2016, a genomics-informed selective breeding programme for enhanced growth (length and weight) was started, while taking co-ancestry into account (Ashton et al., 2019b; Ashton et al., 2019). The first selective breeding run was based on a genotyping by sequencing (GBS) dataset that was able to capture the pedigree in the facility (to reconstruct co-ancestry). This dataset was also used to calculate genomic best linear unbiased predictions (GBLUBs) for growth of the F_2 broodstock to generate the F_3 cohort (Moran et al., 2023). The most recent selective breeding run was based on GBLUBS derived from a custom multi-species single nucleotide polymorphism (SNP) chip (Montanari et al., 2023) to select the best broodstock snapper from several hundreds of candidates to a core broodstock of 138 individuals again, while controlling for relatedness in the spawning tanks. Our current growth improvements are as such capturing a combination of pure domestication selection followed by two generations of genomics-informed selective breeding, and thus, our growth gains of ~40% are very significant and high compared with growth gains achieved in other breeding programmes. For example, generational gains for weight were estimated to be 6% across five generations of selective breeding in Rainbow trout (*Oncorhynchus mykiss*) (Janhunen et al., 2012). Another study on the same species reported an average weight gain per generation of 11% also after 5 generations of selective breeding (Leeds et al., 2016). This is in line with reports from other studies on other salmonids for improved growth rates, and these data generally suggest that gains of 10% to 15% per generation are possible (Kincaid et al., 1977; Gjerde, 1986; Hershberger et al., 1990; Gjedrem, 2010). Similarly, significant generational weight gains were reported for other bream species, e.g. for the sister species of snapper, the red sea bream, a + 90% cumulative weight gain was recorded for the 7th generation (Kato, 2023). These large weight gains are probably related to growth having a high relative heritability compared with other traits, meaning moderate-high breeding gains can be achieved. Support for this in snapper has been demonstrated, and a study by Ashton and colleagues (Ashton et al., 2019) reconstructed the genomic relatedness matrix and found that the heritability (h^2) estimate for body weight was 0.51 in this species. However, it should be noted that the polygenic architecture of growth (Wellenreuther and Hansson, 2016), as well as trade-offs between growth and other traits (Schluter et al., 1991), such as maturation, can complicate efficient selection at times. Thus, careful selection and ideally a genomics-based approach to breeding should be taken to untangle potential negative trade-offs.

We have previously checked the performance of the selected vs unselected, unbred snapper by comparing 3-month-old F_3 vs F_1 snapper over a period of 1 month, to quantify breeding gains due to genetic selection of individuals showing superior growth. Specifically, growth and survival of these two cohorts were compared in relation to different feeding rates using a replicate tank design (Moran et al., 2023). This work showed a significant improvement in survival (100 vs 85% survival in the F_3 vs F_1 cohort, respectively) and in growth rate (28–30% higher growth in the F_3 cohort). Moreover, the study was also able to show that the growth improvement was in part related to an improved feed conversion ratio (FCR) in the elite F_3 cohort (FCR improvement of 33–73%) (Moran et al., 2023). In the current study, we go beyond these findings and add new data from the first 6 months of the most recent F_4 generation to quantify gains. This current study demonstrates an additional improvement, particularly in relation to growth across the evaluation period, of another ~13%. This is in line with what has been found for other teleost selective breeding programmes (Janssen et al., 2017), and indicates that snapper aquaculture shows strong promise to yield high cumulative breeding gains.

During the first 3 months, the elite F_4 line showed superior average growth rates compared with the F_1 cohort, and this pattern was consistent for each month that was sampled. This pattern was evident for both length and weight data, though it should be noted that no weight data could be collected during the first month as the size of snapper at that time was too small to gather accurate weight information (<0.10 g). The overall growth gain during the 3-month period significantly outperformed that of unselected snapper and means that the snapper can be moved more rapidly during the larval and juvenile phases, which is a time when snapper suffer the highest mortality. Survival rates between cohorts showed 4.81% gain in survival over the first 3 months (excluding the first 14 DPH, where survival could not be reliably quantified). All F_4 and F_1 snapper were fed ad libitum during the first 3 months, and while it was clear that the F_4 cohort were able to grow faster, our work is unable to provide insights on whether this was caused by higher feeding rates, better FCRs, or both. Future work to measure FCRs during these early stages could reveal the relationship between these traits, although the size limitations and higher fragility of snapper will make such experiments challenging.

The replicated growth experiments were able to provide detailed individual growth and survival data for snapper from months 3 to 6. Again, growth was significantly enhanced in the F_4 cohort compared to the F_1 cohort, with a difference of 11.4% for length, and 47.7% for weight at the beginning of the experiment (3 months). On completion of the experiment (6 months), no significant differences were seen between snapper of the same generation raised in either a mixed or single cohort, therefore data has been collapsed and was reported across all replicates, by generation (F_4 against F_1). This result means that future trials could confidently employ a mixed cohort approach without any negative consequences arising from the mixing, as long as the individual fish can be traced over time. Individual tracking of individual fish has become easier due to improved biotechnical approaches including the refined use imaging techniques to identify and track individual fish (Fu and Yuna, 2022). Our data also revealed a significant improvement of 10.5% for length and 41.4% for weight of the F_4 cohort. Achieving such rapid growth early on will translate into the snapper being able to be moved out to the sea pen for grow-out at an earlier time. Snapper are spring spawners and an early transfer to the sea pen would mean that the young snapper could benefit for longer from the warm summer temperatures to put on weight before the winter season, which is a season where high mortalities are seen among first-year snapper. Future work to spawn captive broodstock outside of their natural spawning season may also enhance initiatives for the early supply of snapper fingerlings to sea pens. Again, all snapper were fed ad libitum, so it is unclear whether higher feeding rates, FCR, or both, were implicated in the faster growth rates. However, given that previous work has demonstrated improved

FCR rates in F_3 snapper compared with unselected snapper (Moran et al., 2023), it seems likely that improved FCR rates have also contributed, at least in part, to the improved performance of the F_4 cohort.

Condition factor (K) at the beginning of the experiment was already significantly different at 2.17 and 1.97 for F_4 and F_1 cohorts, respectively. This was the same on completion of the experiment with K calculated as 2.45 and 2.26 for F_4 and F_1 cohorts, respectively. This indicates that both cohorts were of excellent quality entering the experiment and remained so on completion. In addition, K tells us that the F_4 cohort were heavier than the F_1 cohort at both time points. Comparisons of the CV in length and growth showed that the F_4 cohort had an overall tighter distribution for these growth variables, indicating a reduced rate of population heterogeneity. This finding is in line with expectations for species that are bred for improved performance, as this exerts directional selection on the population, which is a known factor that reduces genetic and phenotypic variability (Bulmer, 1971). This side effect of selective breeding for directional gains is a desirable output for many production scenarios, however, simultaneous loss in genetic heterozygosity needs to be carefully checked over time to ensure that this loss does not outweigh gains in phenotypic traits and greater trait homogeneity. Benefits arising from more uniform population growth distributions, for example, allows managers to move cohorts simultaneously to a larger feed pellet size, which cannot be done in a synchronised manner if there is large growth heterogeneity (in that case, different feed sizes need to be administered at the same time). Finally, we were also able to measure survival rates, and these showed that, in addition to gains in survival between 14 DPH and 3 months, there were also gains between months 3 to 6, with a 7.2%, and a 13.5% gain overall from 14 DPH to 6 months. Measuring survival differences during this critical time will be an important goal for the future to evaluate potential survival gains in the selected line.

Given that snapper is, like many other bream species, a mass-spawning species (Basurco et al., 2011), future efforts need to ensure that the genetic diversity is maintained at appropriate rates for sustaining the long-term resilience and health of a breeding programme. Previous work has shown that inbreeding has been low and that genetic diversity in snapper is generally high (Ashton et al., 2019b). However, with sustained selection for economic traits such as growth, genetic diversity needs to be maintained and the genetic variance-covariance matrix with other traits needs to be accounted for, to ensure no future high inbreeding loads and trade-offs with survival are produced as side effects of breeding (Stearns, 1989). Trade-offs occur when a beneficial change in a trait is linked to a detrimental change in another trait and is something that some current breeding programmes are actively trying to address to increase resilience and survival (Gallardo-Hidalgo et al., 2021). To support the efforts to maintain low rates of inbreeding and to select the optimal breeding individuals to mitigate potential trade-offs, our group has recently started to develop cryoprotection techniques for the long-term milt storage of elite breeders, so that this can be used to re-introduce diversity from past generations (Wylie et al., 2023). This work will continue and is expected to expand to explore techniques to induce sterility as a measure to address genetic introgression between escapees and wild individuals. It should be noted, however, that while the re-introduction of old genetic diversity through sperm cryopreservation may be one strategy to enhance the genetic diversity of the elite line, this measure needs to be carefully balanced against any losses occurring from the mixing with individuals that have not been selected as strongly for trait improvements. Another effort has been to cross wild snapper into the F_3 broodstock to introduce novel genetic variants into the breeding programme, in an effort to sustain high genetic diversity in the breeding lines. Genetic evaluations of the contribution of wild F_3 snapper to the most recent F_4 cohort will be carried out in the future using whole-genome information.

In conclusion, with growing pressures from climate change, disease outbreaks, market fluctuations and other disturbances, species diversification has become one of the most prominent aquaculture development strategies widely endorsed in the policy and scientific communities. In New Zealand, new species are urgently needed to diversify space use and to add resilience to the sector, and this is particularly pressing now with the increasing pressures from climate change. It has become clear that in the near future, aquaculture will face substantial challenges related to climate changes, e.g. increases in water temperature, which may affect stability and sustainability of this activity (Callaway et al., 2012), both in New Zealand (Chiswell and Sutton, 2020) and on a global level (Grant, 2017; Froehlich et al., 2018; Calado et al., 2021). New species that are more resilient to climate change thus provide a critical next step to not only ensure sustained food production but also to ensure there is a fit between animal needs and welfare and the locations that are used for production.

Ethics statement

This project operated under the conditions of animal ethics application AEC-2021-PFR-05, approved by the Animal Ethics Committee at the Nelson Marlborough Institute of Technology (Te Pūkenga), along with fish-farm licence FW208.03.

CRediT authorship contribution statement

Georgia Samuels: Data curation, Formal analysis, Investigation, Methodology, Project administration, Writing – original draft, Writing – review & editing. **Liam Hegarty:** Investigation, Methodology. **Warren Fantham:** Investigation, Methodology. **David Ashton:** Data curation, Formal analysis, Investigation, Methodology, Resources, Software. **Julie Blommaert:** Formal analysis, Investigation, Writing – original draft. **Matthew J. Wylie:** Investigation, Methodology, Writing – original draft. **Damian Moran:** Conceptualization, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft. **Maren Wellenreuther:** Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing – original draft, Writing – review & editing.

Declaration of competing interest

None.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.aquaculture.2024.740782.

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