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Combining ability and heterosis for growth and survival in interspecific hybrids of *Tor soro*, *Tor douronensis* and *Tor tambroides*

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Abstract

The Indonesian mahseer (*Tor* sp), including *Tor soro* (TS), *Tor douronensis* (TD), and *Tor tambroides* (TT), are local fish with high economic, cultural, and conservation value. Domestication efforts are underway, and breeding programs to support aquaculture are anticipated. This study, conducted at the Research Center for Applied Zoology in Cibinong, Indonesia, aimed to explore the combining ability and heterosis of growth-related traits and survival rate of populations consisting of interspecific hybridization of these species at the early life stage. A complete diallel crossing resulting in nine combinations, three intraspecific and six interspecific hybrid populations, was carried out. The total body weight, body length, and survival were measured following the larval rearing for four months. Growth-related parameters including final weight, final length, absolute growth weight, absolute growth length, specific growth rate of weight, specific growth rate of length, and survival rate were recorded. Combining ability was estimated using griffing approach method 1 and model 1, in which direct hybris, reciprocals, and parental populations were involved. Mid-parent heterosis (MPH) and better-parent heterosis (BPH) were estimated. The results showed significant differences in growth-related traits and survival among the hybrid combinations. General combining ability (GCA), specific combining ability (SCA), and reciprocal effects were significant ($p < 0.001$–$p < 0.01$ in most of the traits). The GCA, SCA, and reciprocals explained 69.12%–83.47%, 4.84%–20.74%, and 8.17%–18.34% of phenotypic variation, respectively. The GCA variances were more remarkable than those of the SCA for most growth-related trait parameters but not for survival. The TT was the best combiner for growth and survival, followed by TS for survival and TD for growth. Based on MPH and BPH, the hybrid combination TT × TD performed best for growth-related traits, with MPH ranging from 5.31% to 14.64%. The performance of direct hybrids differed from their opposite, indicating the significant effect of the reciprocal. Based on the GCA to SCA variance ratio, selective breeding exploiting the additive genetic variance would be effective for long-term genetic improvement. In contrast, a hybrid combination of TT × TD and TD × TS could be recommended for short-term breeding programs.

Keywords: Combining ability, Heterosis, *Tor* spp, Interspecific hybrid

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Introduction

Indonesia's inland waters possess a rich diversity of freshwater fish, with approximately 1,032 species identified in Western Indonesia and Sulawesi (Kottelat & Whitten, 1996). The Indonesian mahseer (*Tor* spp) is of paramount importance, holding significant economic, cultural, and conservation value. Three *Tor* species, *Tor soro*, *Tor douronensis*, and *Tor tambroides*, are found in areas such as Java, Sumatra, and the Kalimantan Islands. Due to their high economic value, these mahseer species have been extensively exploited in the wild, leading to declining natural populations and habitat quality. Efforts to domesticate these species are underway to facilitate their farming and help safeguard their threatened natural stocks (Gustiano et al., 2013; Ingram et al., 2007).

Several phenotypic traits have been characterized as part of the domestication process. *T. tambroides* stands out for its significant body size, with individuals weighing up to 20 kg in the Bukit Batikap area of Central Kalimantan. In the same region, residents have captured fish weighing as much as 50 kg (Haryono & Subagja, 2008). In the Kayan Mentarang National Park in East Kalimantan, *T. douronensis* has an average body weight of 3–5 kg, while *T. soro* weighs less than 10 kg. The average broodstock fecundity is reported as 3,162 eggs/kg for *T. tambroides* and 3,304 eggs/kg for *T. douronensis* (Ingram et al., 2007). Haryono (2006) reported that *T. tambroides* with weights ranging from 5,200–8,700 g and 64–89 cm lengths produced 3.125–8.201 eggs. Additionally, various zootechnical parameters such as fertilization rate, hatching rate, and early-stage growth have also been documented (Kusmardani et al., 2021).

Following domestication, the next step in transitioning a wild fish stock into a farmed fish involves implementing a breeding program. This research provides valuable insights that could guide future breeding programs. Currently, most traditional breeding programs employ either selective breeding or crossbreeding methods. The decision between the two depends on the genetic composition of the population. Selective breeding is more effective when the general combining ability (GCA) proportion is significantly greater than the specific combining ability (SCA) components and vice versa (Fasahat et al., 2016). The assessment of GCA and SCA becomes more crucial when the genetic material consists of multiple lines, whether they are strains, populations, or species.

Combining ability is used to evaluate the genetic architecture underlying phenotypic traits, which helps formulate optimum breeding strategies to harness the genetic potential of a population. Combining ability comprises GCA and SCA. GCA refers to the average performance of a line in hybrid combinations, while SCA reflects the relative performance of specific cross combinations compared to the overall crosses. Genetically, GCA is associated with additive genetic components, while SCA deals with non-additive genetic components (Fasahat et al., 2016). Another related concept is heterosis, which measures the deviation in hybrid performance from their parental lines. Two common types of heterosis are mid-parent heterosis (MPH) and better-parent heterosis (BPH). MPH compares hybrid performance deviation from the average of their parental lines, while BPH measures the deviation from that of the better parent. Due to its predictive nature, combining ability and heterosis analysis is typically conducted at the early stages of establishing a breeding program (Fasahat et al., 2016, Luo et al., 2014).

In the GIFT tilapia breeding program, for example, selecting selective breeding to enhance growth traits was based on evaluating the combining ability components of eight tilapia strains. Some specific crosses showed positive heterosis, but overall, general combining ability played a more significant role in controlling the growth traits in tilapia (Bentsen et al., 1998). A similar pattern was observed in a study with an interspecific hybrid of channel catfish (*Ictalurus punctatus*) and blue catfish (*Ictalurus furcatus*) (Bosworth & Waldbieser, 2014), and a hybrid of female striped bass (*Morone chrysops*) and male striped bass (*Morone saxatilis*) (Wang et al., 2006). Following an evaluation of the relative magnitude of GCA and SCA in interspecific hybrids, Bosworth & Waldbieser (2014) suggested that improvement in growth and carcass traits in the hybrid of channel catfish × blue catfish would be more optimal using selective breeding. A similar case was applied for growth improvement in striped bass hybrid (Wang et al., 2006). Conversely, following the evaluation of GCA and SCA in a synthetic population consisting of five common carp strains (*Cyprinus carpio*) (Ariyanto et al., 2022), and four genetically distant populations of gourami (*Osphronemus goramy*) (Sularto et al., 2017), crossbreeding has been recommended as an effective way of genetic improvement for growth rate. These previous studies showed variations in genetic architecture underlying the phenotypic expression of important traits between species and between traits. Furthermore, a more complex combining ability pattern was observed in a study with northern quahog, *Mercenaria mercenaria*, in which the general combining ability of growth and survival changed at different life stages (Camara et al., 2006). In the present study, we report an analysis of combining ability and heterosis in a population consisting of three interspecific hybridizations involving three species of the Tor Genus: *T. soro*, *T. douronensis*, and *T. tambroides*.

Materials and Methods

Fish

The study was conducted at The Research Station for Freshwater Aquaculture and Fisheries Extension in Bogor. The fish used in this experiment were offspring from reciprocal mating among three *Tor* species: *T. soro*, *T. douronensis*, and *T. tambroides*. A complete diallel crossing was performed, resulting in nine combinations, as shown in Table 1. Sixteen broodstock from the three species were used to produce the fish seed for this experiment. The eggs from female broodstock of each species were combined and fertilized with sperm from male broodstock of the same species to produce a conspecific parental line seed population. Additionally, the eggs were fertilized with sperm from other species to produce seeds of interspecific populations. The detailed technical procedures for obtaining the experimental fish, from artificial spawning to larval rearing, were reported elsewhere (Kusmardani et al., 2021).

Experimental procedure

A hundred two-month-old fry representing each cross were placed in a 50 × 50 × 40 cm aquarium. Before being stocked, the seed samples were weighed using a digital balance with an accuracy of 1 mg and measured for length with a millimetre block with accuracy of 1 mm. To minimize weighing inaccuracy due to water residues, we ensure that the fish's body was thoroughly cleaned using a water -absorbent cloth prior to weighing. During the six weeks rearing period, the fish were fed ad libitum with an artificial powdered feed of 40% protein twice daily. Water quality was maintained by siphoning 20% of the aquarium's water volume once a week. At the end of the experiment, subsamples of 10 fish per replicate were measured for total body weight and length. The measurements were conducted as previously described.

Table 1. Mating design of diallel crossing among three species of the genus Tor

	Male		
	TS (n = 3)	TD (n = 3)	TT (n = 3)
Female			
TS (n = 3)	TS×TS	TS×TD	TS×TT
TD (n = 3)	TD×TS	TD×TD	TD×TT
TT (n = 1)	TT×TS	TT×TD	TT×TT

Crosses in the diagonal are intraspecific seeds, while those below and above the diagonal are interspecific hybrids and their reciprocals, respectively. In hybrid designation, the female lists first.

TS, *Tor soro*; TD, *Tor douronensis*; TT, *Tor tambroides*.

Trait measurements

Growth-related traits, which included final weight (FW), final length (FL), absolute growth of weight (AGW), absolute growth of length (AGL), specific growth rate of weight (SGRW), and specific growth of rate of length (SGRL), were determined at the end of the experiment. The following formulas, as discussed in Ricker (1979), were used. The AGW = W_t–W_0, where W_t = weight at time t and W_0 = initial weight at stocking. The AGL = L_t–L_0, where L_t and L_0 were the length at the time t and length at stocking, respectively.

$$\text{The SGRW}=\frac{LnWt-LnW0}{t}\times 100\%;$$

where LnW_t is a natural logarithmic of weight at time t and time of stocking, respectively, and t was the duration of the experiment.

$$\text{The SGRL}=\frac{LnLt-LnL0}{t}\times 100\%,$$

where LnL_t is a natural logarithmic of length at time t and at the time of stocking, respectively, and t was the duration of the experiment. The survival rate (SR) was calculated as:

$$SR=\frac{Nt}{N0}\times 100\%,$$

where N_t and N_0 were the number of fish at the end and the start of the experiment.

Data analyses

The growth-related traits and survival rate means of all hybrid combinations were analyzed using analysis of variance (ANOVA), followed by Duncan's Multiple Range Test (DMRT) with α = 0.05 to assess the significance among combinations. The general combining ability (GCA), specific combining ability (SCA), and reciprocal effects were calculated using the Griffing's formula as described in Mahgoub (2011).

$$Gi = 1/2p(Xi. + X.i) - 1/p^2(X..),$$
$$Sij = 1/2(Xij + Xji) - (Xi.+X.i + Xj. + X.j) - 1/p^2(X..),$$
$$Rij = 1/2(Xij - Xji),$$

where Gi represents the general combining ability effect of i th parent; p stands for the number of species under evaluation; Xi. is the sum of i th female over all males; X.i is the sum of the i th male over all females; X.. represents the grand total; Xj. is the sum of the j th female over all males; X.j is the sum of the j th male over all females; Xij is the mean for the F1 resulting from crossing the i th female and the j th male parents; Xji is the mean for the F1 resulting from crossing the j th female and the i th male parents; Sij reflects the specific combining ability effect for the cross between the i th female and the j th male parents; and Rij refers to the reciprocal effect involving the i th and j th parents. The Gi effects were then partitioned further into female and male components, as detailed by Mahgoub (2011):

$$Gfi = 1/p(Xi.) - 1/p^2(X..),$$
$$Gmi = 1/p(X.i) - 1/p^2(X..),$$

where Gfi and Gmi are female and male GCA components, respectively.

A variance analysis (ANOVA) of combining ability was conducted to assess the effect of species, interspecific hybrids, and their reciprocals on the various growth-related traits and survival rates. Griffing approach, specifically a combination of method-1 and model-1, was applied to calculate the combining ability. The approach calculates the combining ability under the assumption of a fixed effect, and the population consists of progenies derived from direct crosses, their reciprocal, and parental species (Griffing, 1956). The calculation was implemented using a software package called DiallelAnalysisR (Yaseen et al., 2023), an application run in R environment.

Two kinds of heterosis values were determined to get insight into the performance of hybrid combinations relative to their parental species. They are mid-parent heterosis (MPH) and better-parent heterosis (BPH). The MPH was determined as:

$$\left(F1-\frac{P1+P2}{2}\right):\left(\frac{P1+P2}{2}\right)\times 100\%,$$

where F is a cross, P1 and P2 are mean values of populations derived from species one and species two, respectively. The BPH = F1–BP/BP × 100%, where F1 is the mean of the cross, and BP is the value of the best parent in the crosses.

Results

Analysis of variance of combining ability

The variance analysis of combining ability for growth traits and survival is summarized in Table 2. The results in Table 2 indicate that three main sources of variation, GCA and SCA, contribute significantly to the variations in growth-related traits and survival. The GCA variances for all growth-related traits and survival are statistically significant ($p < 0.001$). The GCA variance explains a significant variation within these traits, ranging from 66.18% to 83.47% for growth-related traits and 69.12% for survival. A similar pattern was also observed for the SCA variances.

The SCA variances in growth traits, except the SGRW, are highly significant ($p < 0.001$. Contribution to the explained variance, however, is much less than those of the GCA. They explain 7.52%–15.02% of phenotypic variation of growth traits. A similar statistically significant *p*-value for the SR trait was

Table 2. ANOVA of GCA and SCA of several growth-related traits and survival in an interspecific hybrid population of three *Tor* species

Source of variations	*df*	FW	FL	AGW	AGL	SGRW	SGRL	SR
GCA	2	0.1477^{***}	0.5617^{***}	0.0872^{***}	0.14112^{***}	0.2085^{***}	0.0128^{***}	737.12^{***}
SCA	3	0.0142^{***}	0.1109^{***}	0.0097^{***}	0.0301^{***}	0.0121	0.0021^{**}	221.22^{***}
Reciprocals	3	0.0263^{***}	0.0640^{***}	0.0206^{***}	0.03908^{***}	0.0237^{*}	0.0026^{**}	87.13^{*}
Error	16	0.00065	0.0017	0.0007	0.0029	0.0055	0.00037	20.94
GCA/SCA ratio		1.8072	0.8549	1.6085	0.8488	5.1760	1.1829	0.5959
Explained variance (%)								
GCA		78.21	76.08	73.77	66.18	83.47	71.63	69.12
SCA		7.52	15.02	8.21	14.12	4.84	11.75	20.74
Reciprocal		13.93	8.67	17.43	18.34	9.49	14.55	8.17

$^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

TS, *Tor soro*, TD, *Tor douronensis*; TT, *Tor tambroides*; FW, final weight; FL, final length; AGW, absolute growth of weight; AGL, absolute growth of length; SGRW, specific growth rate of weight; SGRL, specific growth rate of length; SR, survival rate; GCA, general combining ability; SCA, specific combining ability.

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observed, explaining 20.74% phenotypic variation. A reciprocal effect also significantly contributed to the variation in growth traits ($p < 0.001$ for FW, FL, AGW, and AGL and $p < 0.01$ for SGRL). This variation source explains 8.67% to 18.34% variation in growth traits. The values are almost double those of SCA variance. Meanwhile, the reciprocal effect for the survival rate is statistically significant ($p < 0.05$). These findings suggest that the GCA, SCA, and reciprocal effects contribute significantly to the variation in those traits. Besides the GCA, SCA, and reciprocal effects, Table 2 also shows the GCA to SCA ratios for growth traits and survival. The GCA/SCA ratios for growth traits are greater than for survival. The values ranged from 0.8549 to 5.1760 for the former, while for the latter, it is less than one (0.5959). In brief, the GCA variance was predominant for growth traits, while for survival rate, the SCA variance was predominant.

Combining ability analysis

A complete description of general and specific combining ability values for each evaluated species is presented in Table 3. The results show that for growth-related traits except the SGRW, *T. tambroides* consistently shows positive GCA values (ranging from 0.1389%/day to 0.3357%/day) compared to *T. soro* and *T. douronensis*. All six GCA values for growth-related traits in *T. soro* and four out of six in *T. douronensis* are negative. This means that *T. tambroides* was the best combiner, followed by *T. douronensis* for the growth traits. The GCA value for survival was the best in *T. soro*, followed by *T. tambroides*. The *T. douronensis*, having a negative value (−12.6481%), was the worst combiner for this trait. Partitioning the GCA values into the gender of species found that there was a gender bias. Table 3 shows that female *T. tambroides* contribute more to the GCA than males. A similar trend was observed with sex-specific GCA in *T. soro* and *T. douronensis*, but they were in the opposite direction (negative). In most traits, the female GCA is consistently greater than the males.

The superiority of *T. tambroides* as the best combiner for growth-related traits was confirmed by its performance in hybrid combinations, as shown by SCA values (Table 3). The results show that the hybrid combinations involving male *T. tambroides* result in positive GCA in many growth traits, particularly for males crossing with female TS or TD to form hybrid

Table 3. The GCA of three *Tor* species and the SCA of their interspecific hybrids in several growth-related traits and survival rates

Combining ability	Traits						
	FW (g)	FL (cm)	AGW (g)	AGL (cm)	SGRW (%/day)	SGRL (%/day)	SR (%)
GCA							
TS	−0.0766	−0.0726	−0.0772	−0.1348	−0.1802	−0.0529	8.0185
TD	−0.1039	−0.2631	−0.0618	−0.0320	0.1921	0.0317	−12.6481
TT	0.1805	0.3357	0.1389	0.1668	−0.0119	0.0212	4.6296
GCA by sex							
TS_fi	−0.104	−0.108	−0.059	−0.133	−0.195	−0.030	9.074
TS_mi	−0.049	−0.037	−0.018	−0.137	−0.165	−0.093	6.963
TD_fi	−0.157	−0.349	−0.163	−0.103	0.179	0.032	−17.704
TD_mi	−0.051	−0.177	−0.072	0.039	0.205	0.066	−7.593
TT_fi	0.262	0.457	0.222	0.235	0.016	−0.002	8.630
TT_mi	0.099	0.214	0.089	0.099	−0.040	0.027	0.630
SCA							
TS × TD	0.0413	0.1293	0.0325	0.0464	−0.0343	−0.0023	6.2037
TD × TS	−0.0292	−0.0417	−0.0331	−0.0266	−0.1057	−0.0060	5.1667
TS × TT	0.0402	0.1137	0.0320	0.1175	0.0856	0.0407	−2.2407
TT × TS	−0.0538	−0.0650	−0.0288	0.0333	0.0607	0.0234	−2.0000
TD × TT	0.0628	0.1625	0.0541	0.0331	−0.0594	−0.0175	10.4259
TT × TD	−0.1892	−0.3000	−0.1701	−0.2383	−0.1439	−0.0575	−10.0000

FW, final weight; FL, final length; AGW, absolute growth of weight; AGL, absolute growth of length; SGRW, specific growth rate of weight; SGRL, specific growth rate of length; SR, survival rate; GCA, general combining ability; SCA, specific combining ability; TS, *Tor soro*; TD, *Tor douronensis*; TT, *Tor tambroides*; fi, female; mi, male.

combinations TS × TT or TD × TT, respectively. The SCA of TS × TT for all growth-related traits is positive, while four out of six are in the latter. As illustrated in Table 3, the SCA of reciprocal hybrids does not show symmetrical values to its direct hybrids. Some hybrid combinations show only slight differences, such as in the cases of TT × TS and TS × TT for traits SGRW and SGRL. However, in the most extreme cases, the reciprocal hybrids displayed the opposite performance, being highly positive in direct hybrid and highly negative in the reciprocals, such as the case with the hybrid combination TD × TT and TT × TD for the SR trait (Table 3). The pattern of SCA values among hybrid combinations helps explain the high reciprocal variance in ANOVA, as shown in Table 2. For survival rate trait, Table 3 shows the hybrid combination TD × TT indicates the highest SCA (10.4259%) followed by TS × TD (6.2037%) and TD × TS (SCA = 5.1667%). These results show that hybrid combinations involving *T. tambroides* improve survival rates.

Heterosis

The performance of growth-related traits and survival rate of nine groups consisting of three intraspecific crosses and six interspecific hybrid populations is presented in Table 4. In general, a high variation is observed within each evaluated trait, both among intraspecific and interspecific groups. Within intraspecific groups, the performance of growth-related traits in parental line *T. tambroides* (TT × TT) is the best, followed by *T. soro* (TS × TS) and *T. douronensis* (TD × TD). In terms of survival traits, the most notable observation is the significantly lower survival rate of progenies from the TD × TD parental line (42%), which is approximately half of that the other two *Tor* species. Within the interspecific groups, hybrid combinations involving TT, specifically as females, showed best in most of the traits. The performance patterns of other hybrid combinations are more variable across traits.

The extent of heterosis for growth-related and survival rate traits based on MPH is presented in Table 5. Depending on hybrid combinations, both positive and negative heterosis are observed in both traits. The hybrid combination that shows the best heterosis for growth-related traits is TT × TD. The heterosis level in this hybrid combination is the best in four parameters, including AGW, FW, AGL, and FL, namely 16.39%, 14.64%, 7.51%, and 5.36%, respectively. Heterosis in the other two growth parameters, namely SGRW and SGRL, with 0.69% and 2.01%, respectively, are ranked third and second out of six hybrid combinations. The best heterosis for the last two parameters, SGRW and SGRL, are in the hybrid combination TS × TT, with 3.34% and 5.87%, respectively. The TT × TD combination is the best for the survival parameter, with a heterosis value of 12.79%, and the lowest heterosis is found in the TS × TT hybrid combination (0.50%). By combining information on the heterosis of growth rate and survival into consideration, the results clearly show a more consistent pattern in which TT × TD is the best hybrid combination.

The extent of heterosis estimated based on the BPH performance, as shown in Table 5, shows both positive and negative heterosis across different traits and hybrid combinations. Excluding heterosis values in survival, the ranked of best hybrid combinations, in decreasing order, for heterosis in SGRW are

Table 4. The mean and standard deviation of growth-related traits and survival in interspecific hybrid populations of three *Tor* species

Crosses	Traits						
	FW (g)	FL (cm)	AGW (g)	AGL (cm)	SGRW (%/day)	SGRL (%/day)	SR (%)
TS × TS	0.40 ± 0.028^{g}	3.31 ± 0.10^{d}	0.83 ± 0.068^{d}	0.26 ± 0.019f	0.32 ± 0.024^{d}	1.2 ± 0.011^{c}	96.7 ± 3.06^{a}
TD × TD	0.32 ± 0.018^{h}	2.88 ± 0.051^{e}	1.12 ± 0.032^{c}	0.27 ± 0.012f	0.55 ± 0.012^{a}	2.09 ± 0.105^{a}	42.7 ± 5.77^{c}
TT × TT	0.89 ± 0.092^{ab}	4.09 ± 0.140^{ab}	1.45 ± 0.135^{b}	0.67 ± 0.086 ab	0.49 ± 0.036^{c}	1.57 ± 0.078^{bc}	85.7 ± 9.50^{ab}
TS × TD	0.47 ± 0.008^{f}	3.45 ± 0.021^{d}	1.12 ± 0.080^{c}	0.34 ± 0.014e	0.44 ± 0.040^{c}	1.49 ± 0.078^{bc}	91.3 ± 1.53^{ab}
TD × TS	0.52 ± 0.024^{e}	3.53 ± 0.010^{c}	1.17 ± 0.081^{c}	0.41 ± 0.040e	0.45 ± 0.037^{c}	1.70 ± 0.215^{b}	81 ± 1.0^{0b}
TS × TT	0.72 ± 0.057^{c}	4.01 ± 0.081^{ab}	1.45 ± 0.139^{b}	0.55 ± 0.072b	0.50 ± 0.048^{ab}	1.57 ± 0.185^{bc}	93 ± 2.65^{ab}
TT × TS	0.83 ± 0.008^{b}	4.14 ± 0.023^{ab}	1.38 ± 0.081^{bc}	0.62 ± 0.027b	0.45 ± 0.030^{c}	1.45 ± 0.104^{bc}	97 ± 0.00^{a}
TD × TT	0.58 ± 0.017^{d}	3.63 ± 0.061^{c}	1.20 ± 0.092^{c}	0.44 ± 0.025d	0.44 ± 0.039^{c}	1.59 ± 0.140^{bc}	77 ± 19.05^{ab}
TT × TD	0.96 ± 0.069^{a}	4.23 ± 0.062^{a}	1.67 ± 0.040^{a}	0.78 ± 0.049a	0.56 ± 0.022^{a}	1.88 ± 0.106^{ab}	97 ± 2.00^{a}

$^{a–g}$ Different superscript letters next to figures within the same column indicate statistically significant differences at $p < 0.05$.

TS, *Tor soro*; TD, *Tor douronensis*; TT, *Tor tambroides*; FW, final weight; FL, final length; AGW, absolute growth of weight; AGL, absolute growth of length; SGRW, specific growth rate of weight, SGRL, specific growth rate of length; SR, survival rate.

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Table 5. The heterosis of several growth-related traits and survival rate in the interspecific hybrids of TS, TD, and TT

Heterosis (%)	Traits						
	FW	FL	AGW	AGL	SGRW	SGRL	SR
MPH							
TS × TD	7.27	2.87	6.98	3.62	−2.45	0.05	7.78
TD × TS	11.32	3.54	13.14	4.98	0.76	0.74	4.07
TS × TT	3.05	2.08	4.18	6.75	3.34	5.87	0.50
TT × TS	7.22	2.96	7.25	5.29	1.15	−6.61	1.60
TD × TT	−0.94	1.05	−1.56	−1.75	−3.24	−3.54	5.00
TT × TD	14.64	5.36	16.39	7.51	0.69	2.01	12.79
BPH							
TS × TD	16.62	4.23	25.88	−0.30	−28.94	−20.52	−5.52
TD × TS	31.25	6.75	50.14	4.45	−18.85	−18.33	−16.21
TS × TT	−18.80	−2.04	−18.79	0.00	0.28	2.72	−3.79
TT × TS	−6.72	1.14	−10.24	−4.60	−7.48	−38.81	0.34
TD × TT	−34.51	−11.25	−34.16	−17.47	1.71	−8.48	−10.12
TT × TD	7.91	3.42	16.25	15.40	20.09	15.17	13.23

TS, *Tor soro*; TD, *Tor douronensis*; TT, *Tor tambroides*; FW, final weight; FL, final length; AGW, absolute growth of weight; AGL, absolute growth of length; SGRW, specific growth rate of weight; SGRL, specific growth rate of length; SR, survival rate; MPH, mid-parent heterosis; BPH, best-parent heterosis.

TS × TT (20.09%), TT × TD (1.71%) and TS × TT(0.28%); in SGRL are TT × TD (15.17%) and TS × TT (2.72%); in AGW are TD × TS (50.14%) and TS × TD (25.88%); for AGL TTTD (15.40%) and TD × TS (4.45%); in FW are TD × TS (31.25%), TS × TD (16.62%) and TT × TD (7.91%), and in FL trait are TD × TS (6.75%), TS × TD (4.23%) and TT × TD (3.42%). The TT × TD (13.23%) is the only hybrid combination showing positive and substantial heterosis for the survival rate trait. All the remaining combinations were either less substantial or negative, ranging from 0.34% to −16.21%. Combining heterosis information on growth-related traits and survival, Table 5 shows the TT × TD as the best hybrid combination. In addition to a varying degree of heterosis across parameters of growth-related traits and hybrid combinations, the results also show a significant reciprocal effect, in which the magnitude of heterosis of a direct hybrid differed from that of their reciprocals. For survival rate, based on the MPH, all hybrid combinations showed positive values ranging from 0.5% to 12.79%. Based on BPH, the TT × TD was the only hybrid combination showing a positive value (13.23%), while the remaining five combinations showed a less significant or negative values. Table 5 also shows an opposing pattern between heterosis and SCA value, in which hybrid combinations showing high heterosis seem to have a low SCA value and vice versa.

Discussions

Combining ability

Information on combining abilities, consisting of GCA and SCA, is crucial and helpful for breeders to decide the appropriate breeding method to effectively exploit the genetic potentials in their breeding populations. The information was estimated by hybridization experiments involving several genetic groups, which could be geographic populations (Wang et al., 2024), inbred lines (Hedgecock & Davis, 2007), strains (Ariyanto et al., 2022) or even species (Chaivichoo et al., 2020; Odin et al., 2024). The resulting relevant information from the hybridization studies were GCA and SCA estimates. The GCA value is a function a parental line performance when it combines with other lines, while the SCA is a function of hybrid combinations (Costa et al., 2019). A high GCA variance means that certain parental lines play a greater role in controlling the expression of traits in the hybrid populations of the species under study. A similar explanation holds for the SCA. The high SCA values observed in the variance analysis suggest that certain interspecific hybrid combinations combine better than others.

In the present study, as shown in Table 3, the species showing the best combiner for growth-related traits was *T. tambroides* (TT), *T. douronensis* (TD), and *T. soro* (TS). For the survival traits, the rank in decreasing order was TS, TT, and TD. The survival rate patterns among the groups vary. Despite similar treatment during the experimental period, the progeny of parental line TD × TD showed the lowest survival rate. TD appears to be less adaptive to captive conditions, possibly due to its reproductive characteristics such as egg and larval size. TD, being the most fecund among the three *Tor* species, has the smallest egg size, resulting in smaller larvae which are less fit under captive rearing conditions compared to other groups. Hybridization with other *Tor* species has significantly improved their survival rates.

Table 3 presents a complete description of which species is the best combiner and which combination has performed best in the evaluated traits. The SCA confirmed the superiority of TT as the best combiner, in which several hybrid combinations involving the TT showed high SCA values. Specifically, the hybrid combinations involving TT that showed high SCA are TT × TD and TT × TS. This aligns with the GCA profiles of these two species (TT and TD), which ranked first and second, respectively.

A similar pattern is observed for the survival rate trait.

The high GCA values for *T. tambroides* and *T. soro* are also confirmed by the SCA values in certain hybrid combinations involving these two species. Additionally, it is interesting to note that the SCA results also show reciprocal effects. For growth-related traits, for instance, high and positive values occur in the hybrid combinations TT × TD and TT × TS but not in their reciprocals, namely TD × TT and TS × TT. A similar pattern is observed for survival rate traits. The present results suggest that growth-related traits and survival in interspecific hybrids involving TS, TD, and TT are more governed by additive than dominance genetic effects.

The present study showed that at the early life stage, namely up to 4.5 months old, the components of GCA, SCA, and reciprocal effects significantly affected the variation in growth-related traits among hybrid combinations. These findings conformed with those observed in a study with Pacific abalone (*Haliotis discus hannai* Ino) for growth traits at the spat stage (Deng et al., 2010). In a study evaluating combining ability in Serraselmidae, Costa et al. (2019) found that the GCA contributed greater variation in growth than the SCA. Furthermore, they found that one of the six genetic groups, Tambaqui, had a higher general and specific combining ability than other genetic groups for the evaluated traits. This suggested that the additive gene actions have been predominant in controlling the traits. Meanwhile, another study of combining ability for growth in an interspecific hybrid of female African catfish (*Clarias gariepinus*) and male Bighead catfish (*Clarias macrocephalus*) found that the SCA component was much higher than the GCA (Chaivichoo et al., 2020). It suggested that dominance genetic variance predominated the variation observed in growth.

Heterosis

Hybridization has been widely utilized in exploring the potential of aquaculture, especially when breeders possess various genetic materials to use. It is considered the simplest method of breeding to enhance crucial traits. In fish breeding, interspecific hybridization has been employed to enhance numerous commercial traits in aquaculture. This process takes advantage of the dominance genetic variation of populations. Heterosis, which refers to the deviation of hybrid combinations from their parents, is a foreseeable outcome of hybridization. Heterosis values illustrate the degree of performance deviation, whether it is superiority or inferiority, of the hybrid combination compared to their parents. Several mechanisms that are not mutually exclusive, including dominance, overdominance, and epistasis, have been proposed to explain heterosis. Dominance occurs when the effect of one allele masks the effect of another allele at one gene locus, leading to improved performance. Overdominance refers to the phenomenon where the improved performance in hybrids is associated with allele heterozygous state compared to homozygous in their parental species. A study using molecular analysis in hybrid tilapia (*Oreochromis niloticus* × *O. aureus*) uncovered these hypothesized mechanisms (Xiao et al., 2022).

The present study showed varying levels of heterosis in growth-related traits, supporting the importance of GCA, SCA, and reciprocal effects previously identified. The *T. tambroides* showed a high GCA value, contributing significantly to hybrid combinations with high SCA values. A positive relationship between the SCA and heterosis is expected because both parameters deal with non-additive genetic variance (Gramaje et al., 2020). Hybrid combinations showing substantial positive heterosis were expected to have a high SCA. For instance, the TT × TD showing substantial heterosis in the FL trait was expected to have high SCA for that trait. However, this study found a discrepancy in which hybrid combinations showing substantial heterosis came from those with low SCA values. This phenomenon may reflect several scenarios. First would be the gender-asymmetric contribution in GCA leading to a high reciprocal effect. This was supported by the reciprocal effects explaining almost double the growth-related variation than the SCA. In a two-directional hybridization, performance of a reciprocal, namely the reverse of direct hybrid, could be different from that of its direct hybrid counterpart. Studies showed this could be associated with several possible causes: maternal effect (Ren et al., 2020), nuclear-cytoplasmic interaction (Liu et al., 2017), sex-linked gene (Perry et al., 2005), and epigenetic regulation (Ren et al., 2020). Interspecific hybrid progenies inherit genomic DNA from both male and female parents. Besides genomic DNA, female parents also provide eggs phenotype, cytoplasm, organelles including mitochondria, nutrient and regulatory molecules needed for the early stages of embryonic development (van Dooren et al., 2016). Different female species may provide different provision of these components leading to different outcome to the offspring early traits, such as exemplified by studies in oyster hybridizations (Li et al., 2025; Ren et al., 2020). Nuclear-cytoplasmic interaction may also influence the performance of interspecific hybrids. Nuclear genomes inherited from both parents would interact with cytoplasmic components, including mitochondria, which can influence hybrid performance depending on their compatibility. High performance would arise from co-adapted interaction (Liu et al., 2017),

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whereas incompatibility would cause cellular function to be disrupted (Stolbunova & Kodukhova, 2023). Variation in performance between direct hybrids and its reciprocal may also result from sex-linked gene. When genes linked in chromosomal sex are involved in the expression of traits, their presence or absence would affect the trait performance within the corresponding sex. For example, quantitative trait loci associated with thermotolerance in rainbow trout, are linked with Y-chromosome (Perry et al., 2005). Epigenetic regulation, which involves modification of gene expression without changing the DNA sequence, is also crucial in influencing reciprocal hybrid performance. The differential gene expression between direct hybrids and their reversal in reciprocal hybrids of blunt snout bream (Megalobrama amblycephala) and topmouth culter(*Culter alburnus*) is associated with alternative splicing (Ren et al., 2020). This process results in variation in protein isoforms that affect phenotypic traits. Further research is necessary to elucidate the mechanisms underlying reciprocal effect identified in this study. In addition, epistasis, which consists of additive by additive, dominance by dominance, and additive by dominance interactions, might also be responsible (Yu et al., 2021).

Different studies assessing heterosis for growth-related traits in various taxa have reported diverse results, with some showing positive heterosis and others showing negative heterosis. For example, when Egypt and Ivory Coast tilapia strains were crossed and tested for cold tolerance, the additive genetic variance was predominant. As a result, it was concluded that selective breeding would be the optimal strategy for improving this trait (Tave et al., 1989). Intraspecific hybridization in Pacific oysters revealed low heterosis for growth (Han et al., 2020), and similarly, no heterosis for growth was observed in intraspecific hybrids of salmon (Cheng et al., 1987). In contrast, significant heterosis was observed in intraspecific crosses of different gourami populations (Sularto et al., 2017), and different common carp strains (Ariyanto et al., 2022).

A lack of significant positive heterosis meant the hybrids were not better than their parental line counterparts. Several relevant studies showing similar patterns were reported with the hybrids of Salmon (*Salmo trutta* and *Salvelinus alpinus*). In that work, the hybrid's larval survival to the eyed stage was significantly lower than that of both purebreds, resulting in negative heterosis. A slightly positive heterosis (1.67%) was reported for survival in the first 45 days of nursing (Aras-Hisar et al., 2003). Similar results were reported when crossing a wild and hatchery stock of two strains of chinook salmon (*Oncorhynchus tshawytscha*) and crossbreeding of Catarina scallops (*Argopecten ventricosus*). No heterosis was observed for survival (Cheng et al., 1987; Cruz et al., 1998).

Several theories and hypotheses have tried to explain heterosis in hybrid performance. A classical explanation for heterosis in the hybrids has been the concepts of dominance and overdominance. The first concept proposes that heterosis of the hybrids is associated with the complementation of deleterious alleles from one parent with superior alleles from different parents. The second concept proposed heterosis in the hybrids as a result of allele interaction that the heterozygous class performs better than the homozygous class (Birchler et al., 2003). Positive heterosis may result from genetic diversity or genetic distance of hybridized species. In a study with guppy (*Poecilia reticulata*) Shikano & Taniguchi (2002) found that positive heterosis was consistently found when the genetic variation of individuals among strains was higher than the average genetic variation within a strain. Besides these classics, additional hypotheses have been proposed to explain heterosis phenomena that the classics could not satisfactorily address. These included the hypotheses of epistasis, active gene effect, and epigenetic modifications (Yu et al., 2021). Concerning fitness traits, several possible mechanisms may explain the lower fitness of the hybrids. These included hybridization load, hybrid incompatibilities, and ecological selection disfavoring hybrids (Moran et al., 2021).

Implications for breeding programs

The results of this study provide valuable information on the genetic components governing the growth and survival of a hybrid population of three *Tor* species at the early life stages. This information can help breeders develop effective breeding strategies to enhance the performance of these traits. Analysis of GCA/SCA ratios revealed that growth-related traits are mainly influenced by additive genetic variance, while survival rate is more influenced by non-additive genetic variance such as dominance or epistasis. Since both growth and survival are important in aquaculture, breeding programs should consider improving both traits concurrently. When choosing species for hybridization, selecting combinations demonstrating significant and positive heterosis for both traits is important.

Given the information on combining ability and heterosis obtained in the present study, selective breeding would be effective if a breeding program used these hybrid populations as a base population. This has been the case with the breeding program of GIFT tilapia (Bentsen et al., 1998). This method is mainly effective for breeding programs that are designed in the long run and expect the accumulation of continuous genetic gain from generation to generation. For short-term breeding programs, hybridization of certain combinations could be recommended. Following the identification of prospective hybrid combinations, hybridization as a breeding method certainly will gain immediate results.

Based on the previously described criterion, the hybrid combination TT × TD consistently displayed superior heterosis values compared to the other combinations, making it a strong candidate for further consideration. The TT, with the highest GCA, performed exceptionally well when paired with TD (TT × TD), as evidenced by its impressive heterosis (MPH) value for both growth and survival. The superiority was even more observable when the BPH was used. It was the only hybrid combination showing positive for both growth and survival. Following closely, the TD × TS hybrid also showed promise, supported by the GC values, where TD ranked second in growth and TS ranked second in survival.

It should be noted that the experimental duration during which data were generated in this study represented only a small fraction of the species' generation interval, which can extend up to four years. The patterns of combining ability and heterosis of interspecific hybridaization in this study were readily identifieble. The results of this study, however, should be interpreted with consideration for the representation of a single female brood stock in one of the species. In addition, a study by Wohlfarth (1993) found that heterosis in common carp (*C. carpio*) appeared most noticeable in young and small fish, declining in older animals and influenced by genotype by environment interaction. It is advisable, therefore, to conduct a longer rearing period to confirm the consistency of the observed patterns.

Conclusion

Interspecific hybridization of three *Tor* species (*T. soro*, *T. douronensis*, and *T. tambroides*) has revealed that the GCA, SCA, and reciprocals significantly affected the growth and survival rate trait variation. The GCA variance predominated over SCA, and *T. tambroides* was the best combiner for the evaluated traits. Positive and significant heterosis was observed for growth rate but not survival rate. The extent of heterosis was low to medium and was associated with maternal effect. Based on the combined information of GCA, SCA, and heterosis, selective breeding seems to be the prospective approach to improve growth and survival performances in a long-term breeding program. TT × TD and TD × TS hybrid combinations could be good candidates for short-term breeding programs expecting immediate results.

Competing interests

No potential conflict of interest relevant to this article was reported.

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Availability of data and materials

Upon reasonable request, the datasets used in this study can be made available from the corresponding author.

Ethics approval and consent to participate

This study conformed to the guidance of animal ethical treatment for the care and use of experimental animals.

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