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Examination of survival, physiological parameters and immune response in relation to the thermo-resistant heterosis of hybrid oysters derived from *Crassostrea gigas* and *C. angulata*

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igh temperature is an important environmental stressor leading to summer mass mortality of oysters igni - cant survival heterosis in summer were observed in hybrids between two phylogenetically closely-related oysters, *Crassostrea gigas* and *C. angulata*, but an explicit understanding of heterosis has been lac ing ere, we investigated the survival performance, oxygen consumption rate and en yme activity i e , , and in *C. gigas* GG , *C. angulata* and their hybrids *C. gigas* ♀ × *C. angulata* ♂ G and *C. angulata* ♀ × *C. gigas* ♂ G under acute heat stress containing ve levels , , , and ° ompared with parental strains, the hybrid strains exhibited higher cumulative survival rate at all temperatures, indicating heterosis for thermal tolerance ox regression analysis showed that hybrid strains challenged with heat shoc exhibited lower ha ard ratio and longer expected lifetime oreover, in hybrid strains were signi cantly higher *P* < than those in parental strains under and ° rrhenius brea -point temperature and temperature coef cient *Q10* revealed that hybrids had broader temperature range of aerobic metabolism and lower sensitivity to rising temperature n addition, the activities of and of hybrid strains were signi cantly higher than the parental strains at and ° -level treatment after h and at ° -level treatment after h, whereas the content were reduced, indicating their stronger antioxidant capacity ccordingly, the enhanced aerobic capacity and antioxidant ability of hybrids under high temperature may contribute to the improvement of thermal tolerance ur ndings can facilitate our understanding of the physiological and immune mechanisms underlying thermo-resistant heterosis and facilitate the breeding of thermo-resistant oyster varieties

1. Introduction

he aci c oyster *Crassostrea gigas*, originated from orthern sia, is a hardy and euryhaline species oudry et al , Ghaffari et al , and has become a ey mariculture species globally because of its high growth and yield characteristics edgecoc and avis, n recent decades, however, the farmed *C. gigas* has been heavily affected by recurrent summer mortality syndrome ang et al , uhrmann et al , is caused by multiple factors including elevated temperature, pathogens, and physiologic stress associated with reproduction égremont et al , olomieu et al , igh temperature facilitates the growth of pathogens, inhibits oyster immune system, ma ing them more susceptible to opportunistic pathogens oletchni et al , ang et al , and is therefore considered to be an important incentive for ang et al , t present, several breeding programs for thermal-tolerant oysters have been successfully implemented to address the problem associated with summer mortality ershberger et al , ing et al , Juáre et al , and have been proved to be effective to improve the survival rate of the oyster during summer

he ma ority of research on crossbreeding in plants and animals has been conducted to combine desirable traits alconer and ac ay, n a uaculture, hybridi ation has been fre uently used to increase environmental tolerances when one parental species has a wide range of adaption or speci c tolerance elson and edgecoc , ahman et al , or instance, crosses between o ambi ue and

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ile tilapias resulted in a red tilapia with strong salinity tolerance im et al , hybrid *Haliotis rufescens* × *H. discus hannai* exhibited improved thermostability than both purebred populations afarga de la ru et al , *C. angulata*, a closely related species of *C. gigas*, naturally inhabits the low latitude regions of southern hina, and is characteri ed by excellent warm-water adaptation uvet et al , Ghaffari et al , Jiang et al , a tri ingly, the reciprocal hybrids between *C. gigas* and *C. angulata* exhibited obvious heterosis in survival during the high-temperature months and thermotolerance Jiang et al , b et, little is nown about the physiological and immunological mechanisms of heterosis in thermotolerance of hybrid oysters

hermotolerance assessments of oysters are usually based on the survival curves, which ends with the death of the individuals owd and omero, hen et al , he physiological processes i e , respiration and excretion of marine ectotherms are in uenced by elevated temperature agnuson et al , and is closely related to their thermal resistance lar et al , Elevated or high temperature increase the organism's oxygen consumption rate , which is replenished by increased ventilation Jansen et al , *Q* or an't off's temperature coef cient is fre uently used to evaluate the temperature sensitivity of asas et al , owever, extremely high temperature induces oxygen restriction, leading to a respiration pea , over which anaerobic respiration is stimulated, with a rapid decline in örtner, he temperature at respiration pea , rrhenius brea -point temperature ar er et al , , may represent the thermotolerance threshold of marine organisms Jansen et al ,

igh temperature could induce organisms to produce excessive endogenous reactive oxygen species , resulting in oxidative damage ushcha , , signal transduction disorder ahman and ahman, and increased cellular apoptosis limen et al , alondialdehyde is the part of nal product of lipid oxidation by , and its level is fre uently used to measure the degree of oxidative stress agoudo et al , o protect cells from detrimental effects, a uatic animals have evolved antioxidant defense systems to neutrali e extra and free radicals ang et al , he system consists of non-en ymatic component and antioxidant en ymes, the latter including the en ymes superoxide dismutase and catalase u, lein et al , , which could degrade superoxide into oxygen and water an et al , hus, expression of antioxidant en yme activities may re ect the immune resistance of a uatic organisms under heat stress ahman and ahman,

o address this issue, we evaluated the survival, physiological parameters and antioxidant en yme activity , and in *C. gigas, C. angulata* and their reciprocal hybrids under acute thermal stress he integration of phenotypic, physiological and immunological data is aimed to better understand the heterosis in thermotolerance of hybrids

2. Materials and methods

2.1. Oysters

diallel hybridi ation between *C. gigas* and *C. angulata* was carried out in June *C. gigas* were sourced from ongcheng handong rovince, hina ° ′ , ° ′E , while *C. angulata* were gathered from hang hou u ian rovince, hina ° ′ , ° ′E or each species, eggs from females were pooled and divided e ually into two - bea ers Each bea er of eggs was fertili ed with a mixture of sperm from *C. gigas* or *C. angulata* hus, four crosses were established GG- *C. gigas* ♀ × *C. gigas* ♂, G - *C. gigas* ♀ × *C. angulata* ♂, G- *C. angulata* ♀ × *C. gigas* ♂, and - *C. angulata* ♀ × *C. angulata* ♂ fter months, yearling oysters of GG, and reciprocal hybrids G and G were obtained from ongcheng and transferred to antai aiyi hatchery, handong rovince for heat shoc treatment or each strain, approximately individuals with similar si e able were cleaned to eliminate attaching organisms and acclimated in m concrete pond with ltered, aerated seawater salinity psu, temperature ° for days before the heat shoc treatment ysters were fed daily with fresh *Phaeodactylum tricornutum* ohlin and the animals were not fed one day before heat shoc was applied

Table 1
he summary for the growth characteristics and condition index of four strains

trains	hell height mm	hole weight g	hell-free dry weight g	ondition index
GG	± ab	± a	± c	± b
b	± b	± b	± c	± b
G	± a	± a	± a	± a
G	± ab	± a	± b	± a

2.2. Survival performance under acute heat stress

en - polyethylene buc ets were used for acute heat stress experiment, each divided into e ual sections separated by polyethylene nets, forming a total of trial areas he experimental design was completely random with treatments using a factor design temperature × strains and replicates per treatment n the trial buc et, the temperature was increased from control temperature ° to designed temperatures , , and ° at a rate of ° h⁻ using a water bath unit with heaters or water chiller uring heat shoc period, four strains oysters per strain were transferred directly to the same buc et with designed temperatures urvival data was recorded every -h and stopped at h hen the cumulative survival rates of GG, , G and G were calculated he oyster was regarded as dead when it did not respond to touch with an anatomic needle, and dead individuals are pic ed up of the seawater was exchanged daily, and the oysters were fed *P. tricornutum* three times a day

2.3. Physiological parameters determination

Eight oysters from each strain GG, , G and G with similar si e were randomly selected from the acclimation environment to determine oxygen consumption rate in a closed chamber ysters were fasted for h before measurement Each chamber contained one oyster, and every experiment consisted of eight replicates ll chambers were lled with air-saturated seawater at the control temperature ° and designed temperature , , , ° and bloc ed with li uid paraf n to avoid gas exchange with the external environment ne chamber containing empty shells was included to serve as a control to correct for autogenic trends uring heat shoc , chambers were immersed in a thermostatic bath to maintain a constant temperature ± ° concentrations were determined , at the beginning of heat shoc and h later ubse uently, the soft body of oyster was separated from the shells and dried at ° to measure the shell-free dry weight mg g⁻ h⁻ was calculated as the followings Ghaffari et al ,

$$OR = \frac{(DO_{0\ h} - DO_{1\ h})_{Treat} - (DO_{0\ h} - DO_{1\ h})_{Blank}}{DW \times t} \times V$$

where h and h are the concentrations at the beginning and h, respectively " reat" represents chambers containing oysters " lan " represents chamber does not contain oysters g is the shell-free dry weight represents the volume of water h represents the measuring time

he condition index , an indicator the physiological or nutritional condition of oyster, was calculated as the following bbe and lbright,

$$\mathrm{CI} = \frac{\text{shell} - \text{free dry weight (g)}}{\text{whole wet weight (g)} - \text{shell wet weight (g)}} \times 100$$

2.4. Antioxidant enzyme activity determination

he en yme activity experiment consists of two parts after h of heat shoc treatment, nine oysters each strain were collected from the , , and ° buc ets to examine the effects of different heat shoc temperature on the en yme activities of four strains nine oysters per strain from the ° buc ets were sampled at , , , , , , and h to evaluate the effects of different heat shoc time on the en yme activities of four strains ysters were gill-clipped and the gills were instantly fro en in li uid nitrogen and ept at – ° ll en yme activity measurements were carried out with replicates, and the gills from three individuals were pooled as one sample for each replicate he gills were defrosted in – ° and ° refrigerators, followed by blotting on lter paper and weighing amples were homogeni ed with ice-cold normal saline dilution in an ice bath and then centrifuged rpm for min at ° he supernatant li uid was gathered and the activity of superoxide dismutase , catalase , malondial-

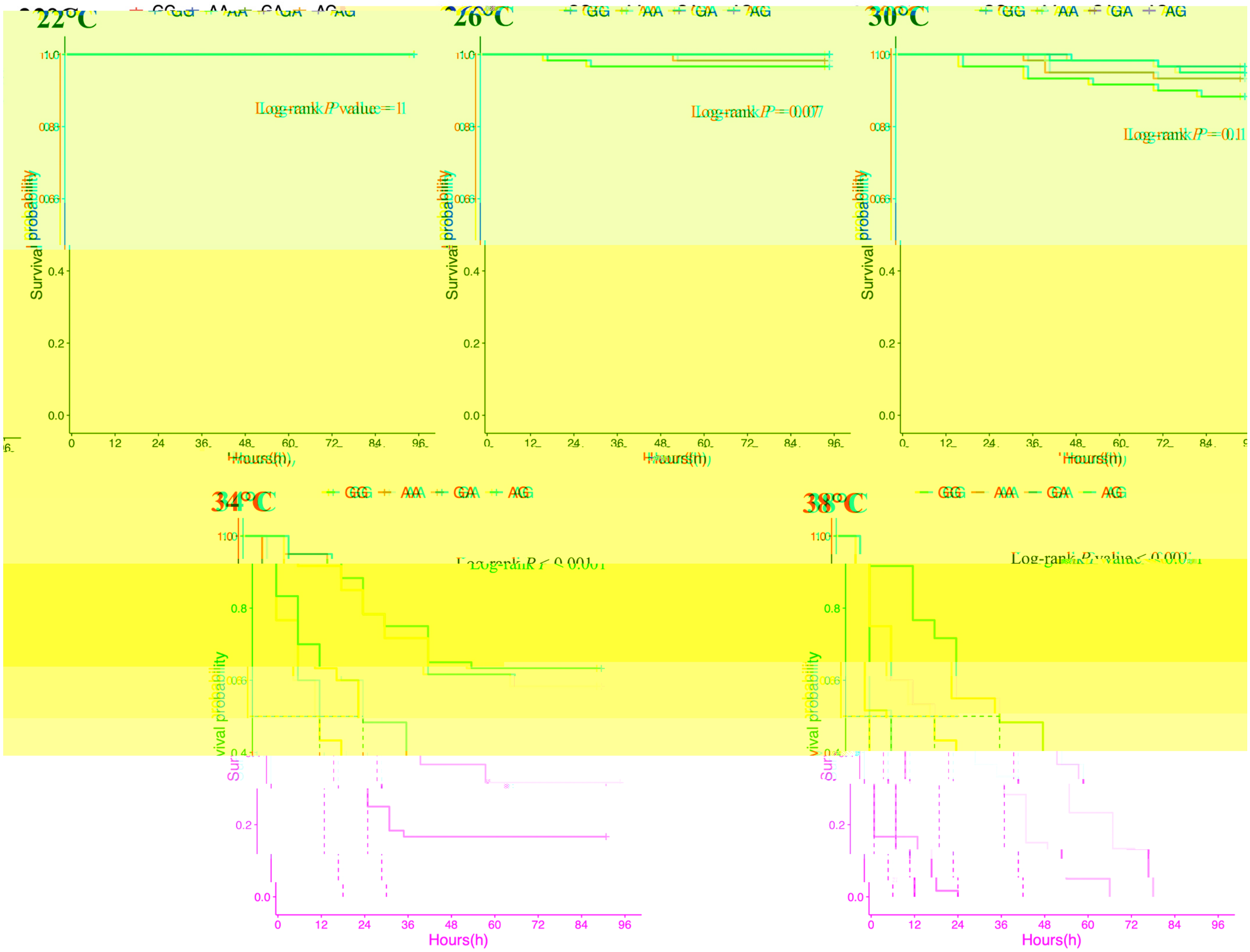

Fig. 1. urvival as a function of time of four strains GG, , G and G under different heat shoc temperature levels , , , and °

strongly affected by strains, temperature and their interaction $P <$ $P <$ $P <$, respectively able i ewise, the activity in GG and increased gradually as temperature elevated, reaching the maximum mgprot⁻ and mgprot⁻ , respectively at ° , and declined afterwards in contrast, the activities in G and G continued to rise with increasing temperature, and was signi cantly higher than the parental strains at and ° ig wo-way revealed clear effects of strain $P <$, temperature $P <$ and strain × temperature interaction $P <$ on the activity levels able dramatic increase in content for GG – nmol mgprot⁻ and – nmol mgprot⁻ was found over temperature, while no obvious changes in content between both G and G up to ° ig tri ingly, levels in G was signi cantly lower $P <$ than the parental

Table 2
ox proportional ha ard model strati ed by heat stress and estimation of expected lifetime h for four strains on ° levels

trains	oef cient estimate	a ard ratio	Estimation of expected lifetime
GG		–	– a
		–	– b
G		–	– c
G		–	– d

trains were signi cantly correlated with survival time $P <$ different lowercase letters in the same line indicating signi cantly different according to the log-ran test $P <$

Table 3
wo-way analyses of variance testing for temperature by strain interaction effects on oxygen consumption rate and antioxidant en yme activity , and

Effect	d f	F-value	d f	F-value	d f	F-value	d f	F-value
train								
emperature			,					
train × emperature								
Error		–		–				

he P-value associated with each F-value are indicated by asteris s – $P <$ – $P <$ – $P <$ – not signi cant

strains at and ° ixed model results indicated signi -
cant

activity or content of the three en ymes $P <$ or $P <$ able

4. Discussion

his study was performed to assess the survival, physiological parameters and immune responses of hybrid oyster under acute heat shoc , with an aim of explaining their survival advantage compared to the parental species e found that the hybrid strains showed larger tolerance to thermal stress since they exhibited higher survival rate and more stable aerobic metabolism when exposed to high temperatures conditions eanwhile, the hybrid strains showed enhanced antioxidant capacity and less oxidative damage at extremely temperature

4.1. Comparison of mortalities under heat stress among cohorts

C. gigas from the coast of northern hina is recurrently exposed to massive mortality events t has been estimated that > of *C. gigas* farmed in handong were lost in the summer of , when seawater temperatures exceeded ° ang et al , onetheless, the survival rate of hybrid oysters was > during warmer months Jiang et al , b his resistance to high water temperature was supported in the current research, since an increase in temperature from ° to ° leads to an obvious increase in survival arr

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in a uatic hybrids, such as *Ictalurus punctatus* × *I. furcatus* with low-oxygen tolerance unham et al , , *Pomacea canaliculata* × *P. maculate* with low-temperature tolerance atsu ura et al , and *Haliotis rubra* × *H. laevigata* with heat tolerance lter et al , esides, the ox proportional ha ards analysis revealed that strain, temperature and their interaction had signi cant in uence on cumulative survival rate, indicating the close dependence of strain and temperature on oyster survival his genotype-environment interaction was associated with the biogeographical distribution of parental lines unham et al , , which may affect the heat tolerance of hybrids ahlhoff and omero, s the main *C. gigas* producing area in hina, handong rovince has an average seawater temperature of – ° in contrast, *C. angulata* is a local species in u ian rovince where temperatures are higher, ranging from ° to ° Jiang et al , b onse uently, the high heat resistance of hybrid oysters may be inherited from one of its parents, the warm-adapted *C. angulata* lter et al , n a similar case in abalone, iang et al reported *H. discus hannai* × *H. gigantea* successfully inherited the high-temperature resistance of *H. gigantea* owever, in this study, G was more tolerant of high temperature compared to G, which may suggest that the maternal effect was small and the paternal effect was large imilarly, ˇim ová et al found that the hybrids with common carp in the paternal position exhibited greater viability than the hybrids with common carp in the maternal position

4.2. Change of oxygen consumption in response to heat stress

or several marine animals such as largemouth bass a et al , , small clam Jansen et al , and esso scallop Jiang et al , , ndings showed that metabolic rate was positively associated with seawater temperature owever, a few studies have reported a negative relationship between metabolic rate and environment temperature in some freshwater animals, including limpets c ahon, and sculpins alsh et al , n this study, the of the four oyster strains rst rose and then fell with rising temperature pregulated respiration rate was thought to be associated with increased digestion rate and protein synthesis rate Jiang et al , , but also indicated the activation energy needed for en yme catalytic reaction was lower at this moment ochach a and omero, eanwhile, the decrease of may be a protection mechanism against excessive metabolism under high-temperature conditions Jansen et al , nimals possessing the capacity to reduce total metabolism was thus thought to be li ely to deal better with extreme temperature than animals without such capacity iao et al , n contrast, other studies concluded that species that could maintain their aerobic capacity at higher temperature have a better heat resistance than species that experience a decline in aerobic performance as temperature rises ing et al , Ghaffari et al , his may be due to the different reaction norms of animals under short-term and long-term stress, allowing them to survive better under different acclimation conditions Glanville and eebacher, he results in this study were consistent with the latter view, as the hybrids with higher survival rates exhibited higher at – ° urther, G had higher metabolic rate compared with G at °, indicating stronger aerobic capacity in G under extreme heat n our study, the s were ° and ° for GG and strain, respectively ne worry is that the measured for GG in this research is close to seawater temperature ° during summer in handong rovince, rendering *C. gigas* vulnerable to temperature rise caused J am steadily over temperature or time – h , which differs from this pattern oreover, the increasing activity of with exposure to stress over time was also found in muscle tissue of gold sh ushcha and agnyu ova, , indicating that no switch from aerobic to anaerobic metabolism occurred in the organism ing et al , part from that, there were other prominent performances of hybrids may be related to their survival advantage under heat shoc G and G gained signi cantly higher $P <$ activities in and than GG at extremely high temperature and ° , ig and activities of G and G were signi cantly higher than those of GG at h ° , ig ccordingly, these two characteristics of hybrids may mean earlier response time and higher response intensity of antioxidant system at extreme temperatures, implying an enhanced capacity to maintain cellular functions of the antioxidative system during thermal stress ahman and ahman, agoudo et al ,

nother stri ing nding in this research was that the hybrids had lower level ig and less variation ig in content at and ° compared to the parental strains is a lipid peroxidation product of polyunsaturated fatty acids in bio lms and represents the degree of biological oxidative damage iang et al , ncreased content have been reported in whiteleg shrimp uan et al , , esso scallop Jiang et al , and red swamp cray sh Guo et al , in response to short-term heat stress otably, an et al found there was a signi cant negative correlation r = – , $P <$ between and in brown scallops, a low-survival population compared to the golden scallops hus, the lower content of hybrids indicated less oxidative damage, which corresponded with their high survival performance under thermal stress

5. Conclusions

his study demonstrated that the hybrids showed higher cumulative survival rate under thermal stress compared with their parental species, *C. gigas* and *C. angulata* he signi cant heterosis of survival rate suggested that crossbreeding improved the thermal tolerance of oysters remar ably eanwhile, the hybrids exhibited broader temperature range of aerobic metabolism and lower sensitivity to temperature rise, which contribute to the stable and great aerobic capacity of hybrids under high temperature environment urther, compared with the parental strains, the antioxidant system and of hybrids exhibited a more rapid and intensive response lso, the hybrids maintained lower levels of content, indicating less oxidative damage hese ndings can facilitate our understanding of the physiological and immune mechanisms underlying heterosis in heat resistance of hybrids and provide a new viewpoint for the future breeding of thermo-resistant oyster

CRediT authorship contribution statement

Gaowei Jiang: nvestigation, onceptuali ation, ormal analysis, riting – original draft **Jianmin Zhou:** nvestigation **Geng Cheng:** nvestigation **Lingxin Meng:** nvestigation **Yong Chi:** nvestigation **Chengxun Xu:** upervision **Qi Li:** upervision, onceptuali ation, esources, riting – review & editing, unding ac uisition

Declaration of Competing Interest

he authors declare no con ict of interest

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