ICES Journal of Marine Science

ICES Journal of Marine Science (2021), 78(1), 360–367. doi:10.1093/icesjms/fsaa080

Contribution to the Themed Section: '*Marine aquaculture in the Anthropocene*'

Original Article

Adaption potential of *Crassostrea gigas* to ocean acidification and disease caused by *Vibrio harveyi*

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Nordio, D., Khtikian, N., Andrews, S., Bertotto, D., Leask, K., and Green, T. Adaption potential of *Crassostrea gigas* to ocean acidification and disease caused by *Vibrio harveyi*. – ICES Journal of Marine Science, 78: 360–367.

Received 26 December 2019; revised 13 April 2020; accepted 16 April 2020; advance access publication 29 June 2020.

The survival and development of bivalve larvae is adversely impacted by ocean acidification and *Vibrio* infection, indicating that bivalves need to simultaneously adapt to both stressors associated with anthropogenic climate change. In this study, we use a half-dial breeding design to estimate heritability (h^2) for survival to *Vibrio harveyi* infection and larval shell length to aragonite undersaturated and normal conditions in laboratory-reared *Crassostrea gigas*. Phenotypic differences were observed between families for these traits with heritability estimated to be moderate for survival to *V. harveyi* challenge ($h^2 = 0.25$) and low for shell length in corrosive ($\Omega_{aragonite} = 0.9$, $h^2 = 0.15$) and normal conditions ($\Omega_{aragonite} = 1.6$, $h^2 = 0.15$). Predicted breeding values for larval shell length are correlated between aragonite-undersaturated and normal conditions (Spearman $r = 0.63$, $p < 0.05$), indicating that larger larvae tend to do better in corrosive seawater. Aquaculture hatcheries routinely cull slow-growing larvae to reduce and synchronize time taken for larvae to metamorphose to spat, thus inadvertently applying size-related selection for larger larvae. This indirect selection in the hatchery populations provides a plausible explanation why domesticated oyster populations are less sensitive to ocean acidification.

Keywords: aquaculture, *Crassostrea*, genetic selection, ocean acidification, *Vibrio*.

Introduction

Ocean change is projected to impact all areas of the ocean, from deep sea to coastal estuaries (Feely *et al.*, 2004), with potentially wide-ranging impacts on marine life. A major goal of climate change research is to determine if species can adapt, via evolution or physiological acclimation, to the rapid pace of ocean change (Munday *et al.*, 2013; Ross *et al.*, 2016). The rapidly rising levels of atmospheric CO_2 are not only causing ocean warming but also lowering seawater pH and altering carbonate saturation state of the oceans (Feely *et al.*, 2004; Orr *et al.*, 2005), which is interfering with shell formation in calcifying animals (Barton *et al.*, 2012; Ross *et al.*, 2016). Ocean warming also influences the prevalence and severity of marine infectious diseases (Burge *et al.*, 2014), such as the emergence of *Vibrio* infections in temperate coastal waters (Le Roux *et al.*, 2016; Vezzulli *et al.*, 2016; Baker-Austin *et al.*, 2017). Most studies investigating the evolutionary potential of marine animals to climate change have focused on a single climate change stressor (Parker *et al.*, 2011; Sunday *et al.*, 2011; Kelly *et al.*, 2013; Malvezzi *et al.*, 2015; Tasoff and Johnson, 2019), although there has been an increasing recognition of the importance of investigating multiple stressors (Foo *et al.*, 2012; Cole *et al.*, 2016; Welch and Munday, 2017). For example, adaption to ocean acidification may result in evolutionary trade-offs with other traits that affect general fitness, such as reproductive output or disease tolerance that constrain adaption potential (reviewed by Kelly and Hofmann, 2013).

Quantitative genetic approaches are increasingly becoming popular in climate change research for measuring narrow-sense

heritability (h^2), the proportion of phenotypic variation in a trait that is controlled by additive genetic effects (Kelly and Hofmann, 2013; Sunday *et al.*, 2014). Knowing a traits heritability is valuable, because highly heritable traits under strong selection evolve rapidly within a few generations, whereas low heritability combined with weak selection results in small or negligible evolutionary change (Morrissey *et al.*, 2010). Quantitative genetic approaches can also be used to determine an individual's genetic merit, or sum of the additive genetic effects of an individual's gene for a given trait, and thus the expected effect of the genes that it passes to its offspring, also referred to as its "breeding value" (Kruuk, 2004). Finally, the magnitude of genetic correlations between two or more traits can also be predicted using quantitative genetics (Kelly and Hofmann, 2013), providing important information on potential trade-offs.

It is widely known that ocean acidification and pathogenic *Vibrio* bacteria have adverse impacts on the development and survival of bivalve larvae (Estes *et al.*, 2004; Elston *et al.*, 2008; Barton *et al.*, 2012). These two stressors have been blamed for failing aquaculture production of the Pacific oyster (*Crassostrea gigas*) in the NE Pacific Ocean (Elston *et al.*, 2008; Barton *et al.*, 2015). Over the coming decades, oceanographic modelling predicts the pH and aragonite saturation of coastal waters of the NE Pacific will shift during spring and summer to levels that cause larval shell abnormalities in *C. gigas* (Evans *et al.*, 2019). *Vibrio* infections of shellfish are also expected to become more frequent with warming coastal waters supporting larger *Vibrio* populations (Le Roux *et al.*, 2016). Determining if *C. gigas* can simultaneously adapt to these two stressors is a key priority. Mass selection for improved growth rate and survival to *Marteilia sydneyi* (QX disease) in the Sydney rock oyster, *Saccostrea glomerata*, has resulted, serendipitously, in reduced effects of ocean acidification on larval shell length (Parker *et al.*, 2011), indicating a potential for a genetic correlation between these traits. Several key studies have estimated narrow-sense heritability for the shell length of bivalve larvae in high pCO_2 conditions (*Mytilus trossulus*, $h^2 = 0.09$; Sunday *et al.*, 2011), or experimental infection with *Vibrio aestuarianus* (*C. gigas*, $h^2 = 0.09$–0.30; Azema *et al.*, 2017) and *Vibrio parahaemolyticus* (*Meretrix petechialis*, $h^2 = 0.31$–0.32; Liang *et al.*, 2017), but these studies did not consider evolutionary trade-offs with other traits. The current study addressed this deficit by using a half-dial breeding design to simultaneously calculate narrow-sense heritability and genetic correlations for ocean acidification (OA) and *Vibrio* resistance in *C. gigas* larvae. This information is crucial to the aquaculture industry as it prepares for climate change. Shellfish farming supports over $300 million in economic activity in rural communities on the west coast of North America, and *C. gigas* comprises >80% of the industry's total annual shellfish harvest by live weight (Dumbauld *et al.*, 2009).

Material and methods

Broodstock collection and conditioning

To maximize genetic diversity in our study, adult diploid *C. gigas* of approximately 2.5 years of age were sourced from three different farms. These adult *C. gigas* were originally purchased by oyster farmers in British Columbia from aquaculture hatcheries in Chile, United States, or collected as wild spat from Pendrell Sound, British Columbia, Canada. Oysters were collected during winter (February 2019) and transported to Vancouver Island University's Deep Bay Marine Field Station, where *C. gigas* were transferred to a 120-l conditioning tank and maintained under continuously flowing seawater. Seawater temperature was gradually increased to 21°C during 6 weeks period, and *C. gigas* were fed a combined algal diet of *Chaetoceros muelleri*, *Isochrysis galbana*, and *Pavlova lutheri*. The reason for collecting broodstock in winter and undertaking reproductive conditioning in a common environment was to minimize paternal effects between broodstock on offspring quality (Parker *et al.*, 2012).

Seawater collection

The North Salish Sea is an ocean acidification hot spot, and deep-water corrosive conditions ($\Omega_{aragonite} < 1$) persist for the entire year (Evans *et al.*, 2019). We exploited a natural depth profile of aragonite saturation for our ocean acidification challenge by using Niskin bottles to collect seawater at 5 and 70 m at Baynes Sound Sampling Station 17 (49.474 N, 124.758 W). We chose to collect seawater with naturally high concentration of pCO_2 for the ocean acidification challenge (Ocean acidification challenge section) to ensure that other variables, such as low pO_2 and microbial community, are representative of aragonite undersaturated conditions experienced in Western Canada (Reum *et al.*, 2016). Niskin bottle target depth was determined using an electronic wire counter (A.G.O. Environmental Ltd), and messengers were used to trip Niskin bottles. Seawater for chemical analysis was collected from each depth in duplicate 350-ml amber soda-lime glass bottles, poisoned with 200 µl of saturated $HgCl_2$, and crimp sealed using polyurethane-lined metal caps. Seawater for OA challenge was collected in triplicate 1-l amber soda-lime glass bottle. Sample bottles were rinsed three times prior to filling with sample and filled from the bottom to minimize gas exchange.

The pH_{NBS} and salinity of seawater samples were measured using a YSI Multilab 4010-2W with IDS 4110-3 pH and IDS 4310 conductivity sensors calibrated with NIST buffers (Fisher Scientific). Total alkalinity was measured using Fisher Scientific Orion Star T910 pH Titrator and HCl titrant (Sigma H1758) standardized against Trizma® base (Sigma T6791). Seawater carbonate chemistry parameters were calculated using CO2Sys (Pierrot et al., 2006) as described in Table 1.

Spawning and crosses

Crassostrea gigas from the Broodstock collection and conditioning section were strip-spawned on 19 March 2019 by making small incisions in the gonad with a scalpel blade and washing gametes into a plastic beaker with filtered seawater. Gametes from each parent were kept separate at room temperature for no longer than 1 h before fertilization. Six females and six males were mated using a half-diallel cross to produce 21 pair-mated families (Figure 1). Each family was reared in an individual 250-l conical tanks maintained at 23°C with gently aeration and at a stocking density of ~10 larvae ml^{-1}. Every 2 days, tanks were drained onto a 40-µm screen to retain larvae, then scrubbed clean with 1% chlorine solution, rinsed, refilled with filtered seawater, and larvae-returned to the tank. Larvae were fed daily with mixed live algal diet consisting of *Chaetoceros calcitrans*, *I. galbana*, and *P. lutheri*. Samples of fertilized eggs on day 0 and larvae on day 6 from each family were used for ocean acidification and *Vibrio harveyi* challenge, respectively.

Table 1. Seawater chemistry used for ocean acidification assay

Sample	Depth (m)	Storage	°C	pH_{NBS}	Salinity (ppt)	Total alkalinity (μmol l)	$\Omega_{aragonite}$
Field	5		9.3 ± 0.0	7.92 ± 0.00	28.9 ± 0.2	2 003.9 ± 4.3	0.9
Field	70		8.5 ± 0.0	7.70 ± 0.01	29.4 ± 0.1	2 079.3 ± 24.3	0.6
OA challenge	5	Sealed	23.0 ± 0.0	7.94 ± 0.01	28.9 ± 0.1	2 048.7 ± 8.4	1.6
OA challenge	70	Sealed	23.0 ± 0.0	7.64 ± 0.02	29.5 ± 0.1	2 071.7 ± 9.0	0.9
OA challenge	70	Aerated	23.0 ± 0.0	8.02 ± 0.01	33.6 ± 0.1	2 307.8 ± 25.1	2.3

Seawater was collected from sampling station 17 (BS17) in Baynes Sound, Canada. Seawater samples were immediately spiked with $HgCl_2$ or kept for OA challenge. The seawater for OA challenge was either stored overnight in sealed amber soda-lime glass bottles or vigorously aerated. Temperature (°C), pH_{NBS}, salinity (ppt), and total alkalinity were measured directly and presented as mean ± standard deviation. Aragonite saturation ($\Omega_{aragonite}$) was estimated from these parameters using CO2SYS (Pierrot et al., 2006).

Table 2. Pearson correlation coefficients (95% CI) between EBVs for larval survival to *Vibrio harveyi* challenge and larval shell length at different aragonite saturation states ($\Omega_{aragonite}$ = 0.9, 1.6, and 2.3)

	$\Omega_{aragonite}$ = 0.9	$\Omega_{aragonite}$ = 1.6	$\Omega_{aragonite}$ = 2.3	*V. harveyi*
$\Omega_{aragonite}$ = 0.9	1	0.63 (0.09–0.88)	0.68 (0.19–0.90)	−0.48 (−0.83 to 0.13)
$\Omega_{aragonite}$ = 1.6		1	0.66 (0.15–0.90)	−0.41 (−0.80 to 0.22)
$\Omega_{aragonite}$ = 2.3			1	−0.25 (−0.72 to 0.38)
V. harveyi				1

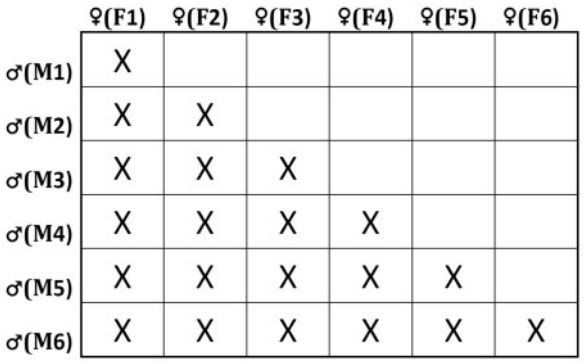

Figure 1. Representation of the 21 pair-mated families produced as a result of a half-diallel mating design. Source of broodstock. USA Farm 1 = F1, M3, M4. USA Farm 2 = F2, F3, M1, M2. British Columbia = F4, F5, F6, M5. Chile = M6.

Ocean acidification challenge

Within the first 2 days post-fertilization, *C. gigas* develop from an egg (0% shell) to D-hinge larvae (~80% shell) (Waldbusser *et al.*, 2015). This period is considered the most sensitive life-history stage of bivalves to ocean acidification (Waldbusser *et al.*, 2015; Kapsenberg *et al.*, 2018) with the shell size of D-hinge larvae being appreciably smaller with decreasing aragonite saturation state (Barton *et al.*, 2012; Frieder *et al.*, 2017). We evaluated genetic differences in larval shell size, as a proxy of larval calcification, to ocean acidification by adding 1 ml of fertilized egg suspension from each family (Spawning and crosses section) to duplicate 15-ml falcon tubes with screw cap lids and filling the tube with seawater collected from BS17 with no head space. The final concentration was 50 fertilized eggs ml^{-1}. Seawater used was collected from 5 and 70 m. We also included a third treatment of seawater collected from 70 m that was vigorously aerated overnight. Aragonite saturation of each treatment was estimated by collecting triplicate seawater samples prior to ocean acidification challenge, poisoning with saturated $HgCl_2$ and measuring temperature, pH, salinity, and total alkalinity as per Seawater collection section. Sealed falcon tubes containing larvae were incubated horizontally in an orbital shaker at 50 rpm and 23°C for 48 h (Eppendorf New Brunswick™ Excella® E-24R). Larvae from each falcon tube were concentrated by centrifugation (1000×*g*, 5 min), and the supernatant was taken for chemical analysis. Larvae were preserved in 10% neutral buffered formalin. Digital images of 30 larvae from each family per treatment were taken using Zeiss Axio Vert.A1 inverted microscope and Axiocam ERc 5s camera to determine shell length (longest axis perpendicular to the hinge) of normally developed larvae only. Normally developed larvae were characterized by a straight hinge, smooth curvature along the edge of the valve, and the appearance of tissue within the translucent shell (Waldbusser *et al.*, 2015). Images were analysed using Zeiss Zen Pro digital imaging software.

Disease challenge

The *V. harveyi* (strain 2018-BS-005) used in the disease challenge is a pathogenic strain isolated from a mass mortality event of juvenile and adult *C. gigas* in Baynes Sound, Canada, during the summer of 2018. *Vibrio harveyi* was grown overnight in tryptone soy broth containing 2% NaCl at 23°C under constant agitation at 200 rpm. The culture was centrifuged (1000×*g*, 15 min), and cell pellet was washed and resuspended in sterile seawater. The titre of *V. harveyi* inoculum was estimated by serial dilution and plating on tryptone soy agar + 2% NaCl. Colonies were enumerated after incubation at 23°C for 48 h.

Larvae from each family (6 days post-fertilization) were dispensed at 150 larvae $well^{-1}$ into 12-well tissue culture plates and resuspended to the final volume of 3 ml $well^{-1}$. A 50-μl aliquot of *V. harveyi* suspension (10^7 *V. harveyi* cells per well) or sterile seawater (negative control) was added to each well. Larvae were fed with 10^6 cells of *C. calcitrans*. Triplicate challenge and control wells were prepared for each family. Plates were incubated at 23°C, and live/dead counts of larvae were performed using a compound light microscope and Sedgewick-Rafter counting

chamber at 4 days post-inoculation according to the criteria outlined in Richards *et al.* (2015). Dead larvae were easily recognized by the lack of movement in their velar cilia and bleached appearance compared with the darker brown of viable larvae.

Heritability

Genetic parameters were estimated using MCMCglmm package in R (Hadfield, 2010), which allows the fitting of variance structures associated with pedigrees under an animal model. Animal models are a form of mixed-effect model used to segregate environmental and genetic effects on an animal phenotype and are especially powerful because they can be used in the absence of a fully crossed breeding design (Wilson *et al.*, 2010). Larval size to ocean acidification challenges (continuous data) and survival to *V. harveyi* challenge (binary data) was fitted to the mixed-effects linear model:

$$y = \mu + \text{Animal} + \text{Dam} + e,$$

where μ is the population mean, Animal is a random effect due to the additive effects of an individual's genetic makeup (additive genetic variance), Dam is a random effect due to the mothers' contribution to offspring phenotype including not only nuclear genes but also all the component within an egg (maternal transcript, organelles, and nutrients), and e is the random residual error. Incorporating maternal effects improved the accuracy of the model. Models were run with 1 500 000 iterations, with a burn-in of 500 000 iterations, and a thinning rate of 500. Estimates of additive genetic and residual variance were calculated from the modes of the posterior distribution, and a Bayesian equivalent of 95% confidence intervals (CI) was obtained by calculating the values of estimate that bound 95% of the posterior distributions. Narrow-sense heritability, or the proportion of total phenotypic variation that is additive genetic in origin, was estimated under the animal model described above as

$$h^2 = \text{Va}/(\text{Va} + \text{Vm} + \text{Ve}),$$

where Va, Vm, and Ve are the variances attributed to additive genetic, maternal, and residual error effects, respectively. The breeding value for each individual broodstock was extracted from the animal model, and linear regression was used to determine genetic correlations between traits.

Results

Seawater profile

Table 1 provides the temperature, salinity, pH, total alkalinity, and aragonite saturation state of seawater samples collected from 5 and 70 m. Physiochemical changes from vigorously aerating 70 m seawater sample are also presented in Table 1. Aragonite saturation for seawater samples at 70, 5, and 70 m + aeration was estimated to be 0.9, 1.6, and 2.3, respectively.

Ocean acidification challenge

Aragonite saturation level of natural seawater samples had a significant effect on shell length of D-hinge larvae at 48 h post-fertilization ($p < 0.05$) with the larval length (mean ± standard deviation) of 67.2 ± 4.4, 72.3 ± 4.2, and 73.2 ± 5.1 at seawater aragonite saturation states of 0.9, 1.6, and 2.3, respectively. There was also a significant family-by-environment interaction on shell length ($p < 0.05$) with families 01 and 04 not developing to D-hinge larvae under conditions of aragonite undersaturation ($\Omega_{\text{aragonite}} = 0.9$), whereas the shell length of four families (13, 19, 20, and 21) was not affected by aragonite saturation ($p > 0.05$). The remaining families had smaller shell lengths when aragonite was undersaturated ($p < 0.05$, Figure 2).

Narrow-sense heritability for larval shell size at 48 h post-fertilization was 0.151 (CI 0.138–0.171), 0.144 (CI 0.130–0.161), and 0.095 (CI 0.085–0.106) for seawater aragonite saturation states 0.9, 1.6, and 2.3, respectively. Maternal effects (m^2) accounted for 14.1% (CI 12.8–15.3%), 13.3% (CI 12.0–14.3%), and 9.1% (CI 8.1–9.9%) of larval shell size at aragonite saturation states of 0.9, 1.6, and 2.3, respectively. A correlation of estimated breeding values (EBVs) revealed that parents whose offspring were larger in normal conditions ($\Omega_{\text{aragonite}} = 1.6$) tended to be larger in aragonite undersaturated conditions ($\Omega_{\text{aragonite}} = 0.9$) [Table 2 Pearson correlation, $r = 0.63$ (95% CI 0.09–0.88), $p < 0.05$].

Vibrio harveyi challenge

The survival of *C. gigas* families to experimental infection with *V. harveyi* (20×10^8 CFU/ml) ranged from 0 to 100% (Figure 3c, average survival = 48.1%). The narrow-sense heritability of this trait (survival: live/dead) was found to be moderate ($h^2 = 0.253$, CI 0.232–0.266). Maternal effects also accounted for 25.2% (CI 23.5 and 26.8%) of the difference in survival between the families.

Genetic correlation between larval shell size and *Vibrio* survival

EBVs did not correlate between larval shell size in aragonite undersaturated conditions ($\Omega_{\text{aragonite}} = 0.9$) and survival to *V.*

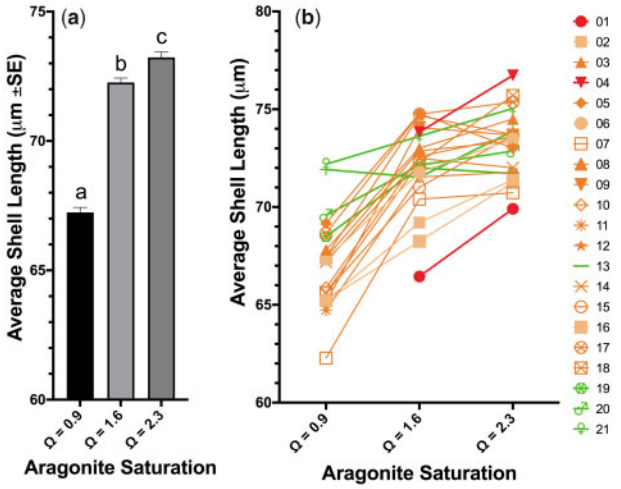

Figure 2. Average shell length of *Crassostrea gigas* larvae at 2 days post-fertilization. (a) Average shell length (μm ± SE) of *C. gigas* population in seawater with estimated aragonite saturation state of 0.9, 1.6, and 2.3. Different letters indicate significant differences between treatments ($p < 0.05$). (b) Genotype reaction norms for average shell length at each aragonite saturation state. Green line represents four families whose shell length was not affected by aragonite saturation state ($p > 0.05$), whereas red line represents two families that failed to develop to D-hinge larvae in aragonite undersaturated conditions.

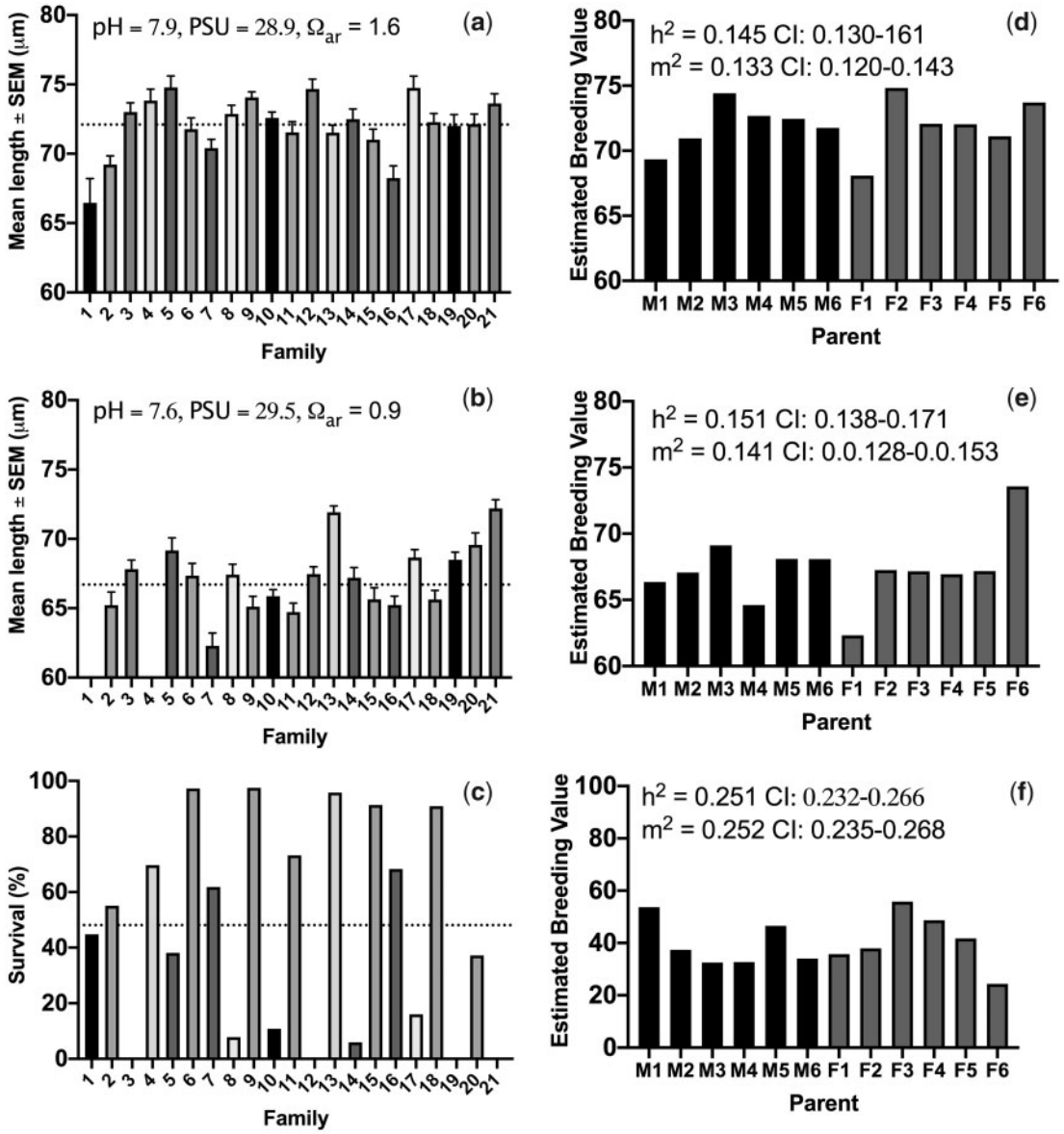

Figure 3. Phenotypic differences for average shell length and survival of *Crassostrea gigas* larvae. Average shell length (μm ± SE) for each family at (a) aragonite undersaturated ($\Omega_{aragonite} = 0.9$) and (b) over-saturated conditions ($\Omega_{aragonite} = 1.6$) at 2 days post-fertilization, respectively. (c) Average survival for each family exposed to *Vibrio harveyi* at 4 days post-inoculation. The EBVs for each sire (M1–M6) and dam (F1–F6) for larval size at aragonite undersaturated (d), normal conditions (e), and larval survival to *V. harveyi* (f). Heritability and maternal effects were estimated using MCMCglmm package in R (Hadfield, 2010). h^2, narrow-sense heritability, m^2, maternal effects.

harveyi (Figure 4, linear regression, $r^2 = 0.24$, $F_{1,10} = 3.052$, $p > 0.05$).

Discussion

The main findings of this study indicate that additive genetic variation explains a low, but nonzero, proportion of the total phenotypic variation in larval shell length of *C. gigas* grown in aragonite undersaturated conditions, and genetic selection of *C. gigas* for increase resistance to *V. harveyi* is unlikely to impact larval sensitivity to ocean acidification. Finally, our data provide compelling evidence that aquaculture hatchery production and domestication may have inadvertently produced populations of *C. gigas* that are less sensitive to ocean acidification. These data are very valuable to the aquaculture industry; *C. gigas* is one of the most important aquaculture species in Northern America (Dumbauld *et al.*, 2009), but summertime aragonite thresholds in the coastal waters of the NE Pacific Ocean are projected, within a few decades, to decline to a level that induces abnormal larval development and survival in *C. gigas* (Evans *et al.*, 2019).

Our research builds upon previous studies investigating adaption of oysters to ocean acidification and disease (Parker *et al.*, 2009; Waldbusser *et al.*, 2015; Goncalves *et al.*, 2017; Stapp *et al.*, 2018). Genetic selection over multiple generations in aquaculture hatcheries for improved growth rate and adult survival has resulted in oyster populations that are less sensitive to aragonite undersaturated conditions compared to non-selected or wild

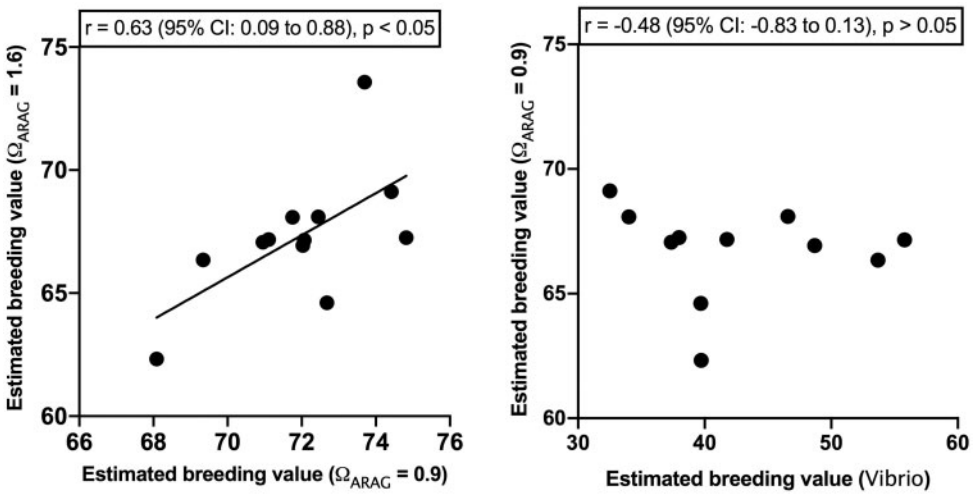

Figure 4. Pearson correlation of EBVs for *Crassostrea gigas* parents. (a) EBVs for larval size at aragonite undersaturated and normal conditions. (b) EBVs for larval size at aragonite undersaturated conditions and survival to *Vibrio harveyi*.

populations (Parker *et al.*, 2011; Durland *et al.*, 2019). Despite comprehensive genetic and physiological characterization of domesticated oysters to corrosive seawater (Goncalves *et al.*, 2017; Stapp *et al.*, 2018; Durland *et al.*, 2019; Fitzer *et al.*, 2019), it is poorly understood why these domesticated populations are more resilient to ocean acidification. A standard aquaculture practice is to cull slow-growing larvae in the hatchery to synchronize and reduce the time taken for larvae to metamorphose to spat (Taris *et al.*, 2006, 2007), and we consider that this size-related selective pressure may have inadvertently produced domesticated oyster populations with increase resilience to ocean acidification. In our experiment, oyster broodstock that produce larger D-hinge larvae in normal conditions have a tendency to also produce larvae with greater resilience to ocean acidification (Figure 4a).

Commercial aquaculture hatcheries in the NE Pacific have installed chemical buffering systems to dose sodium carbonate for repairing the aragonite saturation state of seawater (Barton *et al.*, 2015). Our data indicate that vigorous aeration of seawater for ~12 h can also repair the aragonite saturation state of seawater and increase the mean shell length of D-hinge larvae at 48 h post-fertilization from $67.2 \pm 4.4\,\mu m$ ($\Omega_{aragonite} = 0.9$) to $73.2 \pm 5.1\,\mu m$ ($\Omega_{aragonite} = 2.3$). In the genetic population of oysters we sampled as broodstock, we observed no correlation in the EBVs for resilience to ocean acidification and survival to *V. harveyi*, indicating that selection for one of these traits is unlikely to influence the other (Figure 4). However, we still recommend the breeding objectives for the oyster industry to be focused on disease resistance and use an engineering solution in the hatchery, such as vigorous aeration or pH buffering using sodium carbonate (Barton *et al.*, 2015), to repair aragonite saturation of seawater. The low heritability for larval shell length in aragonite undersaturated conditions means the response to selection, or improvement each generation, would be close to negligible.

Naturalized populations of *C. gigas* also have an important social and ecological role (Katsanevakis *et al.*, 2014), protecting the tidal flat against storm erosion (Walles *et al.*, 2015), increasing the biodiversity and abundance of macroinvertebrates (Markert *et al.*, 2010), and providing important feeding areas for fishes and shorebirds (Herbert *et al.*, 2018). These ecosystems or oyster reefs are also potentially threatened by ocean change (Parker *et al.*, 2013). The measures of heritability and genetic correlations between ocean acidification and disease tolerance are the important first step in evaluating whether natural populations of *C. gigas* have the potential to evolve, but the ability of natural *C. gigas* populations to adapt to ocean change also depends on the selective pressure applied during larval development, which is a complex and nonlinear process (Chevin *et al.*, 2010). For example, periods of carbonate corrosive conditions in coastal waters of western Canada are variable throughout the year and may not coincide with *C. gigas* spawning and stages of early larval development (Evans *et al.*, 2019). Efforts to model population growth rates for *C. gigas* by combining evolutionary genetics with climatic projections, such as a mechanistic population model (Burger and Lynch, 1995), are now warranted. Such information will be critical for understanding if *C. gigas* possess the capacity to adapt to the current pace of ocean change.

Funding

The authors acknowledge funding provided to T. Green from Canada Research Chair Program (950-231856) and Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grant (RGPIN-2018-06761).

Acknowledgements

The authors are grateful of the assistance provided by the team at VIU's Deep Bay Marine Field Station: Carl Butterworth, Rachel Cowling, Sarah Leduc, Shannon Schmunk, and Julie Vandenbor.

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Handling editor: Fabrice Pernet