Direct and indirect responses to selection on individual body weight in the Pacific oyster (Crassostrea gigas)

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Abstract

Three experiments were performed to examine the heritability of body weight among adult Pacific oysters (Crassostrea gigas) evaluated in Yaquina Bay, Oregon, USA, and to determine if selection on individual body weight could result in changes in offspring survival and yield. The first two experiments utilized midparent–offspring regressions to estimate the heritability ($h^2$) of adult oyster body weight and the coheritability ($h_{x,y}$) between adult midparent body weight and offspring performance, including juvenile average body weight, survival and yield as well as adult survival and yield. In Experiment 1 both parents and offspring were evaluated in an “upriver” environment in Yaquina Bay. In Experiment 2 parents were evaluated in a “downriver” environment, while offspring were evaluated in an “upriver” environment. Experiment 3 contrasted average body weight, survival, and yield of offspring (evaluated upriver) derived from three large sires and three small sires mated to the same five females that were chosen at random (all parents evaluated downriver). In Spring 2002, 12 full-sib families from Experiment 1, 19 families from Experiment 2, and 26 families from Experiment 3 were stocked into lantern nets and suspended in Yaquina Bay. Measurements of yield (kg tier$^{-1}$), average body weight (g), and survival (%) were recorded after one and two growing seasons in the field. Heritability estimates for adult body weight at harvest ranged from 0.313 (±0.083) in Experiment 1 to 0.003 (±0.073) in Experiment 2. In Experiment 3, average body weight did not differ between offspring derived from large sires and offspring derived from small sires ($P=0.47$). Significant negative coheritability estimates were observed between adult midparent body weight and offspring survival in both Experiment 1 and Experiment 2. Significant negative coheritability estimates between adult midparent body weight and offspring yield were observed in Experiment 2 but not in Experiment 1. In Experiment 3, offspring derived from large sires had significantly lower survival and yield than offspring derived from small sires. These results show adult oyster body weight to be heritable but also subject to site-specific adaptation such that selection in the downriver Yaquina Bay environment was ineffective at changing average body weight in the upriver environment. Negative coheritability estimates between performance traits indicate that adult oyster body weight may be a poor indirect measure of oyster yield potential, and that selection solely for increased body weight could lead to a decrease in offspring yield.

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Keywords: Pacific oyster; Crassostrea gigas; Heritability; Coheritability; Body weight; Survival; Yield

1. Introduction

Shellfish farmers along the west coast of the United States have expressed interest in developing high-yielding strains of oysters through selective breeding...
(Hedgecock et al., 1997; Pacific Shellfish Institute, 2003). Unfortunately, direct selection for yield is notoriously difficult because it is not yield, per se, but rather it’s many causal components (e.g. feed conversion efficiency, disease resistance, etc.) that are under genetic control (Blum, 1988). As a result, plant and animal breeders have tried to identify easily measured traits that can be used to indirectly score a genotype’s yield potential (i.e. an “indicator trait”; Ceccerelli et al., 1991). An effective indicator trait for yield in any agronomically important species should (1) possess genetic variation (2) be causally or genetically linked to yield, and (3) be easy, inexpensive, and quick to screen (Ceccerelli et al., 1991; Falconer and Mackay, 1996).

An attractive indirect measure of oyster yield is individual growth rate. The heritability of growth traits (including body weight and growth rate) has been estimated for a wide variety of shellfish species such as clams (Rawson and Hilbish, 1990; Hadley et al., 1991), mussels (Mallet et al., 1986; Stromgren and Nielsen, 1989), and scallops (Ibarra et al., 1999; Perez and Alfonsi, 1999). Heritability of growth traits has also been reported for oysters such as Ostrea edulis (Newkirk and Haley, 1983; Toro and Newkirk, 1990), O. chilensis (Toro et al., 1994), Saccostrea commercialis (Nell et al., 1996, 1999), S. cucullata (Jarayabhand and Thavornyutikarn, 1995), and Crassostrea virginica (Haley and Newkirk, 1982; Paynter and Dimichele, 1990). Only two estimates of heritability for body/meat weight exist for adult, harvest-sized Pacific oysters (Crassostrea gigas). Lannan (1972) reported the broad-sense heritability of Pacific oyster whole body weight at 18 months of age to be 0.33±0.19 (±SE), which includes both additive and non-additive sources of genetic variation. Hedgecock et al. (1991) estimated the narrow-sense heritability of meat weight of harvest-sized Pacific oysters to be approximately 0.20.

Although body weight is an important commercial trait, improvement of oyster production will be dependant upon increasing yield, which is a function of both average individual body weight and average family survival. Unlike body weight, survival and yield cannot be measured effectively on a single individual and therefore require family-level measurements to be treated as continuous characters (e.g. Langdon et al., 2003). Unfortunately, family selection has several disadvantages compared with individual (or mass) selection. Selection intensity is typically lower when family selection is applied versus individual selection due to the ability to evaluate more individuals than families. In addition, phenotypic variation among family means is typically smaller than among individuals. Together, these result in a lower selection differential when family selection is applied compared to individual selection (Gall, 1991; Falconer and Mackay, 1996). Furthermore, resources and labor demands associated with the production, maintenance, and tracking of family groups, may prevent the adoption of family-based breeding schemes by commercial farmers (Tave, 1995). Regardless of the advantages, selection for increased body weight using individual selection is only expected to increase yield if a positive genetic correlation exists between the two traits.

In this study, three sets of experimental crosses were produced concurrently to address two primary questions: 1. What is the narrow-sense heritability of body weight among adult Pacific oysters evaluated in Yaquina Bay, Oregon?; and 2. Could selection for individual body weight result in a correlated response in average offspring survival or yield? The first two experiments utilized midparent–offspring regressions to estimate the heritability of individual oyster body weight and coheritability between midparent body weight and offspring survival and yield. The third experiment contrasted the performance of offspring from three large sires with the performance of offspring from three small sires.

2. Methods

2.1. Selection of parents

Individually tagged adult oysters from unselected pedigree families were collected from lantern nets suspended at two locations within Yaquina Bay, Oregon (44.6° N, 124.1° W) during Summer 2001. The first site was located approximately 3 km from the mouth of Yaquina Bay (“downriver”), the second site was located approximately 15 km up the Yaquina River at a commercial shellfish lease-site (“upriver”). Weight of tagged oysters was periodically measured from plant-out in Spring 1998 until harvest in Summer 2001 as a continuation of the research initiated by Brooks (2000). No significant family x site interaction effect on average parental family body weight was found between the upriver and downriver sites after two growing seasons in the field (Spring 1998–Winter 1999), however, a significant site effect was found (unpublished data). Pair-wise, assortative crosses based on live adult body weight after 700 d in the field were made within upriver broodstock (“Experiment 1”) and within downriver broodstock (“Experiment 2”). Crosses among related families were avoided. An additional set of families was created by crossing the three largest males (147 g mean weight after 700 d in the field were made within upriver broodstock (“Experiment 1”) and within downriver broodstock (“Experiment 2”).
live body weight after 700 d in the field) and the three smallest males (68 g mean live body weight after 700 d in the field) from the downriver population with five females from the downriver population (i.e. 6 male × 5 female factorial cross; “Experiment 3”). Dams in Experiment 3 were randomly selected with the only restriction being that they possessed a sufficient number of eggs to contribute to six crosses. The average dam live body weight used in Experiment 3 was 153.56 g.

2.2. Hatchery and nursery protocol

Broodstock were held in 18 °C sand-filtered seawater and fed a mixture of Isochrysis galbana (Iso) and Cheatoceros calcitrans (Cc) at a concentration of approximately 50,000 to 80,000 cells ml⁻¹ until ready to spawn. Animals were stripped-spawned as per Langdon et al. (2003) in Fall 2001. Fertilized eggs were allowed to develop into veliger larvae (D-larvae) for 24 h in cross-specific 20-l containers filled with 25 °C, 0.2-μm filtered seawater. D-larvae from each cross were then stocked into family-specific 100-l larval culture containers at a concentration of 10 larvae ml⁻¹. Larvae were fed daily with a mixture of Iso and Cc at concentrations ranging from 30,000 to 80,000 cells ml⁻¹, depending on age (Breese and Malouf, 1975). Larval tanks were drained and re-filled twice per week with 0.2-μm filtered seawater at 25 °C. During water changes, larvae were retained on 37 μm sieves for the first week and 80 μm sieves for the second week. During the third week, larval cultures were poured onto 243 μm and 80 μm sieves placed in series. All larvae retained on the 243 μm sieve were exposed to 2 × 10⁻⁴ M epinephrine in order to induce metamorphosis (Coon et al., 1986). Larvae retained on the 80 μm sieve were returned to the larval tank and allowed to grow until the next water change. In total, 12 crosses were made for Experiment 1, 23 crosses were made for Experiment 2 and 30 crosses were made for Experiment 3.

Successfully metamorphosed spat were transferred to family-specific 15-cm diameter upwellers held in a semi-recirculating system which received approximately 6 exchanges d⁻¹ of 23 °C UV-irradiated 1-μm filtered seawater. Once all larvae had metamorphosed (approximately 4 weeks post spawn), the number of spat per 15-cm upweller was randomly thinned to 10,000. Spat were allowed to grow until retained on a 1.4 mm sieve, then transferred to larger family-specific 28-cm diameter upwellers. These larger upwellers were supplied with 18 °C 1-μm filtered seawater delivered at approximately 2.8 l min⁻¹ and fed an Iso/Cc mixture at a final concentration of approximately 50,000 to 80,000 cells ml⁻¹. Once all animals were transferred from the 15-cm upwellers, the number of oysters per 28-cm upweller was randomly thinned to 5000. Oysters were allowed to grow until retained on a 6.4 mm sieve before being transferred to family-specific spat bags (2 mm mesh) held in storage tanks. Storage tanks received ambient 1-μm filtered seawater (mean 9.5 °C; range 7.0 °C to 13.68 °C) and batch-fed to a final concentration of approximately 100,000 cells ml⁻¹ of a Cc/Iso mixture for 8 h, twice per week. The reduced temperature and limited feeding were intended to slow oyster growth, minimizing variation in spat weight within (due in part to variable setting dates) and between cultures prior to planting in the field (Langdon et al., 2003). After approximately 80% of the oysters were sieved from the 28-cm upwellers, spat in the storage tank were counted and weighed for subsequent planting in the field.

Due to variable performance in the nursery, some crosses did not produce enough spat to plant-out and evaluate in the field. All 12 crosses made for Experiment 1, 19 of 23 crosses made for Experiment 2, and 26 of 30 crosses made for Experiment 3 were evaluated in the field.

2.3. Field trials

Oyster planting, sampling and harvest methods were the same for all three experimental crosses. In Spring 2002, 50 randomly selected oysters from each family were weighed and stocked into each of two replicate compartments in each of five vertical blocks in ten-tier lantern nets (0.3 m diameter, 2 mm mesh) resulting in a total of 10 replicates per family. Blocking was conducted to account for variation in performance due to water depth (Langdon et al., 2003). Variable survival in the nursery resulted in some families having fewer than the desired number of individuals and therefore less than ten replicates. Stocked lantern nets were suspended from a raft at the upriver field site. In January of 2003 (317 d in the field; oysters referred to as “juveniles”) all live oysters from each replicate were cleaned of biotic and abiotic fouling, counted, and the collective weight of all live animals measured to the nearest gram. After measurements were taken, oysters were stocked into 0.5-m diameter lantern nets (5 mm mesh), and re-suspended at the upriver site. These measurements were recorded again in Fall 2003 (after 640 d in the field; oysters referred to as “adults”). The data collected allowed for replicated estimates of average family bag weight (i.e. yield; kg replicate⁻¹) and survival (%) in the field. Average individual oyster body weight per replicate was calculated by dividing the total bag weight by the number of live oysters. As a result, error terms in
subsequent analyses are based on variation among average bag measurements and not among individual oysters. In addition, note that average body weight includes both the shell and soft tissue. Although, from a commercial standpoint, the desired character is “meat weight” (excluding shell), we chose to use whole live weight for several reasons. It was logistically prohibitive to shuck all oysters used in this study and therefore results would have been based on a sub-sample of the total number of oysters planted in the field. In addition, seasonal variation in reproductive condition can result in soft tissue weight varying dramatically depending upon when measurements are taken (Quayle, 1988). Lastly, Langdon et al. (2003) found live weight to be positively correlated with soft tissue weight across a wide range of growing environments ($r=0.71–0.93$). To confirm this relationship in the present study, the correlation coefficients between live individual body weight and soft tissue weight were determined using a sub-sample of oysters after accounting for block and family effects. StowAway data loggers (Onset Corp, MA, USA) recorded temperature every 2 h at a depth of approximately 1 m for the duration of the 640-day field trial.

2.4. Data analysis

Unless otherwise stated all statistical analyses were performed using SAS statistical software (SAS Institute, Cary, NC, USA). Normal probability plots and residual plots were used to assess normality and equality of variance for all performance measures in Experiments 1, 2, and 3 and to identify appropriate transformations when required.

ANCOVA was used to test for possible bias due to variation in initial plant-out weight on field performance after accounting for the effects of block, experiment (i.e. parental source population), and family nested within experiment. If the covariate term (initial plant-out weight) was significant, field performance values for each replicate unit were adjusted along the slope of the covariate to a common plant-out weight (e.g. Langdon et al., 2003). These adjusted values were used in all subsequent analyses.

2.4.1. Heritability of individual body weight

The slopes of midparent–offspring regressions were used as an estimate of the narrow-sense heritability of adult oyster body weight after two growing seasons in the field for Experiments 1 and 2 (Falconer and Mackay, 1996; Lynch and Walsh, 2000). Due to variable numbers of replicates per family in the field, slopes and standard errors of the midparent–offspring regressions were computed as per Falconer (1963). T-tests were performed to determine if the slopes were significantly greater or less than 0 (Sokal and Rohlf, 1995).

In Experiment 3, analysis of variance and linear contrasts were used to determine if average body weight at harvest differed significantly between offspring of the three large sires and offspring of the three small sires. The fixed-effects model included block, sire, dam and sire x dam interaction.

2.4.2. Coheritability between parental body weight and offspring performance

Coheritability is defined here as the slope of the regression between adult midparent body weight and offspring performance (Falconer and Mackay, 1996) for each measured character except average adult body weight (addressed in Section 2.4.1). Just as heritability ($h^2$) can be used to estimate the expected response ($R_x = h^2_x S_x$) to selection for a single character from selection differential $S_x$, coheritability ($h_{x,y}$) can be used to estimate the expected correlated response in one character ($y$) to selection on a separate correlated character ($x$; $R_y = h_{x,y} S_x$; e.g. Munch et al., 2005).

The coheritabilities of adult midparent body weight with offspring survival and yield as both juveniles (317 d in the field) and adults (640 d in the field) were computed for Experiments 1 and 2. All slopes were again weighted as per Falconer (1963) to account for unequal number of replicates per family. T-tests were performed to determine if the slopes were significantly greater or less than 0 (Sokal and Rohlf, 1995). The coheritability is interpreted as the change in offspring juvenile body weight (g), survival (%) and yield (kg) as well as adult survival (%) and yield (kg), per 1 gram change in adult midparent body weight (Falconer and Mackay, 1996; Munch et al., 2005).

Differences in offspring survival and yield resulting from sire-based selection in Experiment 3 were determined by contrasting the performance of offspring derived from the three large sires with the performance of offspring derived from the three small sires. Contrasts between these two groups were performed for average juvenile body weight, survival and yield as well as adult survival and yield. The fixed-effects model included block, sire, dam and sire x dam interaction.

2.4.3. Impact of density-dependent oyster performance

The growout environment in this study was designed to emulate actual commercial growing conditions. As a result, stocking density within each replicate lantern net compartment was allowed to vary as a function of the growth rate and survival of individuals within each replicate. Two correlations were examined to assess the possible impact of variable stocking density on the phenotypic expression of body weight and survival. First,
the correlation between offspring adult body weight and offspring adult survival was measured to determine if an increase in average family survival (and therefore a higher stocking density) was associated with a decrease in average individual body weight. Second, the correlation between juvenile offspring survival (measured at day 317) and offspring growth rate (g d$^{-1}$) during the second growing season (day 317 to 640) was used to determine if families with high stocking densities entering the second growing season exhibited slower than average second-season growth rate.

3. Results

Average water temperature over the entire field season was 13.9 °C, ranging from a winter low of 7.2 °C to a summer high of 23.2 °C (Fig. 1). Water temperatures exceeded 20 °C for extended periods during the summers of 2002 and 2003.

Initial plant-out body weight was found to have no significant effect on offspring performance as juveniles or as adults. Consequently, no correction for variable plant-out body weight was applied. Survival data in all experiments were arcsine transformed and adult offspring yield in Experiment 3 was log-transformed to meet assumptions of normality [Sokal and Rohlf, 1995].

Trends in body weight, survival and yield over time were similar across all three experiments (Fig. 2). Individual weight, averaged across all three experimental crosses, increased from 46.3 g at day 317 to 128.6 g at day 640 (Fig. 2). Correlation coefficients between live individual body weight (including shell and soft tissue weight) and soft tissue weight were highly significant ($P<0.001$) and ranged from 0.63 to 0.77. Average survival decreased linearly with time, from 58.6% after the first growing season to 26.7% at harvest. Yield increased rapidly during the first growing season to 1.36 kg rep$^{-1}$, and reached 1.72 kg rep$^{-1}$ after the second growing season.

Heritability ($h^2$) of body weight after two growing seasons in the field in Experiment 1 (both parents and offspring raised upriver) was 0.313±0.083 (bold value Table 1). The heritability of body weight at harvest in Experiment 2 did not differ significantly from zero ($h^2=0.003±0.073$; bold value Table 1). In Experiment 3, adult average body weight of offspring derived from the large sires was not significantly different from the adult average body weight of offspring derived from small sires ($P=0.148$; bold value Table 2).

The coheritability between adult midparent body weight and juvenile offspring average body weight did not differ from zero in Experiment 1 ($h_{x,y}=0.022±0.012$) or in Experiment 2 ($h_{x,y}=-0.061±0.036$; Table 1). In addition, contrasts performed in Experiment 3 showed juvenile average body weight of offspring from large sires did not differ significantly from juvenile average body weight of offspring from small sires ($P=0.664$; Table 2).

Coheritability estimates were significant between adult midparent body weight and both juvenile offspring survival (Experiment 1, $h_{x,y}=-0.213±0.090$; Experiment 2, $h_{x,y}=-0.222±0.057$) and adult offspring survival (Experiment 1, $h_{x,y}=-0.262±0.106$; Experiment 2, $h_{x,y}=-0.186±0.053$; Table 1). Similarly, contrasts performed in Experiment 3 indicated that offspring from
large sires had significantly poorer survival than offspring from small sires as both juveniles and adults ($P<0.0001$; Table 2).

Coheritability estimates between adult midparent body weight and juvenile and adult offspring yield were significantly less than zero in Experiment 2 ($h_{x,y} = -0.005 \pm 0.002$ and $-0.011 \pm 0.004$, respectively) but not in Experiment 1 ($h_{x,y} = -0.004 \pm 0.002$ and $-0.011 \pm 0.006$, respectively), although the slopes were also negative and quite similar between the two experiments (Table 1). Contrasts performed in Experiment 3 indicated that offspring from large sires had significantly lower yields as juveniles and as adults.

Table 1

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Parental test site</th>
<th>Offspring test site</th>
<th>Offspring trait</th>
<th>( N )</th>
<th>( \bar{n} )</th>
<th>( N \bar{n} )</th>
<th>Juvenile (day 317)</th>
<th>Adult (day 640)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>( h_{x,y} ) (SE)</td>
<td>( h^2 ) or ( h_{x,y} ) (SE)</td>
</tr>
<tr>
<td>1</td>
<td>Upriver</td>
<td>Upriver</td>
<td>Average body wt (g)</td>
<td>12</td>
<td>9.83</td>
<td>117</td>
<td>0.022 (0.012)</td>
<td><strong>0.313</strong> (0.083)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Survival (%)</td>
<td>12</td>
<td>9.83</td>
<td>117</td>
<td>-0.213* (0.090)</td>
<td>-0.262* (0.106)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Yield (kg rep(^{-1}))</td>
<td>12</td>
<td>9.83</td>
<td>117</td>
<td>-0.004 (0.002)</td>
<td>-0.011 (0.006)</td>
</tr>
<tr>
<td>2</td>
<td>Downriver</td>
<td>Upriver</td>
<td>Average body wt (g)</td>
<td>19</td>
<td>8.53</td>
<td>158</td>
<td>-0.061 (0.036)</td>
<td><strong>0.003</strong> (0.073)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Survival (%)</td>
<td>19</td>
<td>8.53</td>
<td>158</td>
<td>-0.222** (0.057)</td>
<td>-0.186** (0.053)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Yield (kg rep(^{-1}))</td>
<td>19</td>
<td>8.53</td>
<td>158</td>
<td>-0.005* (0.002)</td>
<td>-0.011* (0.004)</td>
</tr>
</tbody>
</table>

\( N \) represents the number of families used in each experiment, \( \bar{n} \) represents the average number of replicate compartments measured per family and \( N \bar{n} \) is the total number of replicates measured per experimental cross. Heritability and coheritability estimates which differed from 0 at the $P<0.05$ and $P<0.01$ levels of significance are indicated with * or **, respectively.
The narrow-sense heritability estimated in Experiment 1 (where parents and offspring were both evaluated in the upriver environment) is consistent with published heritability estimates for adult shellfish body weight and growth rate (see review by Sheridan, 1997). The broad-sense heritability ($H^2$) of adult Pacific oyster body weight was reported by Lannan (1972) to be 0.33±0.19. The narrow-sense heritability of adult Pacific oyster meat weight was reported by Hedgecock et al. (1991) to be approximately 0.2. More recently, Ernande et al. (2004) found heritability of growth in one-year-old Pacific oysters dependent upon growth environment, with $h^2$ estimates ranging from 0.04±0.24 in a high-nutrient environment to 0.60±0.39 in a low-nutrient environment. The heritability estimates found in the present study are comparable to values reported for adult body weight and/or growth rate in other shellfish species such as O. edulis (0.24±0.20; Toro and Newkirk, 1990), Saccostrea cucullata (0.28±0.06, Jarayabhand and Thavornyutikarn, 1995) and Mercenaria mercenaria (0.43±0.06; Hadley et al., 1991).

Stocking density has been shown to affect shellfish growth rate (Jarayabhand and Newkirk, 1989; Holiday et al., 1991; Taylor et al., 1997; Southgate and Beer, 2000). The design of the experiments presented here allowed stocking density to vary as a function of survival and average body weight, which should be addressed when considering bias in heritability estimates. Increased average body weight could lead to elevated biomass per replicate and consequently decreased individual growth rate (e.g. Holiday et al., 1991; Rheault and Rice, 1996; Taylor et al., 1997). If these conditions constrained phenotypic variation, then the observed heritability of body weight would likely underestimate the true population heritability of body weight, and could explain the poor correlation between parent and offspring average body weight in Experiments 2 and 3. However, the significant and relatively high narrow-sense heritability measured in Experiment 1, in which density was also allowed to vary, suggest that variable stocking density was not entirely responsible for the low heritability estimates seen in Experiments 2 and 3. In addition, the absence of correlations between harvest average body weight and harvest survival, and between the number of oyster present at the interim measurement and growth rate during the second growing season (day 317 to day 640), suggests that stocking density did not significantly affect these results. Nevertheless, it is possible, based on research in other

### Table 2

**Direct (in bold) and correlated responses to selection in Experiment 3, where parents were evaluated at the downriver site and offspring evaluated at the upriver site**

<table>
<thead>
<tr>
<th>Trait</th>
<th>Juvenile (day 317)</th>
<th>Adult (day 640)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Large sire</td>
<td>Small sire</td>
</tr>
<tr>
<td>Body weight (g)</td>
<td>47.57</td>
<td>46.74</td>
</tr>
<tr>
<td>Survival (%)</td>
<td>47.55</td>
<td>54.13</td>
</tr>
<tr>
<td>Yield (kg rep$^{-1}$)</td>
<td>1.25</td>
<td>1.47</td>
</tr>
</tbody>
</table>

Linear contrasts were performed between the performance (average body weight, survival, and yield) of offspring derived from large and small sires after 317 and 640 d in the field.

No significant correlations were found between average family body weight at harvest and average family survival at harvest for Experiment 1 ($r=0.031$, $P=0.737$), Experiment 2 ($r=0.061$, $P=0.444$) or Experiment 3 ($r=-0.001$, $P=0.991$). In addition, the correlations between interim survival (i.e. stocking density) and growth rate (g d$^{-1}$) during the second growing season were not significant in Experiment 1 ($r=0.011$, $P=0.902$) and Experiment 2 ($r=0.031$, $P=0.695$), but was significant, and positive, in Experiment 3 ($r=0.184$, $P=0.006$). As a result, no attempt was made to correct performance for variable stocking densities.

### 4. Discussion

Heritability estimates of adult body weight differed dramatically between Experiment 1 (0.313±0.083) and Experiment 2 (0.003±0.073). The primary difference between the two experimental crosses was the environment in which the parents were evaluated. In Experiment 1 both parents and offspring were evaluated at the upriver site, while in Experiment 2 parents were evaluated at the downriver site and offspring were evaluated at the upriver site. These results suggest site-specific adaptations, with the resemblance between parent and offspring dependent upon environment (i.e. a genotype x environment interaction). Tidal influence and seasonal rainfall can result in large differences in temperature and salinity between the upriver (15 km from the mouth of the bay) and downriver (3 km from the mouth of the bay) sites (unpublished data; Kjeldsen, 1966). Tolerance to elevated temperature (Beattie et al., 1980) and variable salinity (e.g. Castagna and Chanley, 1973) could explain variation in relative family performance across sites, resulting in poor correlations between parental performance downriver and offspring performance upriver.

The narrow-sense heritability estimated in Experiment 1 (where parents and offspring were both evaluated in the upriver environment) is consistent with published heritability estimates for adult shellfish body weight and growth rate (see review by Sheridan, 1997). The broad-sense heritability ($H^2$) of adult Pacific oyster body weight was reported by Lannan (1972) to be 0.33±0.19. The narrow-sense heritability of adult Pacific oyster meat weight was reported by Hedgecock et al. (1991) to be approximately 0.2. More recently, Ernande et al. (2004) found heritability of growth in one-year-old Pacific oysters dependent upon growth environment, with $h^2$ estimates ranging from 0.04±0.24 in a high-nutrient environment to 0.60±0.39 in a low-nutrient environment. The heritability estimates found in the present study are comparable to values reported for adult body weight and/or growth rate in other shellfish species such as O. edulis (0.24±0.20; Toro and Newkirk, 1990), Saccostrea cucullata (0.28±0.06, Jarayabhand and Thavornyutikarn, 1995) and Mercenaria mercenaria (0.43±0.06; Hadley et al., 1991).

Stocking density has been shown to affect shellfish growth rate (Jarayabhand and Newkirk, 1989; Holiday et al., 1991; Taylor et al., 1997; Southgate and Beer, 2000). The design of the experiments presented here allowed stocking density to vary as a function of survival and average body weight, which should be addressed when considering bias in heritability estimates. Increased average body weight could lead to elevated biomass per replicate and consequently decreased individual growth rate (e.g. Holiday et al., 1991; Rheault and Rice, 1996; Taylor et al., 1997). If these conditions constrained phenotypic variation, then the observed heritability of body weight would likely underestimate the true population heritability of body weight, and could explain the poor correlation between parent and offspring average body weight in Experiments 2 and 3. However, the significant and relatively high narrow-sense heritability measured in Experiment 1, in which density was also allowed to vary, suggest that variable stocking density was not entirely responsible for the low heritability estimates seen in Experiments 2 and 3. In addition, the absence of correlations between harvest average body weight and harvest survival, and between the number of oyster present at the interim measurement and growth rate during the second growing season (day 317 to day 640), suggests that stocking density did not significantly affect these results. Nevertheless, it is possible, based on research in other
shellfish, that variable stocking density may have biased the reported heritability estimates downward.

Coheritability estimates between adult midparent body weight (700 d in the field) and juvenile offspring average body weight (317 d in the field) did not differ significantly from zero in either Experiment 1 or Experiment 2. Further, there was no difference in average body weight at 317 d in the field between offspring of large sires and offspring of small sires in Experiment 3. These results suggest that either the two characters are not genetically correlated (but see Toro and Newkirk, 1990), average body weight in offspring had not differentiated sufficiently to statistically detect a response (e.g. Kincaid, 1983; McKay et al., 1986; Toro and Newkirk, 1990), or that, as suggested above, genotype × environment interactions mask the genetic similarities between adult parents and juvenile offspring. In the latter case, genotypes could have interacted with location (i.e. upriver versus downriver) and/or time (1997–1998 field trials for parents versus the 2002 field trial for offspring).

In all three experiments significant inverse relationships existed between adult midparent body weight and both juvenile and adult offspring survival (P<0.05), regardless of parental source population (upriver or downriver). In addition, an increase in adult midparent body weight resulted in significant decreases in yield in Experiments 2 and 3. Although stocking density may again bias these results, the literature suggests that survival is much less sensitive to variation in stocking density compared to growth rate (Holiday et al., 1991; Taylor et al., 1997). Further, the decrease in offspring survival with increased midparent body weight was seen at day 317 (after the first growing season), when the animals were still quite small (average individual body weight of 46 g), suggesting that stocking density was not the cause of the observed trend.

The fact that large parents produced poorer surviving offspring than small parents in the present study, implies that there may be a negative genetic correlation between body weight and survival. The biological mechanisms for these inverse correlations are unknown, however, the trade-off between growth rate and/or body size and survival has been reported in a variety of taxa (Li et al., 1996; Bradford et al., 1999; Miller et al., 2000; Norry and Loeschcke, 2002; Olsson and Shine, 2002). The inverse relationship between body weight and survival in shellfish may be in part due to reproductive stress and the tendency for reproductive effort (i.e. proportion of energy resources dedicated to reproduction) to be positively correlated with both mortality rate and body size (e.g. Bayne et al., 1983; Worrall and Widdows, 1984; Emmett et al., 1987; Roff, 1992; Moal et al., 2003; Ernande et al., 2004), resulting in size-specific mortality (e.g. Askew, 1972; Glude, 1975). This theory is consistent with findings of Beattie et al. (1980), who were successful in breeding high-surviving oyster strains by increasing their glycogen content during warm summer months, effectively reducing their reproductive effort. Ernande et al. (2004) suggested allocation of limited resources (food in this case) by Pacific oysters could necessitate a trade-off between energy used for growth and energy used for survival. It is also worth noting that the growing environment in Yaquina Bay during this experiment was stressful for the oysters (as evidenced in the low average survival), possibly due to high water temperatures in the summers of 2002 and 2003 (Fig. 2) as well as fluctuating salinity in winter (unpublished data). Some research suggests that the sign of the correlation between survival and growth rate (Norry and Loeschcke, 2002) and between survival and reproductive effort (Ernande et al., 2004) may be environment-specific. It is therefore possible that in more benign environments midparent size may be uncorrelated or even positively correlated with offspring survival and yield.

The inverse relationships between adult midparent body weight and offspring survival found in the present study differs from other reports in the literature that have considered the effects of selecting for increased oyster body weight on offspring survival. In O. edulis Newkirk and Haley (1983) found no difference in body weight between offspring of parents selected for increased body weight and unselected controls. They did, however, find that offspring of selected parents had significantly higher survival than offspring of unselected control parents, implying a positive genetic correlation between growth and survival. In a study utilizing midparent–offspring regression to estimate heritability of live weight in O. edulis, Toro and Newkirk (1990) found no correlated response in offspring survival. Jarayabhand and Thavornyutikarn (1995) found survival of S. cucullata derived from parents selected for increased growth rate tended to be higher than survival of offspring derived from unselected control parents, but the trend was not significant. The only comment on the cause of the observed mortality was by Newkirk and Haley (1983), who suggested handling mortality may have made differences in survival between genotypes more apparent. Both Beattie et al. (1980) and Boudry et al. (2004) selected for increase survival and saw no correlated response in individual body weight. Lastly, Ernande et al. (2004), found a strong positive correlation between growth and survival in one-year old Pacific oysters raised in France.

Results from this study confirm findings by other authors that suggest adult Pacific oyster body weight is
heritable (Hedgecock et al., 1991; Lannan, 1972). However, these results also suggest that adult oyster body weight may be sufficiently affected by genotype x environment interactions occurring within Yaquina Bay to render selection in the downriver environment ineffective at improving average body weight at the upriver environment. In addition, the negative coheritability estimates between midparent body weight and both offspring survival and offspring yield, suggest that individual body weight is an unreliable indirect measure of average family yield.

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