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Improvements in desirable traits of the Pacific oyster, *Crassostrea gigas*, as a result of five generations of selection on the West Coast, USA

Claudio Manoel Rodrigues de Melo [a], Evan Durland [b], Chris Langdon [b],*

[a] Laboratory of Marine Mollusks, Department of Aquaculture, Federal University of Santa Catarina, Florianópolis, SC 88061-600, Brazil
[b] Department of Fisheries and Wildlife, Coastal Oregon Marine Experiment Station, Hatfield Marine Science Center, Oregon State University, 2030, Newport, OR 97365, USA

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ABSTRACT

The Pacific oyster, *Crassostrea gigas*, is one of the most important global aquaculture species due to its potential high growth rates and tolerance of a wide range of environmental conditions; however, most farmers use seed from wild, non-domesticated stocks for production. In this study we estimated genetic parameters for performance traits of oysters from the Molluscan Broodstock Program (MBP), a family-based selective breeding program designed to improve yields of Pacific oysters on the West Coast, USA. Covariance components were obtained using AIREMLF90, and a multiple-trait animal model. A total of 15,236 records were analyzed from five generations of selectively bred oysters. Heritability estimates for field traits at harvest were all positive over the five analyzed generations, ranging from 0.58 ± 0.03 (3rd generation) to 0.30 ± 0.04 (5th generation) for yield, from 0.55 ± 0.03 (1st generation) to 0.12 ± 0.02 (4th generation) for survival, and from 0.51 ± 0.03 (2nd generation) to 0.40 ± 0.03 (4th generation) for mean individual weight at harvest (growth). Declines in heritabilities for survival and yield in the 4th and 5th generations were perhaps a result of changing ocean conditions due to increased upwelled hypoxic and acidified seawater occurring on the West Coast, USA, that affected the quality of seed from the MBP hatchery/nursery. Realized heritabilities were all positive and medium-to-high across generations, ranging to 0.11 ± 0.42 (for survival in the 3rd generation) to 1.20 ± 0.35 (for individual weight in the 5th generation); however, standard errors for realized heritabilities were high (ranging 0.15 to 1.47), especially in the 5th generation. There was a gradual improvement in genetic gains for survival and yield over the five generations of selection, resulting in accumulated gains of +15.7% and +19%, respectively, in the 5th generation; however, little improvement was achieved after the 2nd generation in genetic gain for individual weight, with an accumulated gain in the 5th generation of +11.3%. Realized gains for performance traits were less than predicted by genetic gains. Realized gain in survival consistently improved over the selection period, resulting in an accumulated gain of 11.7% in the 5th generation compared to that of wild, non-selected controls; however, gains in individual weight and yield at harvest were not consistent across generations and gains in the 5th generation were −9.8% and 0%, respectively, compared with those of controls, perhaps due to inconsistent genetic quality of control broodstock sampled from wild populations. Across generations, there were positive genetic correlations between yield and both survival (0.38 ± 0.04) and individual weight (0.90 ± 0.01) as well as between survival and individual weight (0.25 ± 0.04). Positive medium-to-high genetic correlations among harvest traits suggest that indirect gains in yield can be achieved by selection for either higher growth or survival.

Statement of relevance

The Pacific oyster is an important aquaculture species both globally and on the West Coast, US. This study describes long-term (over 5 generations) genetic and phenotypic responses of Pacific oysters planted at commercial farms, in response to selection for yield, survival and mean individual weight at harvest. The breeding program spanned a period of increased ocean upwelling and acidification on the West Coast, US, that may have reduced heritabilities for survival due to impacts of the quality of hatchery seed. Results will be of interest to other breeding programs for Pacific oysters in France, Australia and New Zealand, as well as breeders of other extensively farmed aquaculture species. Genetically improved broodstock will help support future oyster production under more challenging conditions, due to the global effects of acidification and warming of coastal waters.

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* Corresponding author.
E-mail addresses: claudio.melo@ufsc.br (C.M.R. de Melo), chris.langdon@oregonstate.edu (C. Langdon).

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1. Introduction

The Pacific oyster (*Crassostrea gigas*, Thunberg, 1793) is one of the most widely farmed aquaculture species worldwide (FAO, 2014). This shellfish species is fast growing and displays a wide tolerance to different environmental conditions, making it ideal for farming in many regions of the world (FAO, 2014). However, worldwide production is mainly based on un-improved populations or stocks (Gjedrem et al., 2012), likely limiting profitability and expanded production of this species due to the unrealized potential for genetic improvement.

Shortly after development of hatchery techniques for oyster production in the 1970s, Lannan (1972) reported a positive heritability of 0.37 for growth in adult *C. gigas* in the USA. This estimate is similar to that reported in the USA for body weight at harvest (0.31 ± 0.08; Evans and Langdon, 2006a) and for various growth parameters of *C. gigas* in different parts of Asia: China (0.33 ± 0.03), Japan (0.40 ± 0.02) and South Korea (0.1 ± 0.03) (Li et al., 2011). Estimated heritabilities for growth are strongly affected by rearing conditions and source populations for broodstock, as demonstrated by Langdon et al. (2003) who observed heritability values for yield ranging from 0.22 to 0.77 for *C. gigas* cultured in different locations in the Pacific Northwest, USA.

Family-based selection programs for improving desirable traits of the Pacific oyster have been initiated in the USA (Evans and Langdon, 2006b; Langdon et al., 2003), France (Dégremont et al., 2007, 2010), China (Li et al., 2011; Wang et al., 2012) and Australia (Kube et al., 2011), obtaining genetic gains per generation between 7.2% for growth (Li et al., 2011) to 25.5% for yield (Langdon et al., 2003). In Australia, Nell et al. (1996, 1999) obtained genetic gains of 4% and 8% for individual weight in the first and second generation of mass selection, respectively, for the rock oyster *Saccostrea commercialis*.

Positive heritability values and genetic gains reported for oysters and a variety of other bivalve species across the world indicate that selection has the potential to improve desirable traits of Pacific oysters. In this study, we report on heritabilities, genetic correlations as well as estimated genetic and realized gains for yield, survival and individual weight at harvest, obtained after five generations (17 years) of selective breeding with 1235 families of Pacific oysters planted at 11 different sites on the West Coast, USA (Table 1; Supplementary Table S1).

2. Material and methods

2.1. Husbandry of MBP families and control groups

MBP families were selected and produced according to methods described by Langdon et al. (2003). Briefly, parental families were selected based on their yields at harvest. Pair sire/dam matings were carried out between individuals from unrelated families to maintain a low coefficient of coancestry ($\theta ij < 0.1$). Individual parents used for crosses were selected from within each family based on size and shell shape, and were typically from the top third largest oysters per family. From 50 to 100 families were simultaneously produced and included in each cohort. Beginning in the 2nd generation, groups of control crosses were also incorporated in each cohort by pooling 5 to 10 single pair matings among individuals collected from naturalized "wild" populations in the Pacific Northwest. These naturalized stocks were mainly sourced from Willapa Bay (46°33′00.0″N, 123°58′12.0″W) because populations from this bay were primarily used by commercial hatcheries for their broodstock, but some cohorts included progeny from broodstock collected from Dabob Bay (47°45′02.1″N, 122°50′00.3″W) in Washington State (WA) as well as from Pipestem Inlet (49°01′36.0″N 125°15′36.3″ W) on Vancouver Island, British Columbia, Canada.

Cohorts were produced by rearing separate families from larval to early juvenile (spat) stages at Oregon State University's facilities at the Hatfield Marine Science Center (HMSC) in Newport, Oregon, USA. Larval and spat cultures for each family were not replicated due to limited space and labor in the hatchery/nursery as well as to meet the goal of maximizing the number of families included in the breeding program. In support of this approach, Evans and Langdon (2006a) reported that variation among replicates during this early phase of family rearing contributed only 1.5%, 0.3% and 5.2% to the total phenotypic variance (10%, 6% and 14% expressed in terms of family variance) in yield, average individual weight and survival at harvest, respectively.

Larval and spat culture techniques were based on those described by Langdon et al. (2003). Briefly, larvae were raised for 2–3 weeks on an algal diet of *Isochrysis galbana* (Tahitian strain T-ISO) and *Chaetoceros* sp. Larvae were induced to metamorphose using epinephrine. Single spat were reared in upwellers for 2–3 months until they were 3 to 5 mm in size. At this size, they were either transferred to a nursery in Yaquina Bay to grow to 10–15 mm in size before planting at field test sites in the 1st and 2nd generations or, in subsequent generations, directly planted at field test sites at a small size (3–5 mm; see Table 2 for initial weights at planting).

Test sites were located on commercial farms in the western coastal states of Alaska, Washington, Oregon and California, USA (Fig. 1). At each site, 35 to 100 spat were placed in grow-out containers (bags or purses at inter-tidal sites or lantern net compartments at sub-tidal sites; Fig. 2; Supplementary Table S1) at densities that were below typical farm densities of adult oysters at harvest. Oyster densities were not adjusted during the plant-out period. Typically, two replicate grow-out containers were randomly placed within each of four or five blocks that were positioned across different tidal heights at inter-tidal sites or at different depths at sub-tidal sites (Langdon et al., 2003).

Spat were initially planted in small-mesh (2–4 mm) bags, but as the spat grew, they were transferred to larger-meshed containers to maximize the exchange of water and supply of suspended food. Containers were cleaned of fouling organisms at each bag change and dead spat removed. After 2 to 4 years, depending on grow-out conditions, oysters were harvested when they reached market size, typically with shell lengths of 5 to 10 cm. At harvest, the total weight of all living oysters (yield) and the number of live oysters per container (survival) were determined and from these values, average individual weights were estimated per family.

Table 1
Structure of the data used in analysis.

No. of records	15,236
No. of families with records	1235
No. of sites	11
No. of tidal exposures	2
No. of generations	5
No. of families[§]	1274
No. of sires[*]	263
No. of dams[†]	277
No. of years	14
No. of cohorts	23
No. of blocks at test sites	159

[§] Including parents without records and dummy identities for unknown dams.
[*] With progeny in the data.
[†] With progeny in the data, including dummy identities assigned for animals with missing dam identities.

2.2. Statistical model

Performance records for family yield (kg), survival (%) and individual mean weight (g) at harvest, as well as initial weight (g) at planting, were obtained for five MBP generations of selectively bred Pacific oysters and 23 cohorts produced between 1996 and 2012 (Fig. 2). The cohorts were planted at 11 sites in Oregon, Washington, California, and Alaska, USA (Fig. 1).

After eliminating a total of 86 outlier records (containers of oysters at harvest), using descriptive and graphical analyses to identify biologically improbable values, 15,236 records of field performance remained for statistical analyses (Table 1). These data were analyzed using a linear