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Relationship Between Shell Color and Growth and Survival Traits in the Pacific Oyster *Crassostrea gigas*

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Abstract Shell color is regarded as an economic trait in many breeding programs of bivalve mollusks, but the relationship between shell color and production traits remains controversial. In our breeding program of *Crassostrea gigas*, solid white, black, and orange shell lines were obtained, and second-generation (F2) and testcross families with segregating shell colors were constructed by crossing these three lines. These segregating families provided ideal samples for investigating the relationship between shell color and production traits in *C. gigas*. The growth and survival of 7-month-old oysters with different shell colors sampled within the same families were compared in seven F2 families and 13 testcrosses. In addition, the growth and survival of oysters from the three shell color lines were compared at 4 and 16 months of age. The growth and survival rates of the orange shell line were significantly lower than those of the white and black shell lines. However, no significant difference in growth between oysters with different shell colors was observed within segregating families, except the testcrosses produced by crossing orange- and white-shelled grandparents, and no significant difference in survival was observed in any family. Overall, no significant correlation was observed between shell color and production traits in *C. gigas*. These results suggest that shell color cannot be used as a marker to guide the selection of growth and survival traits. Thus shell color and production traits should be selected independently in oyster breeding programs.

Key words *Crassostrea gigas*; shell color; growth; survival; relationship

1 Introduction

Molluscan shellfish have traditionally been a major global aquaculture product, and their shells are extremely diverse in color and pattern (Williams, 2017; Gjedrem and Rye, 2018). Shell color plays an important role in increasing the commercial seafood value of mollusks because it can influence the preference of consumers at seafood markets (Nell, 2001; Alfnes *et al*., 2006). Previous studies established inheritance models of various shell colors (Ky *et al*., 2016; Han and Li, 2020), and shell color served as a targeted trait of many breeding programs for oysters (Wada and Komaru, 1994; Evans *et al*., 2009; Adzigbli *et al*., 2020; Vu *et al*., 2020), scallops (Zheng *et al*., 2013; Wang *et al*., 2017), and clams (Liang *et al*., 2019; Nie *et al*., 2020). The possible association of shell color with production traits must be considered in designing breeding programs (Brake *et al*., 2004). Whether shell color can be used as a marker to guide the selection of production traits and whether the production traits of rare shell color variants can be improved independent of shell color need be determined.

Growth and survival are important production traits in economically important bivalves, and their relationship with shell color has been investigated from two levels nowadays. First, growth and survival were compared between wild or selected populations with different shell colors (Zheng *et al*., 2005; Han and Li, 2018; Adzigbli *et al*., 2020; Nie *et al*., 2020). The yellow variants are inferior in growth and survival rates to the brownish purple variants in *Argopecten purpuratus* (Wolff and Garrido, 1991). However, these two populations differ in genetic background (Song *et al*., 2017; Han *et al*., 2019). The inconsistency in genetic background between these two populations means that growth and survival cannot be entirely attributed to shell color alone.

Second, correlations between shell color and production traits were estimated by comparing families in a selection program. For the oyster, a lack of significant correlation was found between shell pigmentation and production traits among the families of the Molluscan Broodstock Program on the West Coast, US (Brake *et al*., 2004). By contrast, medium–high genetic correlations were observed between shell pigmentation and growth-related traits in families from the selected black shell line of the Pacific oyster in Shandong Province, China (Xu *et al*., 2017). These con-

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flicting results indicate that additional information is necessary to clarify the relationship between shell color and production traits.

The Pacific oyster (*Crassostrea gigas*) is an important global commercial bivalve. Shell color, as an economic trait of *C. gigas*, has attracted the attention of many breeders and scientists worldwide (Nell, 2001; Evans *et al*., 2009; Kang *et al*., 2013; Xu *et al*., 2017). In our breeding program, three lines with either solid white shells (Xing *et al*., 2017), black shells (Xu *et al*., 2019a), or orange shells (Han *et al*., 2019) have been obtained by artificial selection. Moreover, the orange shell is recessive to the white and black shells, and the shell colors of offspring are separated into white (or black) and orange in second-generation (F2) families and testcross families from crosses between white (or black) and orange lines (Fig.1) (Han and Li, 2020). The genetic background of individuals with different shell colors from the same family is more consistent than that of individuals from different populations or families. Differences in growth and survival between oysters from the orange shell line and black or white shell lines were observed in the full-sib families generated by these three lines (Han *et al*., 2020). Therefore, families with sibs showing segregated shell colors are ideal materials for investigating the relationship between shell color and production traits in *C. gigas*.

In this study, the growth and survival of *C. gigas* with different shell colors were compared among lines and within families to investigate the relationship between shell color and production traits.

2 Materials and Methods

2.1 Shell Color Lines

The orange, white and black shell lines of the Pacific oyster were used in this study (Han *et al*., 2020). The orange shell line was established based on only four parental oysters (two females and two males) with left and right orange shells (Han and Li, 2018). Three generations of family selection were performed from 2011 (G1) to 2013 (G3) to fix the orange trait. Then, three generations of mass selection were performed from 2014 (G4) to 2016 (G6) to improve growth trait. For each generation of mass selection, about 50 females and 50 males were used as parents, and the selection intensity was about 1.90 (Han *et al*., 2019). The orange shell line had no advantages in growth and survival compared with the wild population after six generations of selection (Han and Li, 2018). Previous studies assessed the genetic diversity of the orange shell line by using microsatellites and the mitochondrial COI region. Only one haplotype was observed in all generations from G4 to G6 of the orange shell line. The mean allelic richness of G4 to G6 ranged from 3.51 to 4.08, and heterozygosity ranged from 0.48 to 0.50; the mean allelic richness of wild populations of *C. gigas* ranged from 12.82 to 13.99, and heterozygosity ranged from 0.76 to 0.79 (Han *et al*., 2019).

The white and black shell lines were initiated in 2010 based on relatively white- and black-shelled *C. gigas* collected from Rushan, Shandong Province, China, respectively (Xing *et al*., 2017; Xu *et al*., 2019a). For the two lines, four generations of family selection (G1–G4) and three subsequent generations of mass selection (G5–G7) were performed to fix the white or black traits and improve their growth traits. For each generation of mass selection of the white and black shell lines, the number of parents ranged from 75 to 100, the selection intensity was about 1.40, and genetic gain for shell height (the straight-line distance from the hinge of oyster to its bill) was around 10% per generation (Wang *et al*., 2016; Xu *et al*., 2019a). After this selection, the growth performance of the black and white shell lines significantly improved compared with those of the wild population (Xing *et al*., 2017; Xu *et al*., 2019a). For the genetic diversity of G5–G7 of the black shell line, only two haplotypes were observed in all generations; the mean allelic richness ranged from 5.60 to 5.80, and heterozygosity ranged from 0.65 to 0.68 (Xu *et al*., 2019b). For the genetic diversity of G5–G7 of the white shell line, the mean allelic richness ranged from 6.80 to 7.10, and heterozygosity ranged from 0.67 to 0.70 (Xing *et al*., 2017). After this selection, no other shell color phenotypes were observed for all three shell color lines.

Artificial fertilization and larval rearing were performed using the procedure described by Li *et al*. (2011). Strings of scallop shells were used as spat collectors. After all eyed larvae adhered to shells and metamorphosed to spat, they were transferred to the sea around Rongcheng (37.11˚N, 122.35˚E), Shandong Province and allowed to grow. Before the spat reached 4 months of age, they were cultured by the long-line method and then placed in 10-layer lantern nets to harvest. Spat density was 30 oysters per layer to avoid crowding.

2.2 F2 and Testcross Families

The F2 and testcross families used in this study were the same as previously reported (Han and Li, 2020). In 2017, 1-year-old sexually mature oysters randomly selected form the orange shell line (O-G6), black shell line (B-G7), and white shell line (W-G7) were used as parents for F1 crosses. Reciprocal crosses were carried out between O-G6 and B-G7 (O♀B♂ and B♀O♂, Fig.1a) and between O-G6 and W-G7 (O♀W♂ and W♀O♂, Fig.1b). Twelve F1 families with four reciprocal crosses and three replicates were generated.

In 2018, 12 F2 families were generated by single-pair mating between progeny of F1 families, and 13 testcrosses were generated by single-pair mating between progeny from F1 families and 1-year-old orange shell oysters randomly selected from the seventh generation of the orange shell line (O-G7). In this study, the growth and survival of seven F2 families and 13 testcrosses were used for the subsequent analysis. The artificial fertilization, larvae rearing, and growth were the same as described above. Details about the parents of each F1, F2, and testcross family are shown in Table 1.

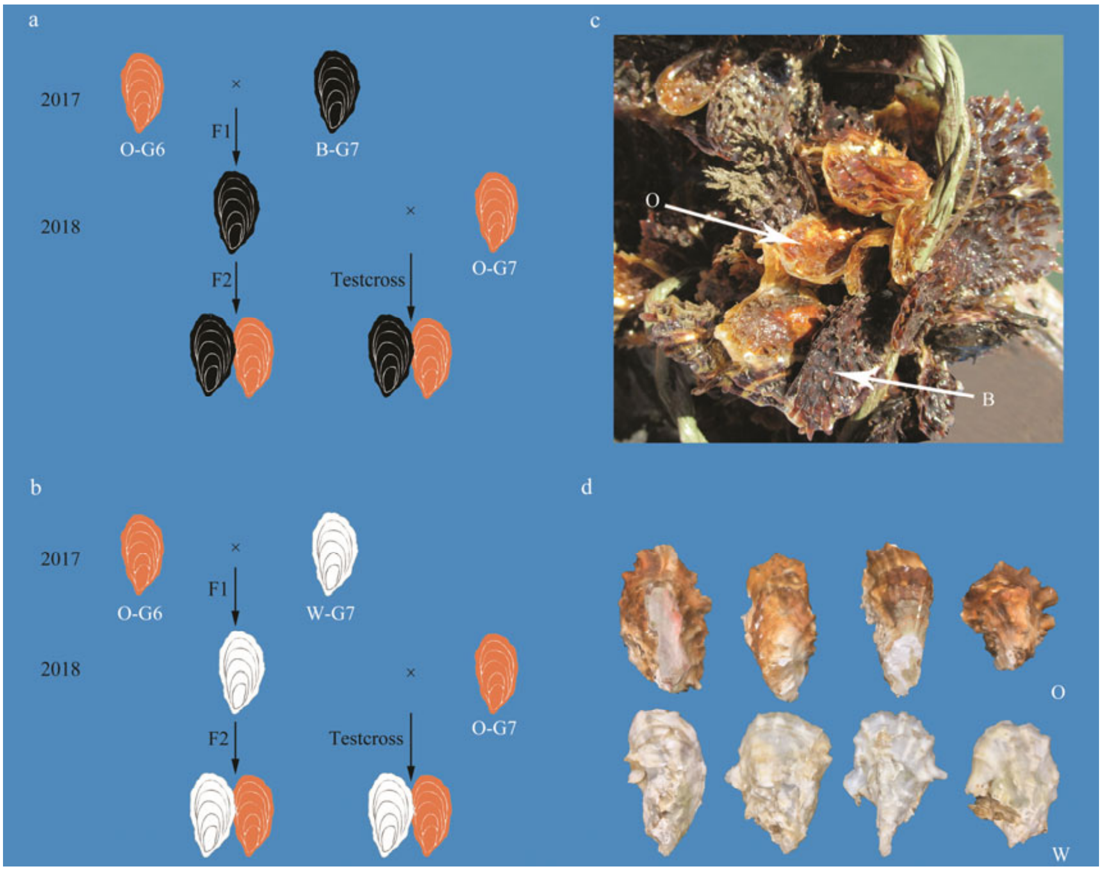

Fig.1 Schematic of the F2 and testcross families generated by crossing orange with black shell oysters (a) and with white shell oysters (b), and representative offspring with segregating shell colors in the F2 or testcross families of crosses between orange and black shell oysters (c) and between orange and white shell oysters (d). O, orange shell oyster; B, black shell oyster; W, white shell oyster.

Table 1 The parents of the F1, F2 and testcross families

Family		Parents		Number†	Family		Parents		Number†
		Female	Male				Female	Male	
F1	O♀B♂$_1$	O-1	B-4		F2	10	B♀O♂$_2$-1	B♀O♂$_2$-7	O: 17, B: 30
	B♀O♂$_1$	B-1	O-4			11	B♀O♂$_2$-2	B♀O♂$_2$-8	O: 10, B: 30
	O♀B♂$_2$	O-2	B-5			12	B♀O♂$_2$-3	B♀O♂$_2$-9	O: 4, B: 30
	B♀O♂$_2$	B-2	O-5		Testcross	13	O♀W♂$_1$-4	O$_{G7}$-3	O: 19, W: 30
	O♀B♂$_3$	O-3	B-6			14	O$_{G7}$-1	O♀W♂$_1$-9	O: 22, W: 30
	B♀O♂$_3$	B-3	O-6			15	O♀W♂$_3$-4	O$_{G7}$-4	O: 30, W: 30
	O♀W♂$_1$	O-1	W-4			16	O♀W♂$_3$-5	O$_{G7}$-5	O: 11, W: 23
	W♀O♂$_1$	W-1	O-4			17	O♀W♂$_3$-6	O$_{G7}$-6	O: 7, W: 30
	O♀W♂$_2$	O-2	W-5			18	W♀O♂$_2$-4	O$_{G7}$-7	O: 15, W: 30
	W♀O♂$_2$	W-2	O-5			19	W♀O♂$_2$-5	O$_{G7}$-8	O: 30, W: 30
	O♀W♂$_3$	O-3	W-6			20	O$_{G7}$-2	W♀O♂$_2$-9	O: 20, W: 30
	W♀O♂$_3$	W-3	O-6			21	B♀O♂$_1$-6	O-G$_7$-9	O: 19, B: 24
F2	5	O♀W♂$_3$-3	O♀W♂$_3$-9	O: 8, W: 30		22	B♀O♂$_2$-4	O-G$_7$-10	O: 5, B: 28
	7	W♀O♂$_2$-3	W♀O♂$_2$-8	O: 9, W: 30		23	B♀O♂$_2$-5	O-G$_7$-11	O: 24, B: 30
	8	B♀O♂$_1$-2	B♀O♂$_1$-8	O: 5, B: 30		24	B♀O♂$_2$-4	O-G$_7$-12	O: 15, B: 30
	9	B♀O♂$_1$-3	B♀O♂$_1$-9	O: 24, B: 30		25	B♀O♂$_2$-6	O-G$_7$-13	O: 30, B: 30

Note: † The number of oysters of each color (O, orange; W, white; B, black) being measured.

2.3 Measured Traits

To compare the growth of these three lines, 40 oysters were randomly selected from each line at 4 (November 2016) and 16 months of age (November 2017). The shell height, length, and width of each oyster were measured by digital calipers (0.01 mm), and their body weights were determined by a digital electronic balance (0.01 g). Three lantern nets were randomly selected for each line as replicates to compare the survival rate of these three lines. The survival rate of each lantern net was calculated based on the total number of live oysters in the lantern net at 16 months of age.

Oysters with different shell colors were randomly selected from each F2 or testcross family at 7 months of age to compare growth among oysters with orange, white, or black shells from the same families. Their shell heights, shell lengths, and shell widths and body weights were measured using the same method as described above. The numbers of oysters of each shell color recorded in each family are shown in Table 1. Five families (families 15, 19, 9, 23 and 25) with the largest number of oysters in these 20 families were selected to compare the survival of oysters with different shell colors from the same families. Seven-month-old oysters of each family were then divided into two groups: orange and non-orange (white or black) groups. For each group, 10 oysters were randomly selected and placed in the lantern net (10 oysters per layer) with three replicates. The survival rate of each layer was calculated based on the number of 11 month-old live oysters in the layer.

2.4 Statistical Analyses

Differences in shell heights, shell lengths, shell widths, total weights, and survival rates among the three lines at 4 and 16 months of age were analyzed with one-way ANOVA followed by Tukey's test. The shell heights, lengths, and widths and the total weights of families were analyzed using two-way ANOVA, with color as the fixed factor and family as the random factor. Differences were considered statistically significant at $P<0.05$. All analyses were performed using SPSS 20.0 software.

3 Results

3.1 Growth and Survival of Oysters from the Three Color Lines

No significant differences ($P>0.05$) in growth traits (shell height, shell length, shell width, and body weight) or survival traits were observed between the black shell (G7) and white shell lines (G7) (Fig.2). However, the shell heights and body weights of the orange shell line (G6) were significantly lower ($P<0.05$) than those of the black and white shell lines at 4 and 16 months of age (Figs.2a and 2d). No significant difference ($P>0.05$) in shell length was found among the three color lines at 4 months of age,

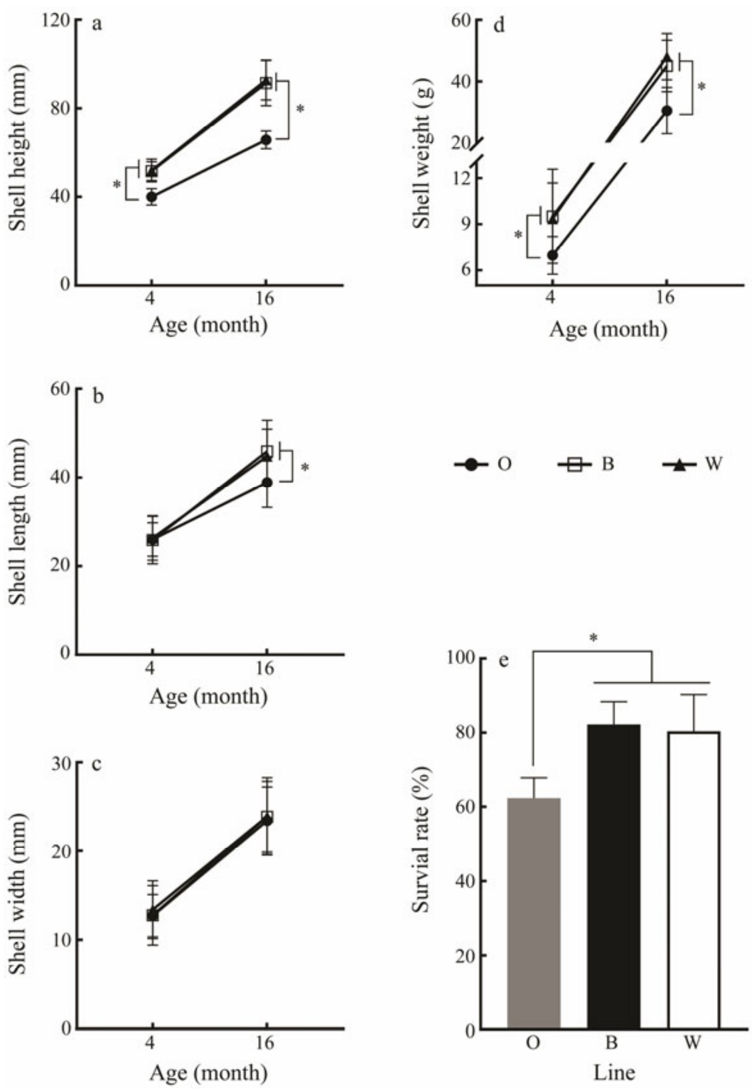

Fig.2 Shell height (a), shell length (b), shell width (c), body weight (d), and survival rate (e) of the orange (O, G6), black (B, G7), and white (W, G7) shell lines at 4 and 16 months of age. * represents $P<0.05$.

whereas 16-month-old oysters from the black and white shell lines were significantly larger (P<0.05) than those from the orange shell line (Fig.1b). At 4 and 16 months of age, no significant difference (P>0.05) in shell width was observed among the three lines (Fig.2c). In addition, the survival rate of the orange shell line was significantly lower (P<0.05) than those of the black and white shell lines (Fig.2e).

3.2 Growth of Oysters with Different Shell Colors Within Each Family

For all four growth traits, shell color exerted no significant influence (P>0.05) on F2 families produced by crossing orange- and white-shelled grandparents and on F2 and testcross families produced by crossing orange- and black-shelled grandparents (Table 2). By contrast, shell color showed significant influences on the shell height and total weight of testcross families produced by crossing orange- and white-shelled grandparents, and it interacted with family to influence the shell length, shell width, and total weight (Table 2).

3.3 Survival of Oysters with Different Shell Colors Within Each Family

The survival rates between oysters with different shell colors from the same family were compared in one F2 family (family 9) and four testcrosses (families 15, 19, 23 and 25), and no significant difference (P>0.05) was observed in any family (Fig.3).

Table 2 P values of ANOVA analysis on the shell height, shell length, shell width, and total weight of F2 and testcross (TC) families

Type	Family	Source	Shell height	Shell length	Shell width	Total weight
W×O	F2	Color	0.196	0.425	0.328	0.196
		Family	0.123	0.629	0.875	0.339
		Color×Family	0.538	0.324	0.215	0.495
	TC	Color	**0.000**	0.147	0.561	**0.048**
		Family	**0.002**	0.285	0.193	0.213
		Color×Family	0.825	**0.000**	**0.020**	**0.027**
B×O	F2	Color	0.446	0.972	0.894	0.660
		Family	**0.047**	**0.018**	**0.016**	0.106
		Color×Family	0.817	0.425	0.778	0.438
	TC	Color	0.351	0.061	0.794	0.062
		Family	0.348	**0.010**	0.070	**0.015**
		Color×Family	0.100	0.517	0.602	0.452

Notes: W×O, white shell and orange shell lines as grandparents; B×O, black shell and orange shell lines as grandparents. Bold indicate significant difference, P<0.05.

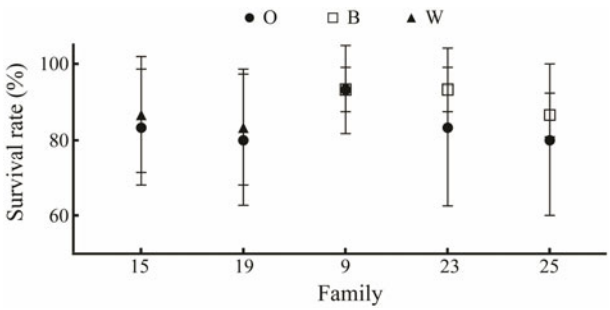

Fig.3 Survival rates of orange (O) and non-orange (W or B) oysters within F_2 and testcross families. No significant difference was observed in any family.

4 Discussion

The growth and survival of oysters from the orange-shelled line were significantly lower than those of the black- and white-shelled lines. By contrast, no significant differences were observed between oysters sampled form the black- and white-shelled lines (Fig.2). This result is consistent with those previously observed in full-sib families generated for these three lines (Han *et al*., 2020); however, differences among these lines and relationships between shell color and production traits could be affected by differences in the genetic diversity of the orange-shelled line, which is lower than those of the black- and white-shelled lines (Xing *et al*., 2017; Han *et al*., 2019; Xu *et al*., 2019b). Comparisons of growth traits of individual oysters sampled within the F2 and testcross families are suitable to investigate the relationship of shell color with growth and survival, considering the genetic diversity should be similar for oysters within the same family even their colors are different.

Growth (shell height, shell length, shell width, and body weight at harvest) and survival were compared among different-colored oysters within the same family. For growth, no significant difference was found between oysters with different shell colors in any of the families, except in the testcrosses produced by crossing orange- and white-shelled grandparents. In all the results with significant differences, orange-shelled oysters showed a poorer performance than black or white ones. These results suggest a weak linkage between the genetic loci controlling these three shell colors and growth traits. Moreover, no significant difference in survival was observed in all five families, although one of the five families showed significant differences in shell height, shell length, and body weight. A lack of correlation between shell color and survival suggested the absence of a linkage between the genetic loci controlling these three shell colors and survival, although further molecular data are needed for verification. Overall, no correlation was observed between shell color and growth and survival traits in most families. These results support the conclusion of Brake *et al*. (2004) that a significant correlation does not exist between shell pigmentation in almost all growth and survival traits when comparing the average performances among families, although this finding differs from the conclusion of Xu *et al*. (2017) that medium-to-high genetic correlations between shell pigmentation and growth-related traits were found after comparing the averages among families of the black shell line of *C. gigas*. Moreover, the evidence provided by this study is stronger than that provided by Brake *et al*. (2004) because the genetic background of individual oysters from the F2 and testcross families is more consistent than that of individuals from different families.

5 Conclusions

No overall correlations were found between three shell colors (black, white, and orange) and growth and survival traits in *C. gigas* sampled within 20 families. These results indicate that shell color cannot be used as a marker to guide the selection of growth or survival traits. In addition, shell color can be selected independently in an oyster breeding program without affecting the production traits. These findings will be helpful for the selection of elite lines of Pacific oysters with desired shell color.

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