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A NOVEL SHELL COLOR VARIANT OF THE PACIFIC ABALONE *HALIOTIS DISCUS HANNAI* INO SUBJECT TO GENETIC CONTROL AND DIETARY INFLUENCE

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ABSTRACT Molluscan shells may display a variety of colors, which formation, inheritance, and evolutionary significance are not well understood. Here we report a new variant of the Pacific abalone *Haliotis discus hannai* that displays a novel orange shell coloration (O-type) that is clearly distinguishable from the wild green-shelled abalone (G-type). Controlled mating experiments between O- and G-type abalones demonstrated apparent Mendelian segregations (1:1 or 3:1) in shell colors in F_2 families, which support the notion that the O- and G-types are under strict genetic control at a single locus with a recessive *o* (for orange shell) allele and a dominant *G* (for green shell) allele. Feeding with different diets caused modifications of shell color within each genotype, ranging from orange to yellow for O-type and green to dark-brown for the G-type, without affecting the distinction between genotypes. A previously described bluish-purple (B-type) shell color was found in one of the putative $oo \times oG$ crosses, suggesting that the B-type may be a recessive allele belonging to the same locus. The new O-type variant had no effect on the growth of Pacific abalone on the early seed-stage. This study demonstrates that shell color in Pacific abalone is subject to genetic control as well as dietary modification, and the latter probably offers selective advantages in camouflage and predator avoidance.

KEY WORDS: color adaptation, *Haliotis discus hannai*, Pacific abalone, predator avoidance, shell color variation

INTRODUCTION

Shells of molluscs are extremely diverse in morphology and rich in color. They have been the subject of fascination throughout human history and well sought after by conchologists and shell lovers. However, we have little understanding of how molluscs produce such remarkably delicate and colorful shells. Whereas shell morphology is typically unique and characteristic for a given species, shell color may vary from mostly single color in some species (e.g., the blood cockle *Scapharca broughtonii* and the razor clam *Sinonovacula constricata*) to a wide array of colors in others (e.g., Manila clam, *Ruditapes philippinarum* and noble scallop, *Chlamys nobilis*). The ecology, genetics, and evolution of shell color have been studied in some species (Hoagland 1977, Raffaeli 1982, Cowie 1990). It is known that both environmental and genetic factors affect shell color. Effects of lights, salinity, and climate on colorations have been reported in some studies (Heath 1975, Precht & Plett 1979, Cowie 1990, Sokolova & Berger 2000). Dietary influence on shell color has also been documented in some marine gastropods (Harry & Turner 1958, Leighton 1961, Underwood & Creese 1976). Although environmental modifications of shell color are typically not inheritable, they are stable and long lasting once formed.

Genetic factors may play a major role in the determination of shell color. Genetic determination of shell color was first reported in the conch *Urosalpix cinerea* where a single-locus genetic model controlled three color types (Cole 1975). Similar simple patterns of inheritance were later found in a number of bivalves such as *Mytilus edulis*, *Argopecten irradians*, and *Fulvia mutica*) (Innes & Haley 1977, Adamkewicz & Castagna 1988, Fujiwara 1995), and gastropods including *Helix aspersa* and *Biomphalaria glabrata* (De Matos 1984, Richards 1985). More recently, a study on the gene expression in the mantle of vetigastropod *Haliotis asinina* has revealed a complex secretome and characterized a number of genes involved in shell construction and coloration in this tropical abalone (Jackson et al. 2006, 2007). However, despite these progresses, genetic studies on the coloration of molluscs, particularly on the abalones, are still limited, largely because of the lack of well-defined genetic models, the long life/breeding cycle, and complications caused by environmental factors.

The Pacific abalone (*Haliotis discus hannai* Ino) is a marine gastropod naturally distributed in the northwestern Pacific from northern China to Korean peninsula and Japan. The shell color of wild Pacific abalone is usually dark-brown or green (G-type), depending on dietary source. Thus, it has been long believed that shell color in the Pacific abalone is environmentally determined and not inheritable (i.e., Sakai 1962, Ogino & Ohta 1963). Recently, however, a new bluish shell color (B-type) was discovered in a full-sib family of this species, and segregation data indicated that the bluish and greenish variants were genetically controlled by a recessive and a dominant allele, respectively, at a single locus (Kobayashi et al. 2004).

Apart from the bluish variant, orange-colored (O-type) Pacific abalone individuals have been sporadically spotted in some hatcheries in China since 1986 when large-scale breeding of abalones began in the country. Little attention was paid to the O-type variant until a relatively large number of orange-type individuals were found in a hatchery in 1992. The O-type individuals were then collected and mated to each other in 1996, which produced all orange offspring (Zhao et al. 1999). The shell color of these orange-type abalones ranged from solid orange to yellow depending on diets, and the color patterns were stable over the time, and clearly distinguishable from the greenish G-type. These observations indicate that the orange shell coloration may be under genetic control, although its inheritance and relationship with the other two color variants are not clear.

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In the present study, we conducted controlled mating experiments and determined that the O-type shell color is genetically controlled and belongs to the same locus as the wild G-type. We also demonstrate that different diets cause stable modifications of the shell color mimicking colors of the diet, which may provide camouflage and have some evolutionary significance in avoiding predation.

MATERIALS AND METHODS

Source of the Orange (O) Type Abalone

Pacific abalones with O-type shells were found and collected in one of our breeding stocks at the Dalian Institute of Fisheries in 1992. The parental abalones were wild with the typical greenish brown G-type shells collected from Fujiazhuang bay, Dalian, Liaoning Province, China (near 38°52′N, 121°36′E). Some of the O-type individuals were collected and conditioned to spawn (32 ♀ and 3 ♂) in 1996. The first generation offspring were cultured in a land-based cultivation facility into adults (~9 cm shell length), which in turn were used as the parents (P_1) for this study in 2002. In addition, two O-type adults (♀ O-w and ♂ O-h) were independently discovered in one of the commercial stocks in Weihai, China (near 37°25′N, 122°23′E) in 2001, which were acquired and used in this study in 2002.

Mating Experiments

Mating experiments between the O-type and wild G-type abalones were performed from 2002 to 2006. Two experiments were separately carried out in Dalian and Qingdao in 2002 to produce F_1 hybrids between the O- and G-type abalones. In the experiment conducted in Dalian, the O-type parents (P_1) were the offspring from our initial collection produced in 1996. G-type parents were originated from Iwate, Japan (39°17′N, 141°56′E). Eight experimental groups, four multiple parent crosses, and four full-sib families were produced by 2 × 2 factorial mating. The experiment performed in Qingdao produced 14 full-sib families using the O-type (O-w and O-h) individuals from Weihai and G-type individuals derived from Iwate, Japan or Zhangzidao, Dalian, China (39°1′N, 122°44′E). A total of 22 F_1 groups were obtained in this study, including three O × O, 13 O × G and G × O, and six G × G groups (Table 1). Among them, the coloration and preliminary growth features of eight family lines were previously reported (Liu et al. 2005). In addition, F_2 families were produced by single-pair mating between F_1 individuals. Eighteen F_2 families were produced, 6 were lost because of unexpected mortality during metamorphosis, and 11 families with expected 0:1, 3:1 or 1:1 segregation ratios plus one with apparent cross-contamination survived (8 from 2005 and 4 from 2006) (Table 2).

For all mating experiments, spawning induction and larval rearing were conducted following standard procedures as previously described (Uki & Kikuchi 1984, Zhao et al. 1999). Cares were taken to avoid cross-contamination of gametes. The F_1 larvae from different groups were separately cultured in an array of 20-L tanks before being transferred to individual 1,000-L fiberglass tanks for metamorphosis and juvenile rearing. The F_2 full-sib families were similarly placed in fiberglass tanks for juvenile rearing, whereas some replicates were cultured in 60-L barrels. Both F_1 and F_2 lines were maintained under the same condition to minimize environmental effects.

TABLE 1.

Shell color of offspring from F_1 crosses between O- and G-type abalone as determined on day 30 after fertilization.

		Parents (P_1)[c]		Offspring Shell Color	
Group	Site[b]	Female	Male	Green (G)	Orange (O)
OO1	D	O-1	O-2	0	39,500
OO2 [a]	D	15 O-type individuals	4 O-type individuals	0	177,100
OO3	Q	O-w	O-h	0	34,500
OG1	D	O-1	G-f	17,300	0
OG2 [a]	D	15 O-type individuals	3 G-type individuals	155,600	0
OG3	Q	O-w	G-m	32,500	0
GO1	D	G-a	O-2	1,600	0
GO2 [a]	D	15 G-type individuals	4 O-type individuals	229,500	0
GO3	Q	G-1	O-h	43,500	0
GO4	Q	G-2	O-h	5,900	0
GO5	Q	G-4	O-h	10,500	0
GO6	Q	G-5	O-h	1,300	0
GO7	Q	G-6	O-h	8,000	0
GO8	Q	G-7	O-h	3,800	0
GO9	Q	G-9	O-h	18,500	0
GO10	Q	G-10	O-h	5,200	0
GG1	D	G-a	G-f	4,800	0
GG2 [a]	D	15 G-type individuals	3 G-type individuals	205,100	0
GG3	Q	G-1	G-m	18,000	0
GG4	Q	G-2	G-m	25,500	0
GG5	Q	G-9	G-m	14,000	0
GG6	Q	G-10	G-m	1,200	0

[a]Groups produced from multiple P1 individuals (i.e., mixed oocytes from 15 ♀ individuals and sperms from 3 or 4 ♂ individuals), whereas all other groups were derived from single pair of parents as specified in column "Parents (P_1)".
[b]Site = Site for cross-mating experiments. D = Dalian; Q = Qingdao.
[c]All G-type parents were from Iwate, Japan except for the G-10 that was collected from Dalian, China. All O-type parents were collected in 1992 and bred in 1996, except for the O-w and O-h that were collected from Weihai, China in 2002.

Shell color of offspring derived from each mating experiment was recorded when the O-type individuals were clearly distinguishable from the wild G-type ones, typically at 30 days postfertilization. The proportions of O- and G-type individuals in the F_2 generations were analyzed under the assumption of a single-locus, two-allele model where deviations of the observed from the expected color type ratios were tested with chi-square test.

Growth Comparison Between O- and G-type Abalone

To determine whether the orange coloration affects the growth of abalone, we measured the shell length of offspring at 12 or 14 months in all groups occurring shell color segregations described in Table 2. Shell lengths of O- and G-type abalones within each group were compared in triplicates with a Student *t*-test.

Influence of Diets on Shell Color

Although the O-type abalone never turned into the greenish color as in the G-type individuals, color variation within the orange-yellow spectrum was occasionally observed probably

TABLE 2.

Shell color segregation in F_2 families of Pacific abalone.

Family*	Parents (P_2)		Observed Color Segregation		Expected Ratio	χ^2-test (P value)	Deduced F_1 Genotype
	Female	Male	G	O			
1	OO1–6	OO1–10	0	114	0:1	N/A	o/o, o/o
			0	213		N/A	
2	OG1–5	OO1–10	114	97	1:1	0.2419	o/G, o/o
			117	95		0.1308	
3	GO1–1	OO1–10	64	60	1:1	0.7194	G/o, o/o
			54	44		0.3124	
4	OO1–6	OG2–12	84	64	1:1	0.1002	o/o, o/G
			156	144		0.4884	
6	GO1–1	OG2–12	162	49	3:1	0.5510	G/o, o/G
			151	41		0.2433	
12	GO2–3	GO2–34	84	19	3:1	0.1245	G/o, G/o
			368	107		0.2131	
13	GO2–3	OG2–14	222	67	3:1	0.4757	G/o, o/G
			199	60		0.4955	
14	GO2–4	GO2–35	93	28	3:1	0.6367	G/o, G/o
			76	21		0.4460	
15	OO1–3	OG3–15	211†	239	1:1	0.1869	o/o, o/G
17	GO3–2	OO1–14	540	556	1:1	0.7026	G/o, o/o
18	GO1–4	OO2–14	364	336	1:1	0.4018	G/o, o/o

*Families #1 to #14 were established in 2005, and families #15 to #18 were established in 2006. Lines #5 and #7 to #11 were lost during metamorphosis.

†This family also contained 65 bluish-purple individuals that were assigned to the G-type group based on presence of dark-brown color in early developmental stages (also see Fig. 1C).

caused by dietary difference. We tested the effects of various diets on the shell color of both O- and G-type abalones between 2002 and 2006. Specifically, large numbers of juveniles from selected F_1 groups (i.e., OO2, OG2, GO2, and GG2) were raised in isolated tanks and fed with diatoms for 2 mo (up to 0.3–0.5 cm shell length [SL]), followed by an artificial/commercial diet for 5 mo (up to 0.8–1.5 cm SL), and then three different types of macro-algae for additional 5 mo (up to 1.5–3.0 cm SL). Variations in shell color in response to different diets were recorded, and the experiment was repeated three times.

RESULTS

Shell Color Follows a Single-locus, Two-allele Model

We produced 22 F_1 groups (18 full-sib families and 4 multiparental crosses) covering all possible crosses between the orange (O-type) and wild green (G-type) Pacific abalones (Table 1). All juveniles were fed with diatoms (mainly *Navicula* sp.) until their shell lengths reached to 1.0–1.5 mm, when their shell color was determined. With the diatoms as their diet, the O-type F_1 abalones displayed orange colored shells, whereas the G-type individuals had dark-brown shells (Fig. 1). All offspring from the O × O crosses had orange shells as their parents did. Similarly, all progeny from G × G crosses had the same dark-brown shells as their parents. All offspring from between-type crosses, O × G and G × O, had only dark-brown shells, which are the same as the wild G-type (Table 1). These observations indicate that there is no segregation in shell color in all F_1 crosses; the O- and G-types are homozygotes of a single locus with the *o* allele being recessive and the *G* allele being dominant.

To further test the hypothesis that the O- and G-types are controlled by a single locus, we produced 18 F_2 families with various F_1 abalones as parents, although only 11 survived beyond metamorphosis (Table 2). Among the other seven families, six were lost because of unexpected mortality during metamorphosis and one was excluded from analysis because of an undefined, but apparent cross-contamination. Shell color in all 11 survived families segregated according to a single locus, two-allele (*G* for green and *o* for orange) model (Table 2). As expected, the F_2-1 family with two O-type F_1 parents (♀ OO1–6 and ♂ OO1–10) produced only O-type individuals. All crosses between ♀ GO and ♂ OG (or GO) produced G- and O-type individuals in 3:1 ratio as supported by chi-square-test (i.e., lines F_2-6, F_2-12 to F_2-14). Furthermore, all crosses between ♀ OO and ♂ OG, or ♀ GO (or GO) and ♂ OO parents, produced G- and O-types in 1:1 ratio. These observations clearly demonstrate that the two color types are controlled by one locus with the *G* allele dominant to the *o* allele.

It is also noticed that family F_2-15 also contained a significant number (65 or 14.4% of total) of individuals with purple shells. These purple-shelled F_2 individuals displayed about the same coloration as those reported as bluish by Kobayashi and colleagues (Fig. 1C, also see Fig. 1 in Kobayashi et al. 2004). We hence designated these individuals as bluish-purple to be consistent with the description by Kobayashi and colleagues. It is likely that the bluish-purple phenotype is determined by a third allele, but further investigations are needed.

No Difference in the First-year Growth Between O- and G-type Juveniles

We selected nine families and measured shell length of juvenile abalones for 3–5 times at one year of age (with 2 lines at 14 mo). Data of family 1 and 12 in F_2 were excluded because of no shell

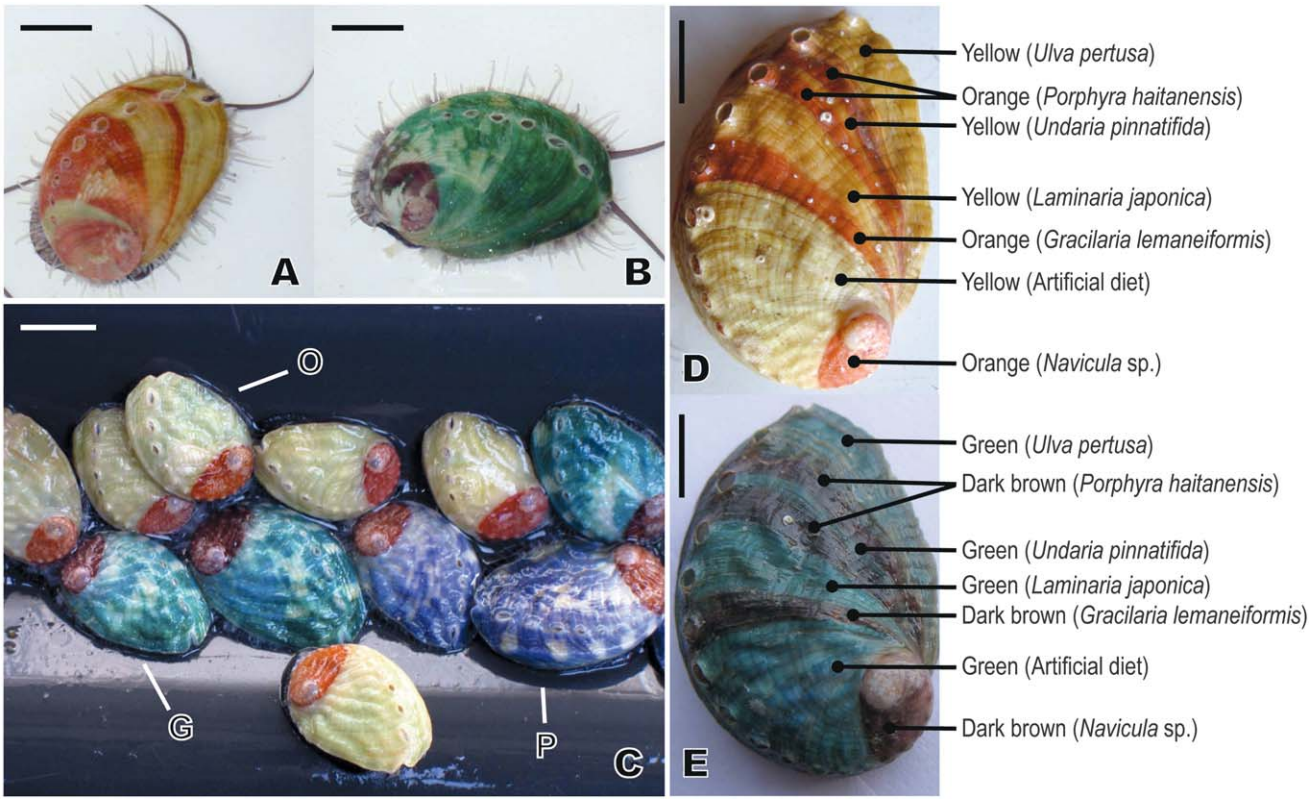

Figure 1. Illustration of shell color variations in the orange (O) and green (G) types of Pacific abalone, *Haliotis discus hannai*. (*A*) Typical O-type shell color; (*B*) Typical G-type shell color; (*C*) Example of F_2 individuals with orange, green and bluish-purple colored shells obtained in mating experiments (family line F_2-15); (*D* to *E*) Coloration patterns in O-type (*D*) and G-type (*E*) abalones in response to various diet supplies. Scale bar = 1 cm.

color segregation or a lack of sufficient replicates. There were no significant differences in size between O- and G-type juveniles in all groups except for the family 17 in which the G-type individuals are statistically bigger than O-type ones (Table 3). Collectively, our observations suggest that the O-type mutation has no apparent effect on the first-year (seed-stage) growth of abalone.

Dietary Influence on Shell Color

Although the orange and green shell colors are under genetic control, diets may still cause some limited variations in shell color within each genotype. In our feeding experiments, we observed that the O-type individuals (line OO2) might display orange to yellow colors, whereas all wild G-type individuals (lines OG2, GO2, and GG2) might show dark-brown to green colors, depending on diet (Fig. 1, D to E). There were apparent patterns of color change in response to different diets within each genotype (Table 4). For example, O- or G-type abalones always had orange or dark-brown colors when fed with diatoms or red algae, but they might change to yellow or green, respectively, when fed with brown or green algae, or a commercial diet whose exact composition is unknown. On the other hand, the diet-caused color shift occurs in both O- and G-type abalone but never causes overlaps between the genotypes or confusion, which permitted us to safely assign orange to yellow as the O-type and dark-brown to green as the G-type in this study. These observations further support the notion that the shell coloration in Pacific abalones is under genetic control, but can be modified by diets.

DISCUSSION

Shell color of wild Pacific abalone typically ranges from green to dark brown. A bluish variant has been found and shown to be recessive to the wild G-type (Kobayashi et al. 2004). This study provides the characterization of yet another novel shell color type, the orange (O-type) variant. Data from the mating experiments show that the O-type variant and wild G-type are

TABLE 3.

Growth comparison between O-type and G-type Pacific abalone from F_2 families.

Phenotype (Genotype)	363 days		412 days	
	O (o/o)	G (G/o)	O (o/o)	G (G/o)
Line 2	20.24 ± 3.54	19.29 ± 2.34	n/a	n/a
Line 3	17.92 ± 4.60	17.86 ± 2.84	n/a	n/a
Line 4	17.96 ± 2.42	17.88 ± 3.25	n/a	n/a
Line 6	21.96 ± 3.60	21.99 ± 3.26*	n/a	n/a
Line 13	19.98 ± 2.69	19.59 ± 2.55*	n/a	n/a
Line 14	18.03 ± 4.02	17.30 ± 3.77*	n/a	n/a
Line 15	16.88 ± 3.48	17.81 ± 3.33	n/a	n/a
Line 17†	n/a	n/a	25.62 ± 4.39	27.84 ± 6.31
Line 18	n/a	n/a	25.02 ± 4.84	25.47 ± 4.88

*Family lines contained both G/o and G/G genotypes.
†Growth differences are statistically different between O- and G-type individuals ($P = 0.044$).

TABLE 4.

Shell color of O- and G-types of Pacific abalones fed with different diets.

Age (mo)	Shell Length (cm)	Observed No.	Diet	Family Line	Type	Shell Color
1–2	0.3–0.5	150 × 3	Diatoms (*Navicula* sp.)	OO2	O	Orange
				OG2/GO2/GG2	G	Dark-brown
2–7	0.8–1.5	3000 × 3	Artificial diet* (with undisclosed ingredients)	OO2	O	Yellow
				OG2/GO2/GG2	G	Green
7–12	1.5–3.0	200 × 3	Brown algae (*Laminaria japonica* or *Undaria pinnatifida*)	OO2	O	Yellow
				OG2/GO2/GG2	G	Green
7–12	1.5–3.0	200 × 3	Green algae (*Ulva pertusa*)	OO2	O	Yellow
				OG2/GO2/GG2	G	Green
7–12	1.5–3.0	200 × 3	Red algae (*Gracilaria lemaneiformis* or *Porphyra haitanensis*)	OO2	O	Orange
				OG2/GO2/GG2	G	Dark-brown

*Artificial diet was acquired from Zhaohui Tech, Co. Ltd., Dalian, China.

genetically controlled by a single-locus. Further, the *o* allele is recessive and when homozygous produces O-type abalones. The O-type shells have no effects on abalone growth and survival in their seed-stage. Although data on the long-term effect of the mutation in these family lines are lacking, it is noticed that the mature O-type parents were generally much smaller than the wild-type siblings among the 1992 stocks and their 1996 breeds.

Although O-type shells show no negative effects on fitness in the laboratory at their seed stage, the orange variant is rare in wild populations. In fact, orange shells have not been reported in natural populations of Pacific abalone in China. Wild Pacific abalones are usually hidden under brown or green algae. In such environment, O-type abalones stand out from the environment and are more prone to be spotted. Visually selective predation may be a major contributing factor to the low frequency of the O-type abalones in the wild.

The unexpected bluish-purple shells observed in a F_2 family suggest a more complex genetic control of shell color in the Pacific abalone. As suggested by Kobayashi and colleagues (2004), bluish-purple and the wild G-type belong to one locus, with the *b* allele being recessive and responsible for the expression of the bluish-purple type. Our study shows that allele *o* and *G*, responsible for the expressions of O- and G-types, belong to one locus. Therefore, we conclude that all three alleles, *b*, *o*, and *G* must belong to the same locus. Phenotypes observed in family #15 can only be explained by the assumption that the third allele *b* is recessive to both *G* and *o*, and the genetic model in family #15 should be modified as the following:

$$o/b \times G/b = o/G + o/b + G/b + b/b$$

Where o/b and G/b are the deduced genotypes of the parents, and b/b is the proposed genotype of the bluish-purple abalones. However, the observed number of each type (G:O:B = 146:239:65) differs from the expected ratios (G:O:B = 2:1:1) predicted by the genetic model proposed earlier. The discrepancy may be explained by segregation distortion caused by linkage between the *G* allele and a recessive deleterious gene. Recessive deleterious genes are common in marine molluscs and often cause segregation distortion (Launey & Hedgecock 2001, Yu & Guo 2003). Because we observed bluish-purple shells in only one family, further studies with replicated matings between bluish-purple and other types of abalone are needed to test our hypothesis.

This study shows that shell color in the Pacific abalone can change considerably depending on diet. Dietary influence on shell color has been observed in some marine gastropods before (Harry & Turner 1958, Leighton 1961, Underwood & Creese 1976). Findings of this study are significant because the dietary modifications of shell color observed here provide a direct link between the color of the natural diet and the color of the surrounding environment where the Pacific abalone lives. The fact that wild G-type abalones are predominantly green when fed with green algae and change into dark reddish brown when fed with red algae (Fig. 1) is probably no accident. Even the normally yellow O-type changes to a reddish orange when fed with red algae. Such dietary modifications of shell color may have great adaptive significance. By absorbing and depositing color pigments from the diet onto the shell, it may provide a mechanism for abalone to avoid predation. Color selection by visual predators is common in marine animals such as *Littorina saxatilis* (Allen 1988, Ekendahl 1998). Dietary inputs to shell color make it possible for abalones to align their shell color with that of the surrounding background provided by their dietary algae, so that abalones are camouflaged for sake of avoiding predation. We argue that dietary modification of shell color in abalone is not a simple coincident, but a significant mechanism for camouflage and predation avoidance developed through evolution and adaptation.

The importance of abalone shell color in predation avoidance is further supported by the rare occurrence in wild populations of the yellow to orange O-type and the bluish-purple B-type variants. These variants do not provide effective camouflage to the Pacific abalone and may be strongly selected against by predation. The Pacific abalone usually lives in environments with large, brown algae such as *Ecklonia*, *Nereocystis*, *Macrocystis*, *Laminaria*, and *Eisenia* (Lindberg 1992), which is probably why the green to brown G-type shells are predominant in wild populations. Mutations such as the O- and B-types do occur but are selected against in normal environments.

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