MALACOLOGIA, 1984, 25(2): 477–491

SPECIES COHESIVENESS AND GENETIC CONTROL OF SHELL COLOR AND FORM IN *THAIS EMARGINATA* (PROSOBRANCHIA, MURICACEA): PRELIMINARY RESULTS

A. Richard Palmer

Department of Zoology, University of Alberta, Edmonton, Alberta T6G 2E9
and
Bamfield Marine Station, Bamfield, British Columbia V0R 1B0, Canada

ABSTRACT

Thais (or *Nucella*) *emarginata* has one of the largest geographical ranges of rocky-intertidal, prosobranch gastropods of the northeastern Pacific, nearly 35° latitude. *T. emarginata* has direct development from benthic egg capsules with no pelagic larvae. Throughout its latitudinal range, *T. emarginata* is restricted to the mid- and upper-intertidal zone of rocky shores, and is generally restricted to areas with intermediate to high wave exposure or moderate currents. Consequently, expanses of deep water, sand beaches and quiet estuaries or inlets all act to inhibit gene flow. In addition, lateral movements along rocky shores are not very great; mean distances moved by marked individuals over a 12 month period were less than 5 m.

Pairwise crosses of *T. emarginata* from southeast Alaska (U.S.A.) and Vancouver Island (Canada) revealed that in spite of restricted gene flow, individuals from these distant populations (circa 1500 km) were capable of producing F1 offspring that grew to adult size, mated and produced egg capsules. F2 viability remains to be determined. Females from Alaska produced fewer egg capsules (avg. <50%) in the laboratory than those from Vancouver Island, but there were no differences between within- or between-population crosses. No consistent differences in juvenile survivorship were noted among crosses of each type.

T. emarginata also exhibits variation in shell color, banding and sculpture. Shell-morph frequencies of F1 offspring suggest that: 1) there are at least three discrete color alleles (black, orange, white), 2) the color black is dominant to orange and white,[1] 3) banding assorts independently of color, 4) the capacity to produce spiral sculpture may be controlled by a single switch gene or a block of tightly linked genes, and 5) spiral sculpture assorts independently of color.

Key words: *Thais*; shell; variation; genetics; breeding; marine; dispersal; geographic range; speciation.

INTRODUCTION

It is a common view that genetic divergence results from reduced or interrupted gene flow among populations, either due to genetic drift or to selection (Mayr, 1963; Endler, 1977; Lessios, 1981). If of sufficient magnitude, such divergence may ultimately lead to speciation, a process which remains poorly understood (Ayala, 1975; Avise, 1976; Bush, 1982). One approach to the study of speciation is to examine the degree of genetic divergence among populations of a geographically wide-ranging species via breeding experiments. Such experiments provide information about offspring viability as a function of geographic separation of parents and may also provide information about the nature

---

[1] NOTE ADDED SEPTEMBER 1983: F2 progeny have revealed a more complicated set of dominance relationships for color than indicated below. In Alaskan populations, the color black is clearly dominant to brown, and both are dominant to orange; F2 phenotype frequencies indicate a simple, single-locus, three-allele basis of color variation in lineage 16 (now 80–16). In Vancouver Island populations [e.g. lineages 17 and 18 (now 80–17 and 80–18)], however, either more alleles are present, more loci are involved or epistatic effects on expression of color are greater since the color orange exhibits considerable variation in intensity of expression. Of greater significance, orange can be completely dominant to black, although black exhibits weak and variable penetrance in some crosses, and black so far exhibits no evidence of dominance over orange. At the present time, I am not certain whether the color loci in Alaskan and Vancouver Island populations are the same; however, differences clearly exist in the phenotypic dominance hierarchy among color alleles between these distant populations. Thus, the interpretation presented below that regulation of color expression may have broken down in between-population crosses, appears to be supported.

of differences that lead to speciation (Ayala, 1975; Marcus, 1980).

I report here the results of some breeding experiments with individuals from geographically distant populations of the rocky-intertidal gastropod, *Thais* (or *Nucella*) *emarginata* (Deshayes, 1839). In addition to information on genetic divergence, these crosses permit a preliminary interpretation of the genetic basis of variation in color, banding and sculpture in a marine, prosobranch gastropod. Data of these types have been reported for few such gastropods (*Littorina picta* [Struhsaker, 1968], *Urosalpinx cinerea* [Cole, 1975], and *Littorina saxatilis* [Newkirk & Doyle, 1975]).

METHODS

Geographic ranges of prosobranch gastropods that occur in the rocky intertidal zone of the central and northern Pacific coast of North America were obtained from Abbott (1974) and McLean (1966). Species that were largely or strictly intertidal were distinguished from those that were predominantly subtidal.

Data on vertical distribution of *Thais* in the intertidal zone and lateral distribution along a wave-exposed gradient were obtained in Torch Bay, Alaska (58°20′ N, 136°50′ W), a deep, 6 km long fjord that opens on the Gulf of Alaska. Six replicate 0.1 m^2 quadrat samples were taken at 0.5 m or 1.0 m intervals along two permanent vertical transects in an area of intermediate wave exposure in 1974, 1978 and 1979. Counts were made of all three species of *Thais* that occurred at these sites [*T. canaliculata* (Duclos, 1832), *T. emarginata* and *T. lamellosa* (Gmelin, 1791)]. The distribution along a wave exposure gradient was determined by inspecting the shores of Torch Bay in June 1978 as indicated in Fig. 3, and recording the presence or absence of *T. emarginata*.

Movements of *T. emarginata* were determined by recording the distance moved by marked individuals from their point of release. Vertical movements of *T. emarginata* were compared to those of the lower shore *T. canaliculata* at Iceberg Point, Lopez Island, Washington (U.S.A.) in July, 1974. Individuals of both species were collected and returned to the laboratory where they were marked by writing numbers on their shells with india ink and coating them with a clear cement (Dekophane, Rona Pearl Corp., Bayonne, New Jersey). The day after collection, 50 marked individuals of each species were released at two positions on the shore: high, at the base of the *Balanus glandula* refuge zone and low, in the lower third of the *Semibalanus cariosus* zone. Two weeks after release, the positions of all marked snails that could be located were noted. Lateral movements along the shore were measured on marked *T. emarginata* at two sites in Torch Bay, Alaska from June 1978 to June 1979 relative to their point of release in 1978.

Breeding experiments were initiated in September 1980 with *T. emarginata* collected from Torch Bay, Alaska and Wizard Rock, near the Bamfield Marine Station (Bamfield, British Columbia, Canada; 48°53′ N, 125°10′ W). Immature snails were sexed by anaesthetizing them overnight in a $MgCl_2$ solution ($MgCl_2$ mixed with tap water to a specific gravity the same as seawater at approximately 32‰ then diluted 1:3 with seawater). The feet of the relaxed animals were pulled gently out of the aperture until it was possible to determine the presence or absence of a penis behind the right tentacle. As nearly all *T. emarginata* had a penis when small, it was necessary to rank individuals by penis size; those with a large penis were considered males and those with a small penis were considered females. To date, sexing errors have occurred in fewer than 10% of the crosses as verified by penis size when mature. Snail sizes were measured as shell length to the nearest 0.1 mm with vernier calipers.

Pairs of sexed, immature snails were held in plastic freezer containers with sides of 3 mm mesh VEXAR (Dupont) plastic screen and supplied with small stones covered with the barnacle *Balanus glandula*, one of their preferred prey (Palmer, 1980). The cages were immersed in aquaria with continuously running sea water at the Bamfield Marine Station and barnacles were replenished after they were consumed. Egg capsules were allowed to remain in these cages until close to hatching (10 to 14 weeks) at which point they were transferred to freezer containers with NITEX screen sides (335 μm mesh). Newly hatched snails were supplied with recently metamorphosed *B. glandula* on small stones collected from the field. When large enough (>3 mm), juveniles were transferred to coarser mesh, freezer-container cages where they were grown to adult size on larger *B.*

glandula. As adult coloration became discernible (8–10 mm shell length), the F1 progeny were photographed at approximately 8 week intervals to record the pattern of color maturation.

RESULTS

Of species of prosobranch gastropods that occur in the rocky intertidal, only three of 91 have latitudinal ranges as great or greater than *Thais emarginata* (Fig. 1). Of strictly rocky-intertidal prosobranchs, only one of 35 species (the limpet *Collisella pelta*) has a latitudinal range as great as *T. emarginata* along the Pacific coast of North America (Fig. 1).

The vertical transects in Torch Bay revealed that even though the distribution of *Thais emarginata* changed rather dramatically over time (Fig. 2), this species rarely occurred below +1.0 m above MLLW. In Washington, marked individuals released at or below this point actively crawled upshore while individuals released within this zone tended to remain there (Table 1).

The shore survey of Torch Bay revealed that *T. emarginata* did not occur in the protected portions of the bay and occurred infrequently on the most exposed headlands (Fig. 3). In addition, in Torch Bay, *T. emarginata* was rarely found on cobble beaches unless the snails were immediately adjacent to a stretch of bedrock shore. Lateral movements of marked animals along continuous bedrock at two sites on the north-central shore of Torch Bay varied as a function of wave exposure (Fig. 4). At neither site, however, were individuals recovered that had moved more than 10 m over 12 months. I have observed movements of greater distances for *T. emarginata* in the San Juan Islands, Washington (U.S.A.), but they were not common; only 6 of 92 marked animals recovered more than 10 m over 2 months along the shore of Deadman Island (Palmer, unpublished).

TABLE 1. Mean distances moved following reciprocal vertical transplants of *Thais emarginata* and *T. canaliculata* at Iceburg Point, Lopez Island, Washington (U.S.A.) in July 1974. Distances were measured along the rock surface relative to the release point. Fifty animals of each species were released at each location. The upper release point was at the base of the *Balanus glandula* refuge zone, the lower release point was in the lower third of the *Semibalanus cariosus* zone. Tabled values are means ± one standard error. P = probability value for two-tailed t-test.

Species	N	Mean	P
Distance moved down from upper release point (m)			
T. emarginata	12	0.44(0.147)	0.19
T. canaliculata	4	0.87(0.335)	
Distance moved up from lower release point (m)			
T. emarginata	25	4.05(0.885)	<0.001
T. canaliculata	17	1.19(0.505)	

Egg capsule production varied widely among pairs (Table 2). In general, Alaskan females produced fewer than half the number of egg capsules produced by those from Vancouver Island; however there were no consistent differences in egg capsule production or juvenile survivorship between within- and between-population crosses (Table 2).

Tables 3–5 present parental and offspring phenotypes from within- and between-

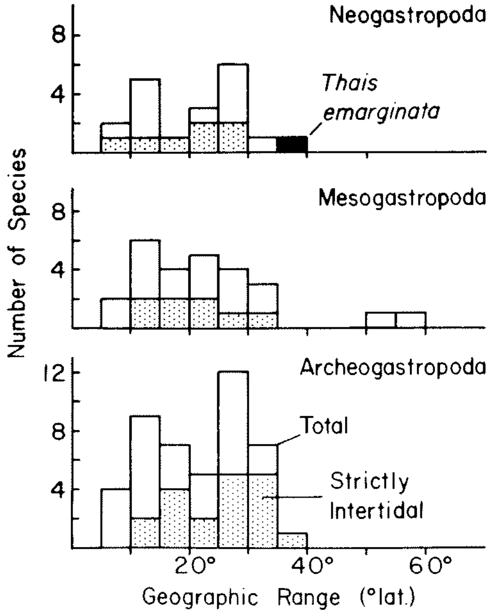

FIG. 1. Frequency distribution of geographic ranges (degrees latitude) of prosobranch gastropods recorded from the rocky intertidal zone of the central and northern Pacific coast of North America. Ranges of archeogastropods from McLean (1966), all others from Abbott (1974). Stippled bars represent species restricted largely to the intertidal zone.

TABLE 2. Egg capsule production rates and survivorship of juveniles of *Thais emarginata* from within- and between-population crosses of animals collected from Torch Bay, Alaska (U.S.A.) and Bamfield, British Columbia (Canada). Tabled values include the total number of egg capsules produced by pairs in the laboratory from Sept. 2, 1980 to Dec. 28, 1981, and the number of juveniles surviving per capsule on Dec. 29, 1981.

	Female					
	Torch Bay			Bamfield		
Male	Cross	Caps.	Juv.	Cross	Caps.	Juv.
Torch Bay	15	44	0.32	1	110	0.33
	16	50	0.26	2	101	0.84
				11	124	0.02
				12	58	0.00
	Means	47.0	0.29		98.3	0.30
Bamfield	3	59	0.25	17	95	0.48
	4	47	0.49	18	102	0.26
	13	52	0.46			
	14	19	0.14			
	Means	44.3	0.34		98.5	0.37

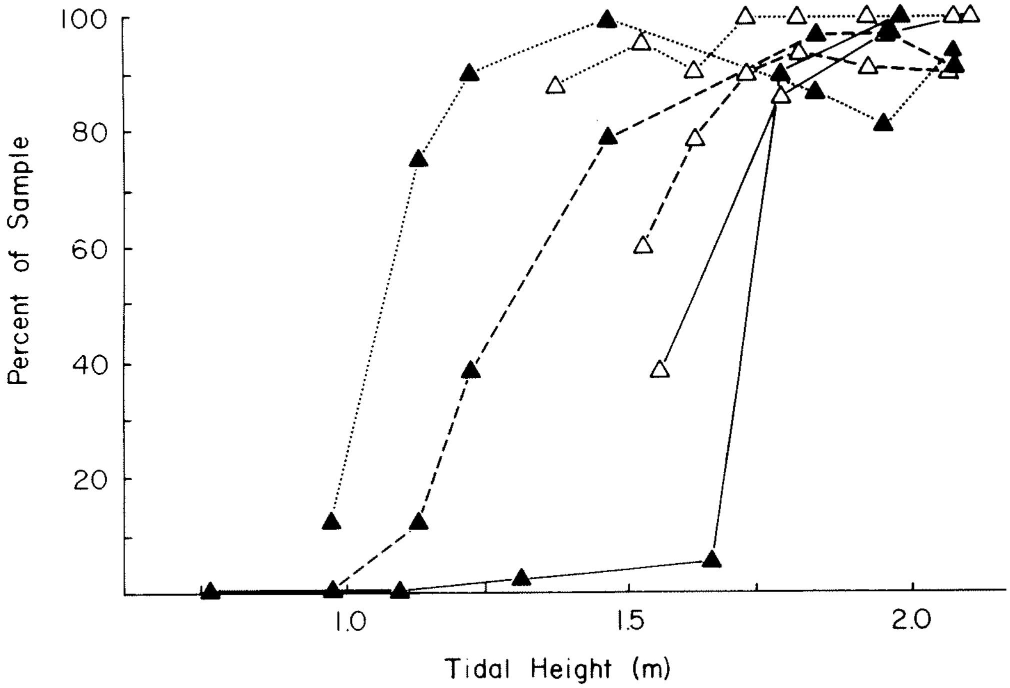

FIG. 2. Vertical distribution of *Thais emarginata* in Torch Bay, Alaska (U.S.A.) for three different years: 1974 (solid lines), 1978 (dashed lines) and 1979 (dotted lines). Solid symbols and open symbols represent data from two separate transects. Tidal height was measured in meters above MLLW. Mean maximum tidal range in the vicinity of Torch Bay is 3.1 m (Anonymous, 1982).

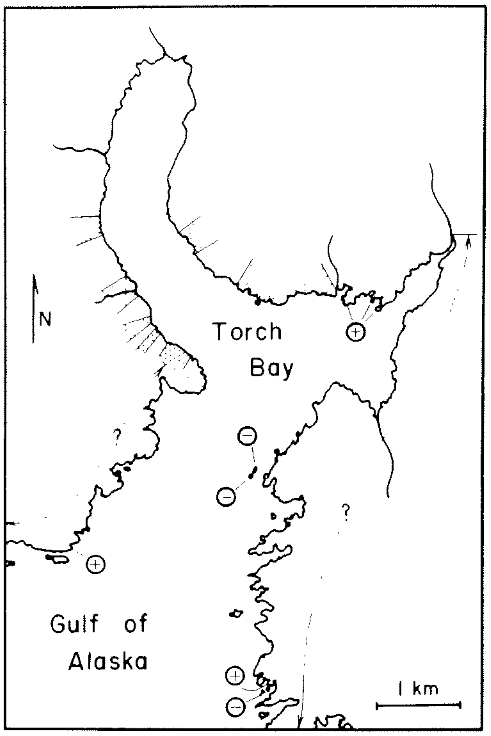

FIG. 3. Lateral distribution of *Thais emarginata* along the shore of Torch Bay, Alaska (U.S.A.) in June 1978. Stippled areas indicate continuous populations. '+' and '−' indicate presence or absence at isolated sites. Regions of the shore not surveyed are indicated by question marks.

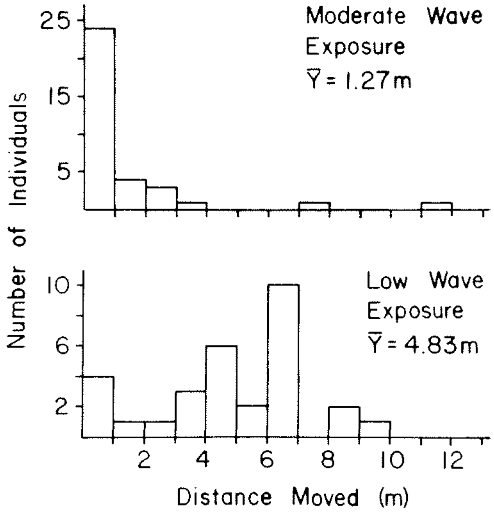

FIG. 4. Frequency distribution of distances moved by marked *Thais emarginata* at two sites of differing wave exposure in Torch Bay, Alaska (U.S.A.) over 12 months, from June 1978 to June 1979. At both sites the shore was searched for 15 or more meters in both directions from the site of release.

population crosses. Three discrete color morphs could be recognized clearly: black, orange and white. Variable shades of brown, orange-brown, grey-orange and grey also existed but were difficult to score among broods reliably. Black appeared dominant to orange (crosses 1 and 16) and white appeared to be recessive to black and orange (cross 15, Table 3), although there was some evidence of blending. While most crosses yielded an intermediate range of sculptural development, one (cross 18, Table 5) yielded two distinct phenotypes: strong spiral sculpture and smooth. In this cross, sculpture assorted independently of the colors orange and black (Table 6). Banding also assorted independently of color (cross 17, Table 6). Finally, the offspring of cross 4 exhibited a rather dramatic linkage between growth rate (or possibly time of hatching) and shell color: after 8 months of growth, the seven brown-banded individuals were significantly larger (mean shell length = 21.1 mm, SE = 1.02) than the 13 orange-brown individuals (mean = 13.0 mm, SE = 0.57; $P < 0.001$, t-test).

DISCUSSION

Geographic distribution

The geographic range of *Thais emarginata* is clearly large relative to other prosobranch gastropods that occur in the rocky intertidal (Fig. 1). This species thus appears capable of persisting under a wide range of physiological and ecological conditions. Its range includes three 'marine-climate' and four 'wave-climate' regions along the Pacific coast of North America (Hayden & Dolan, 1976), and spans three biogeographic provinces described by Valentine (1966) based on molluscs and four faunal associations recognized by Hayden & Dolan (1976) using molluscs, decapod crustaceans and ascidians. Environmental conditions thus appear to have resulted in shorter geographic ranges for most other gastropod species along this coastline; *Thais emarginata* appears unusually resistant to those forces influencing range determination or speciation.

TABLE 3. Inheritance of shell color in *Thais emarginata*. Parental phenotypes and frequencies of offspring phenotypes are presented for between- and within-population crosses. Color abbreviations: BL = black, OR-BRN = orange-brown, OR = orange, GR-OR = grey-orange, GR = grey, WH = white. Source population abbreviations: B = Bamfield, British Columbia, Canada, TB = Torch Bay, Alaska, U.S.A. Tabled values are numbers of progeny. Question marks indicate uncertain scoring.

		Parent		F1 Phenotypes					
Cross	Sex	Phenotype	Source	BL	OR-BRN	OR	GR-OR	GR	WH
1	m	OR	TB	10	6		2?		
	f	BL	B	10	7		1?		
2	m	OR	TB	9	5	23?			
	f	BL	B	11	12	26?			
3	m	BL(BRN?)	B		3?		4?		
	f	OR	TB		3?		5?		
4	m	BL(BRN?)	B	3	4		6?		
	f	OR	TB	2	3		2?		
11	m	BL	TB					1?	
	f	WH	B					2?	
13	m	WH	B	10					9
	f	BL	TB	7					10
14	m	WH	B						1
	f	OR-BRN	TB			1			
15	m	WH(GR?)	TB	3	1	2			
	f	OR-BRN	TB	1	4	3			
16	m	BL	TB	6	4				
	f	OR	TB		3				
17	m	OR	B	13		14			
	f	BL	B	13		14			
18	m	BL	B	5	1?	5			
	f	OR	B	11	1?	6			

This observation is in rather sharp contrast to the patterns observed by Shuto (1974) and Hansen (1978, 1980) that species with low dispersal (lecithotrophic development) tend to have shorter geological durations and geographic ranges than those with greater dispersal (planktotrophic development). In *Thais emarginata* the lack of a pelagic larva is associated with a wide geographic range. While it is not surprising that species with greater dispersal ability should have larger geographic ranges, the claim that reduced dispersal ability precludes a wide geographic range (Shuto, 1974; Hansen, 1978, 1980) appears unsubstantiated.

Gene flow

As for many other mid- to high-latitude prosobranchs, *Thais emarginata* has direct development from benthic egg capsules (Thorson, 1950; Lyons & Spight, 1973). This species breeds in pairs, or groups of 5 or 6, and lays small clusters of egg capsules (10 to 20 per snail) in crevices or under algae (personal observation). Hatchlings leave the egg capsules after approximately 3 months development. Active dispersal thus is accomplished solely by movements of animals along the shore (but see below).

The distributional data and results of the vertical transplants revealed not only that *T. emarginata* occurs high on rocky shores (Fig. 2), but that this distribution is actively maintained (Table 1). *T. emarginata* is also normally absent from protected bays or inlets (Fig. 3), except in areas where there are strong tidal currents (personal observation). As a consequence, expanses of deep water and protected bays or inlets should act as barriers to gene flow. Since the Pacific coast from Alaska through British Columbia is

TABLE 4. Inheritance of banding in *Thais emarginata*. Parental phenotypes and frequencies of offspring phenotypes are presented for between- and within-population crosses. Source population abbreviations: B = Bamfield, British Columbia, Canada, TB = Torch Bay, Alaska, U.S.A. Tabled values are numbers of progeny.

		Parent		F1 Phenotypes	
Cross	Sex	Phenotype	Source	Banded	Unbanded
1	m	Banded	TB	12	6
	f	Banded*	B	11	7
2	m	Banded	TB	14	22
	f	Banded**	B	23	26
3	m	Unbanded	B	4	3
	f	Banded**	TB	6	2
4	m	Unbanded	B	13	
	f	Banded	TB	7	
11	m	Banded	TB		1
	f	Unbanded	B		2
13	m	Unbanded	B	10	9
	f	Banded	TB	7	10
14	m	Unbanded	B		1
	f	Banded	TB	1	
15	m	Unbanded	TB	6	
	f	Banded	TB	8	
16	m	Banded	TB	10	
	f	Banded*	TB	3	
17	m	Banded	B	15	12
	f	Unbanded	B	10	17
18	m	Unbanded	B		11
	f	Unbanded	B		18

*Unbanded when small.
**Banding very weak.

TABLE 5. Inheritance of shell sculpture in *Thais emarginata*. Sculpture was measured as the depth (mm) of the grooves between the middle spiral ribs of the body whorl at the lip of the aperture. F1 offspring were ranked visually into four approximate sculpture categories: SM = smooth (<0.14 mm), WK = weak (0.15–0.29 mm), MOD = moderate (0.30–0.44 mm), STR = strong (>0.45 mm). Tabled values are numbers of progeny.

	Parental Sculpture(mm)		F1 Phenotypes			
Cross	Male	Female	SM	WK	MOD	STR
1	0.30	0.00		13	23	
2	0.40	0.00		21	39	25
3	0.00	0.40		3	10	2
4	0.00	0.40		6	5	7
11	0.30	0.10			1	2
13	0.05	0.40		19	17	
14	0.30	0.25			1	1
15	0.35	0.40				14
16	0.40	0.50				13
17	0.05	0.15	40	14		
18	0.35	0.30	14			17

heavily dissected by fjords and estuaries, it seems likely that gene flow among these populations on the scale of hundreds of kilometers is extremely low.

It is, of course, almost impossible to document rigorously the absence of gene flow, since migration of as few as one individual per population per generation to an adjacent population can be adequate to maintain uniform gene frequencies over an extensive geographic range in the absence of selection (Lewontin, 1974). However, I believe several hypotheses about passive mechanisms of gene flow may be ruled out or minimized. First, movement by birds is unlikely to be important. While adult *Thais emarginata* may be taken from the intertidal by gulls, crows or oystercatchers to be consumed on adjacent rocks, they are usually taken above the high-tide line (Zach, 1979; personal observation) and would thus die whether they were eaten or not. Second, movement of egg capsules by dislodgment is also probably unimportant. If capsules were dislodged, they would most likely either be consumed by intertidal anemones (Sebens, 1977), drift into the strand line and die, or settle into the subtidal among drift algae where hatchlings probably would not survive.

A mode of dispersal which might occur but which would be very difficult to document is transport of hatchlings or very small juveniles on drifting algae (e.g. *Fucus*). Although drifting algae would also end up in the strand line, a juvenile could be dislodged from the alga on another shore before its final deposition. The lack of data for any of these modes precludes a definitive conclusion regarding actual levels of gene flow. The most promising test of this hypothesis of extremely low gene flow will be an analysis of the geographic distribution of rare, electrophoretically detectable alleles following the procedure of Slatkin (1981). If sufficient electrophoretic variation is present, such an analysis would provide a direct measure of the rates of gene flow in *Thais emarginata.* Preliminary electrophoretic scanning is underway.

Genetic divergence

Patterns of egg-capsule production and juvenile survivorship for between- and within-population crosses from Alaska and Vancouver Island (Table 2) suggest that in spite of reduced gene flow, there has not been sufficient genetic divergence on this geographic scale to reduce F1 viability substantially, even though physical and ecological conditions change substantially over this range (Hayden & Dolan, 1976). Crosses in progress will provide information on F2 viability. To date (July, 1982), 7 of 23 mated pairs of F1 progeny from between-population crosses have produced egg capsules and several clutches are clearly developing. In addition, crosses have been established with *T. emarginata* collected from Santa Barbara, California (U.S.A.) to try to assess the degree of divergence on a larger geographic scale. It thus appears either that gene flow is greater than expected or that selection has not been strong enough to induce genetic differentiation which would influence viability of between-population crosses. Alternatively, these data could be interpreted as consistent with the currently popular view that species are entities resistant to change except during the speciation process (Schopf, 1981; Gould, 1982).

Perhaps the most interesting pattern observed among broods was that difficulties scoring offspring color phenotypes were restricted largely to between-population crosses (e.g. 1, 2, 3, 4, and 11; Table 3). In crosses 1 and 2, many of the darker morphs that were difficult to score appeared to have a superposition of a lighter band color (orange) upon a ground shell color of black: spiral ribs were black and grooves in between appeared to be an uneven mixture of orange and black. In banded individuals, ribs most commonly are unpigmented. The four within-population crosses (15–18) exhibited more discrete color morphs. One interpretation of this pattern is that the integration of loci which regulate production of pigment and control banding is different in these distant populations, and crosses between these populations may have resulted in a breakdown of this regulation. Backcrosses and crosses in progress among F1 progeny will shed additional light on this hypothesis of disrupted regulation.

Confidence of paternity

It is well known that prosobranch gastropods have the capacity to store sperm for periods of from weeks to months (Fretter & Graham, 1962). Thus, to interpret patterns of inheritance accurately it is necessary to know either that females were virgin when established in pairs or that any stored sperm had been resorbed or become inviable. To guard against the possibility of stored sperm I used animals that were approximately half

TABLE 6. Independent assortment of banding, color and sex, and sculpture, color and sex in *Thais emarginata* crosses 17 and 18. Tabled values are numbers of progeny.

		Banding Cross 17		Sculpture Cross 18	
Color	Sex	Unbanded	Banded	Smooth	Sculptured
Orange	m	6	8	2	3
	f	11	3	3	3
Black	m	6	7	4	1
	f	6	7	4	7

adult size (mean initial shell length of parents when isolated = 13.8 ± 2.2 mm, range = 11.8–15.3 mm; mean shell length of laboratory grown adults = 25.5 ± 3.1 mm, range = 22.4–29.6 mm). The possibility that copulation occurred prior to isolation, though, cannot be ruled out entirely.

There is evidence, however, suggesting that females in these crosses produced offspring using only the sperm of the male with which they were caged. In a recent backcross where a mature female was caged with a male offspring half its size, the female produced three successive clutches at approximately one month intervals. In the first of these clutches, nearly all capsules appeared to contain developing embryos. In the second, only about 10%, and in the third none of the eggs exhibited normal development. Storage of viable sperm thus would appear limited to a period of approximately two to three months. Since none of the initial pairs produced capsules until over three and a half months after isolation, it seems likely that the progeny were derived only from the isolated parents. Mature females brought into the laboratory and fed usually produce capsules within one month or less of collection (personal observation). Crosses are currently underway between mature females and males with known color markers to determine the length of sperm storage in *Thais emarginata.*

Genetics of color, banding and sculpture

Although color, banding and sculpture polymorphisms have been described for many marine, prosobranch gastropods (Moore, 1936; Struhsaker, 1968; Berry & Crothers, 1968, 1974; Spight, 1973, 1976; Cole, 1975; Campbell, 1978; Reimchen, 1979; additional refs. in Vermeij, 1978), the genetic basis of these polymorphisms appears to have been documented for only a few species. Struhsaker (1968) found that offspring of different sculpture morphs in *Littorina picta* tended to resemble the average parental phenotype as did Newkirk & Doyle (1975) for shell shape in *Littorina saxatilis,* but phenotypes were not discrete and no genetic model was proposed. Juvenile shell color in *Urosalpinx cinerea* was explained by a tri-allelic, single locus model (Cole, 1975). In this species, however, as in *T. emarginata,* juvenile shell colors were largely transient. Thus the precise genetic basis of adult coloration and sculpture of the shell remains to be determined.

In *Thais emarginata,* F1 phenotype frequencies (Tables 3–6) suggest that there is a simple genetic basis to several aspects of variation in shell color, banding and sculpture. Mendelian ratios from crosses between black and orange (crosses 17 and 18), and black and white individuals (cross 13, Fig. 5) suggest minimally that there is a single locus with three discrete color alleles which controls adult coloration. The lack of orange offspring from crosses 1 and 16 (Table 3) indicates that black can partially or completely override the contribution of the orange allele in a heterozygote.[2] White also appears to be recessive to black and orange since only black, orange-brown and orange progeny were produced in cross 15 even though one parent was white (Table 3). The parental phenotypes of this cross, however, were not distinct and the interpretation is thus tentative.

Not all color phenotypes were clearly defined. In particular, several shades of brown and orange-brown appeared to intergrade (crosses 1–5, 15 and 16; Table 3). These could be black/orange heterozygotes or they may indicate the existence of more than one black allele or perhaps the presence of alleles

---

[2] See Footnote 1 (Abstract).

for brown coloration. Alternatively, more than one locus may be involved; other loci may affect hue or intensity as described for the pulmonates *Partula taeniata* (Murray & Clarke, 1976) and *Cepaea nemoralis* (Cain & Sheppard, 1957). Additional crosses will be required to clarify the number of alleles and loci controlling adult coloration in *Thais emarginata.*

Diet appears to have little if any effect on the shell color of *T. emarginata,* in contrast to results reported by Moore (1936) for another thaidid gastropod, *Nucella lapillus.* Young individuals of both *T. emarginata* (mean initial shell length = 13.7 mm) and *T. canaliculata* (16.8 mm) held in cages at two tidal heights in the field (+ 0.15 m and + 0.76 m; Friday Harbor Laboratories, Friday Harbor, Washington, U.S.A., 48°33′ N, 123°01′ W) and fed pure diets of barnacles *Balanus glandula* for approximately one month (25 and 33 days respectively) followed by a pure diet of mussels *Mytilus edulis* for approximately one month (32 and 25 days respectively) exhibited at most very slight changes in the hue of the shell even though they increased substantially in total weight both on barnacles (mean ± SE, N = 8: 141.1 ±4.07% and 99.6 ± 7.65% for *T. emarginata* and *T. canaliculata* respectively) as well as on mussels (51.2 ± 9.06% and 50.2 ± 2.93% respectively; Palmer, unpublished). A similar result was obtained with 100 individuals of juvenile *T. emarginata* (shell length range 12.7–16.9 mm) collected from Wizard Rock (Vancouver Island, British Columbia, Canada; 48°53′ N, 125°09′ W and grown nearly 360° (one full whorl) on average on either a pure diet of barnacles (50 animals on *B. glandula*) or mussels (50 on *M. edulis*) over a period of 58 days while continuously immersed in running seawater in the laboratory. In neither experiment was a dramatic loss of pigment observed in individuals with dark-colored shells when grown on barnacles, or an increase observed in shell pigmentation when grown on mussels.

In a widely cited work, Moore (1936) reported that dark-shelled *N. lapillus* produced white shell when transferred to a diet of barnacles in the laboratory and in the field, and also that the % pigmented shells in natural populations was significantly correlated with the availability of *Mytilus edulis* as food. His conclusion that brown/black or mauve shell color is a product of consuming *Mytilus edulis,* however, is open to question on several grounds (see also Berry & Crothers, 1968, 1974). First, no pigmentation was observed to appear in white-shelled animals from a *Balanus* fed community that were grown on mussels even though they were fed mussels for six months (Moore, 1936: 80). Second, I have observed many instances of abrupt shell-color changes in animals from the field as well as those transferred to and grown in the laboratory; these changes, however, were almost invariably from darker shell to either a lighter or an unpigmented shell. In the laboratory, these changes in shell color appeared to result from some kind of trauma as they were associated with an abrupt cessation and reinitiation of growth. Thus, the cessation of pigmentation observed by Moore in some transplanted snails may have been due to the trauma of transplantation rather than a change in diet. Further, these animals often regained their previous pigmentation if grown long enough, a pattern Moore concluded was due to a return to a mussel diet. The lack of quantitative data on frequency and intensity of the experimentally induced color changes makes Moore's results difficult to evaluate. Third, the observed correlations between shell color and availability of *Mytilus* on the shore need not have been produced by dietary differences; they could have resulted from differential mortality due to visual predators. Finally, among the studies with which I am familiar, all of the other reported cases of conspicuous shell-color change with diet are for archaeogastropods [*Turbo cornutus* (Ino, 1949), *Haliotis rufescens* (Leighton, 1961), *H. cracherodii* (Leighton & Boolootian, 1963), *Austrocochlea constricta* (Underwood & Creese, 1976)], a pattern consistent with Comfort's (1951) interpretation that the Meso- and Neogastropoda are fundamenally different from the Archaeogastropoda in the chemistry of their pigment systems. The direct effect of diet (as opposed to rate of growth or trauma) on shell pigmentation remains to be demonstrated conclusively in meso- and neogastropods.

Banding appears to be controlled by two alleles at a single locus. Within-population crosses yielded broods that were either uniformly banded (crosses 15 and 16), uniformly unbanded (cross 18) or contained an equal number of banded and unbanded individuals (cross 17, Table 4; Fig. 6). The lack of unbanded offspring where one parent was unbanded (cross 15) and the presence of unbanded offspring where both parents were

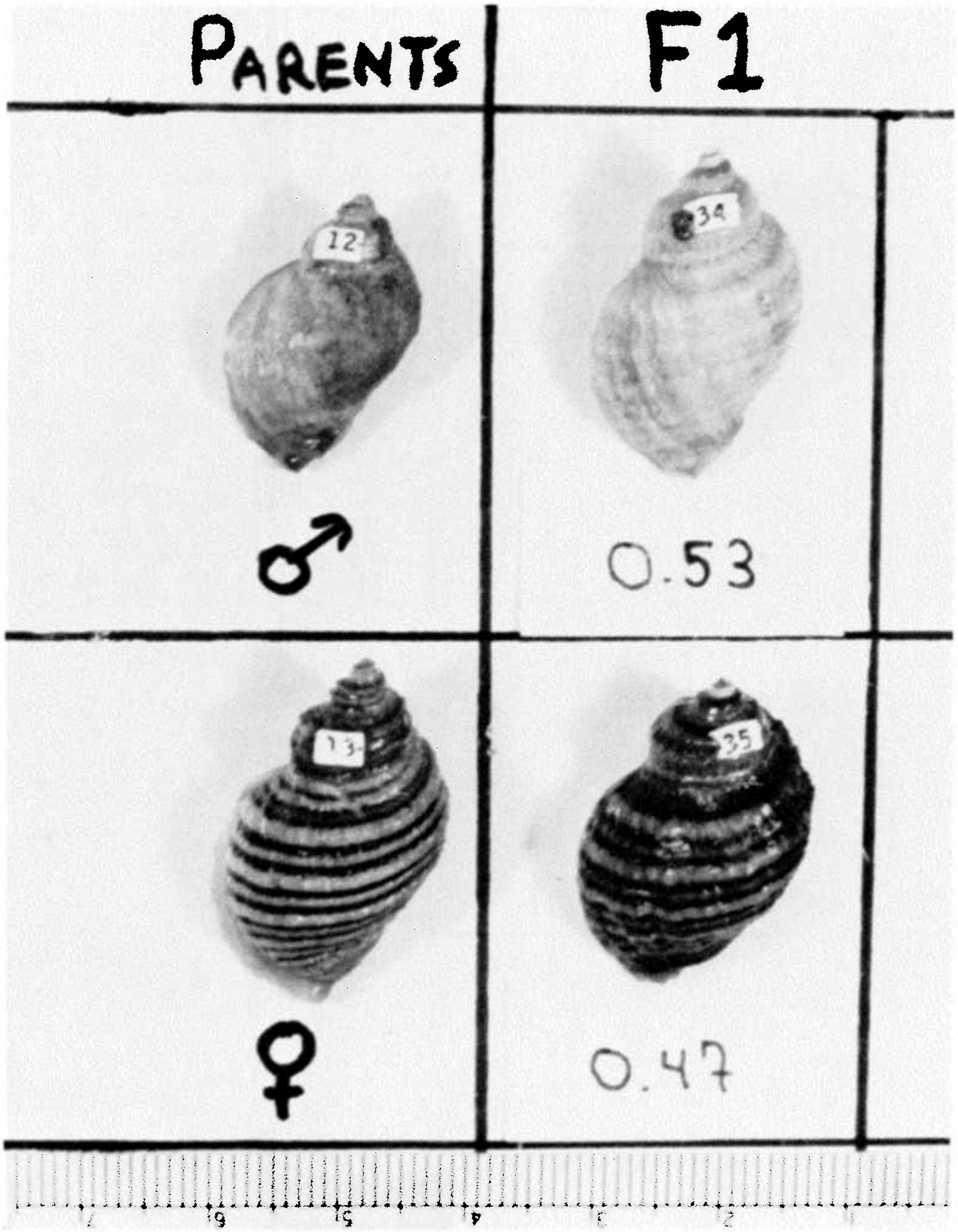

FIG. 5. Phenotypes of parents and F1 offspring from cross 13. The white male parent was from Bamfield, British Columbia, the black banded female from Torch Bay, Alaska. The total number of offspring was 36; numbers under progeny indicate proportions of each phenotype. Scale units in cm.

banded (cross 1) suggests that banding is dominant as in the pulmonate gastropods *Partula taeniata* (Murray & Clarke, 1966) and *Arianta arbustorum* (Cook & King, 1966). However, the offspring of cross 11 were all unbanded even though one parent was banded, so dominance remains to be determined decisively. Crosses 1 and 11 were both between-population crosses and, as suggested above, the integration of color and

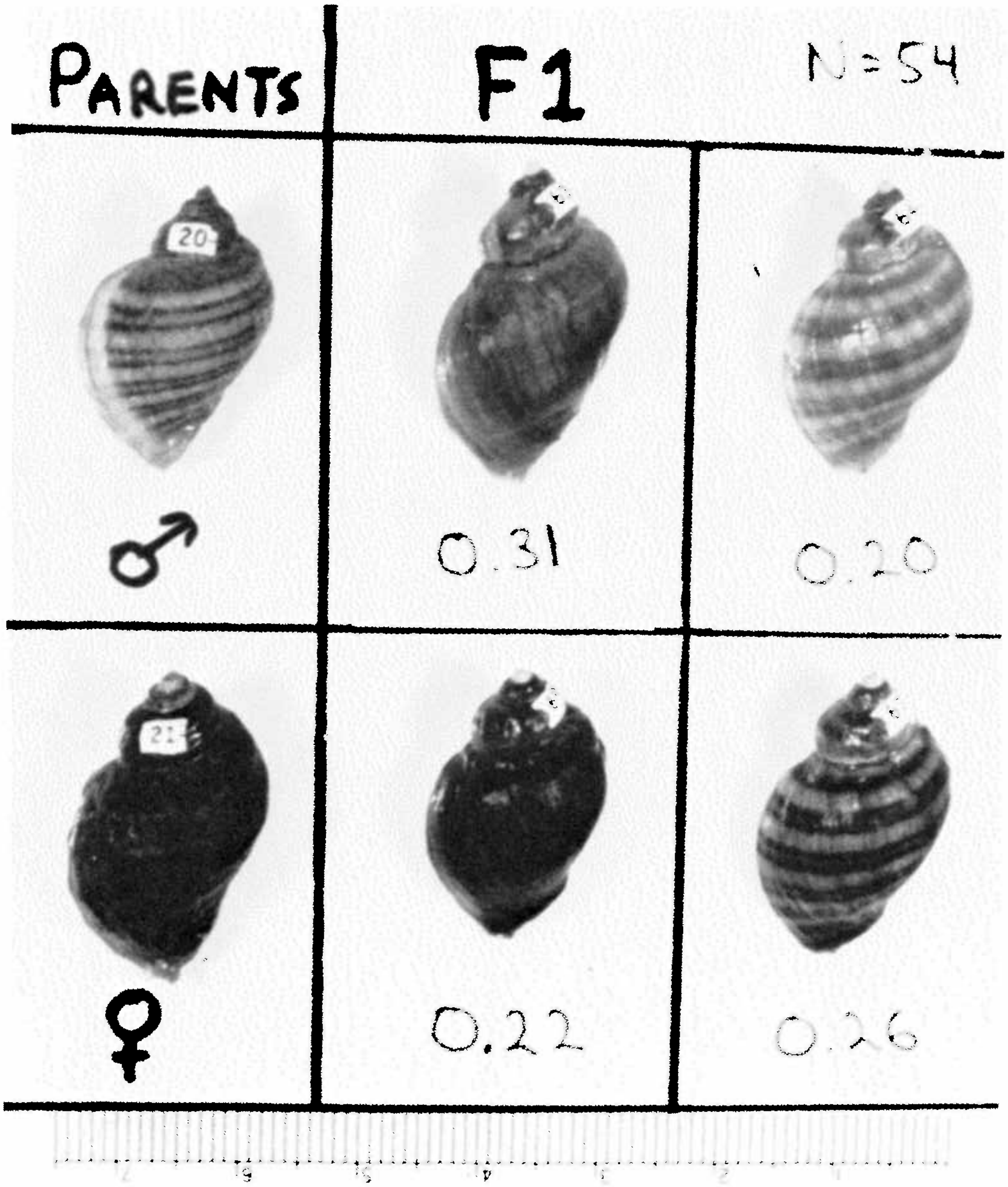

FIG. 6. Phenotypes of parents and F1 offspring from cross 17. Both parents, the orange banded male and the black unbanded female, were from Bamfield, British Columbia. F1 phenotypes, clockwise from upper left: orange unbanded, orange banded, black banded, black unbanded. The total number of offspring was 54; numbers under progeny indicate proportions of each phenotype (see also Table 6). Scale units in cm.

banding may have been disrupted in the progeny.

Perhaps the most striking outcome of these breeding experiments was the production of approximately equal proportions of two discrete sculpture morphs in the progeny of a single cross (cross 18, Table 5; Fig. 7). Expression of shell sculpture in *Thais emarginata* thus may be controlled by a single locus, or by a block of very tightly linked genes. In

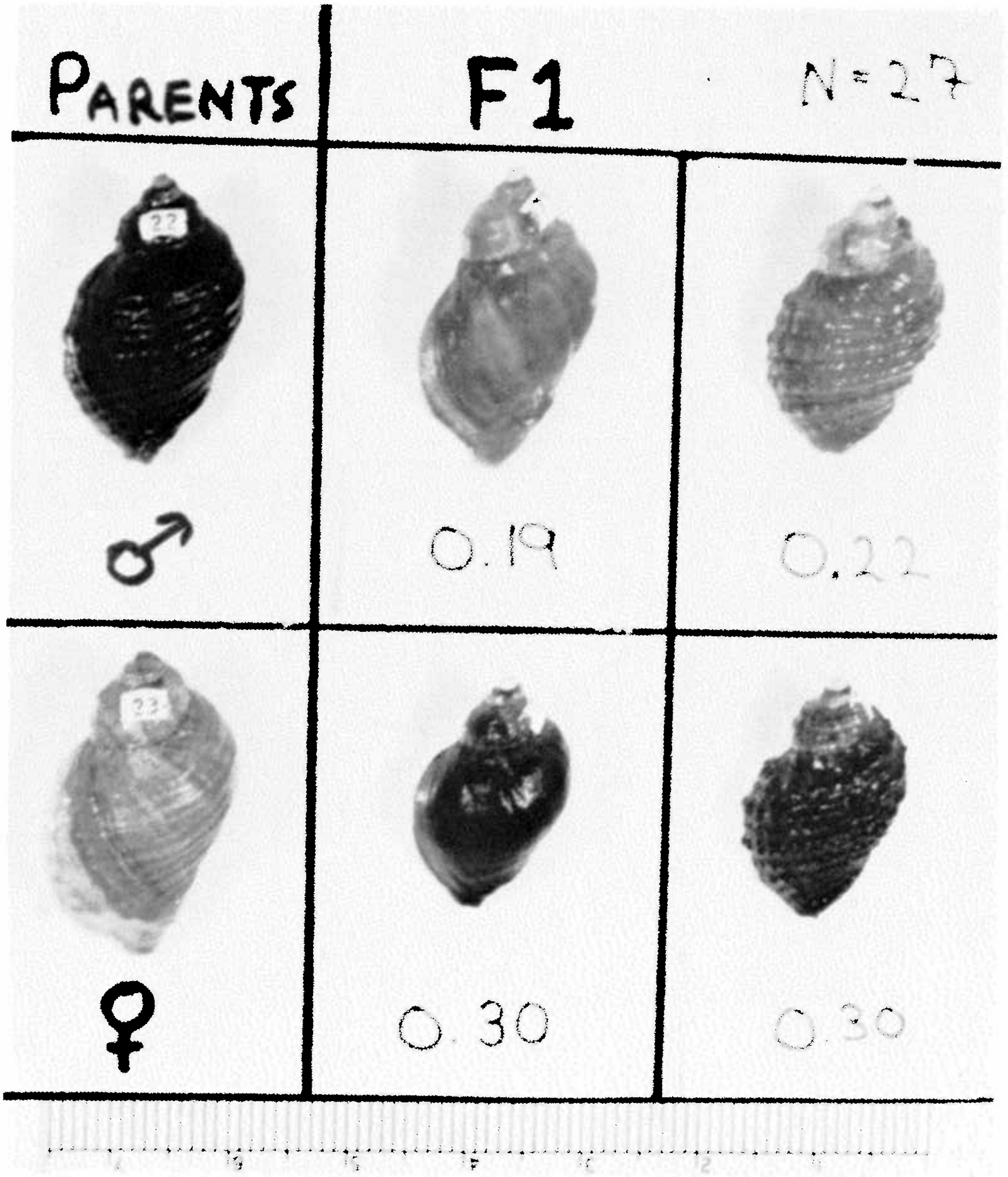

FIG. 7. Phenotypes of parents and F1 offspring from cross 18. Both parents, the black unbanded male and the orange unbanded female, were from Bamfield, British Columbia. F1 phenotypes, clockwise from upper left: orange smooth, orange sculptured, black sculptured, black smooth. The total number of offspring was 27; numbers under progeny indicate proportions of each phenotype (see also Table 6). Scale units in cm.

nearly all other crosses, an intermediate range of sculpture was produced (Table 5), suggesting that several genes actually are involved. There is strong evidence that the development of sculpture can be suppressed by environmental cues in *Thais lamellosa* (Palmer, unpublished); thus *T. emarginata* may have a similar control. If true, the discrete sculpture morphs of cross 18 may represent two alleles at a locus involved with sensing or responding to environmental stimuli rather than coding for sculpture directly.

Brood sizes were too small in most cases to assess intermediate levels of linkage; however both banding and sculpture appeared to assort independently of color (Table 6, Figs. 6 and 7). These data indicate that shell phenotype is not controlled by a supergene as suggested for several terrestrial pulmonates (Cook & Murray, 1966; Murray & Clarke 1976a,b). There also was no consistent evidence for sex linkage of color, banding or sculpture (Tables 3–6). In cross 16, black offspring were all males (Table 3) but this pattern was not observed in any other crosses. Also, in cross 18 seven of eight black, sculptured offspring were females (Table 6). Sample sizes were sufficiently small, however, that these frequencies could have resulted by chance.

In spite of difficulties associated with typing color morphs, *Thais emarginata* appears to offer tremendous potential for understanding the genetic basis of color, banding and sculpture variation in a marine, prosobranch gastropod. Further, additional crosses between adults from more widely separated populations offer the opportunity to examine how the regulation of shell phenotypes may break down when coadapted gene complexes are mixed.

ACKNOWLEDGEMENTS

Long term studies of this type could not be conducted without the cooperation of research granting agencies and marine station staff. I am grateful to the National Sciences and Engineering Research Council of Canada for operating grant A7245 which has provided most of the funding for this study, and to the staff of the Bamfield Marine Station, Bamfield, British Columbia, Canada for their continued cooperation. I am grateful to Greg Streveler and Gary Vequist of the U.S. National Park Service, Glacier Bay National Monument, both for permission to do research in the Monument and for substantial logistical support. Critical comments on a draft of this MS by Drs. M. LaBarbera (University of Chicago), R. R. Strathmann (University of Washington) and G. J. Vermeij (University of Maryland) were much appreciated.

LITERATURE CITED

ABBOTT, R. T., 1974, *American seashells,* ed. 2, Van Nostrand Reinhold, New York, [vii +] 663 p., 24 pl.

ANONYMOUS, 1982, *Tide tables 1982, west coast of North and South America.* U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Washington, DC, 231 p.

AVISE, J. C., 1976, Genetic differentiation during speciation. In AYALA, F. J. ed., *Molecular Evolution.* Sinauer Associates, Sunderland, Mass., p. 106–122.

AYALA, F. J., 1975, Genetic differentiation during the speciation process. *Evolutionary Biology,* 8: 1–78.

BERRY, R. J. & CROTHERS, J. H., 1968, Stabilizing selection in the dog-whelk *Nucella lapillus. Journal of Zoology, London,* 155: 5–17.

BERRY, R. J. & CROTHERS, J. H., 1974, Visible variation in the dog-whelk *Nucella lapillus. Journal of Zoology, London,* 174: 123–148.

BUSH, G. L., 1982, What do we really know about speciation? In MILKMAN, R. ed., *Perspectives on evolution.* Sinauer Associates, Sunderland, Mass., p. 119–128.

CAIN, A. J. & SHEPPARD, P. M., 1957, Some breeding experiments with *Cepaea nemoralis* (L.). *Journal of Genetics,* 55: 195–199.

CAMPBELL, C. A., 1978, Genetic divergence between populations of *Thais lamellosa* (Gmelin). In BATTAGLIA, B. & BEARDMORE, J. A., eds., *Marine organisms: genetics, ecology and evolution.* Plenum, New York, p. 157–170.

COLE, T. J., 1975, Inheritance of shell colour of the oyster drill *Urosalpinx cinerea. Nature,* 257: 794–795.

COMFORT, A., 1951, The pigmentation of molluscan shells. *Biological Reviews,* 26: 285–301.

COOK, L. M. & KING, J. M. B., 1966, Some data on the genetics of shell character polymorphism in the snail *Arianta arbustorum. Genetics,* 53: 415–425.

COOK, L. M. & MURRAY, J., 1966, New information on the inheritance of polymorphic characters in *Cepaea hortensis. Journal of Heredity,* 57: 245–247.

ENDLER, J. A., 1977, *Geographic variation, speciation, and clines.* Princeton University, Princeton, New Jersey, 246 p.

FRETTER, V. & GRAHAM, A., 1962, *British prosobranch molluscs.* Ray Society, London, 755 p.

GOULD, S. J., 1982, Darwinism and the expansion of evolutionary theory. *Science,* 216: 380–387.

HANSEN, T. A., 1978, Larval dispersal and species longevity in Lower Tertiary gastropods. *Science,* 199: 885–887.

HANSEN, T. A., 1980, Influence of larval dispersal and geographic distribution on species longevity in neogastropods. *Paleobiology,* 6: 193–207.

HAYDEN, B. P. & DOLAN, R., 1976, Coastal marine fauna and marine climates of the Americas. *Journal of Biogeography,* 3: 71–81.

INO, T., 1949, The effect of food on growth and coloration of the topshell (*Turbo cornutus* Solander). *Journal of Marine Research,* 8: 1–5.

LEIGHTON, D. L., 1961, Observations on the effect of diet on shell coloration in the red abalone, *Haliotis rufescens* Swainson. *Veliger,* 4: 29–32.

LEIGHTON, D. L. & BOOLOOTIAN, R. A., 1963, Diet and growth in the black abalone *Haliotis cracherodii. Ecology,* 44: 227–238.

LESSIOS, H. A., 1981, Divergence in allopatry: molecular and morphological differentiation between sea urchins separated by the isthmus of Panama. *Evolution,* 35: 618–634.

LEWONTIN, R. C., 1974, *The genetic basis of evolutionary change,* Columbia University Press, New York, 346 p.

LYONS, A. & SPIGHT, T. M. 1973, Diversity of feeding mechanisms among embryos of Pacific Northwest *Thais. Veliger,* 16: 189–194.

MARCUS, N. H., 1980, Genetics of morphological variation in geographically distant populations of the sea urchin, *Arbacia punctulata* (Lamarck). *Journal of Experimental Marine Biology and Ecology,* 43: 121–130.

MAYR, E., 1963, *Animal species and evolution.* Harvard University, Cambridge, Mass., xiv + 797 p.

McLEAN, J. H., 1966, *West American Gastropoda: superfamilies Patellacea, Pleurotomariacea, and Fissurellacea.* Ph.D. dissertation, Stanford University, Stanford, Calif., 255 p.

MOORE, H. B., 1936, The biology of *Purpura lapillus.* I. Shell variation in relation to environment. *Journal of the Marine Biological Association of the United Kingdom,* 21: 61–89.

MURRAY, J. & CLARKE, B., 1966, The inheritance of polymorphic shell characters in *Partula* (Gastropoda). *Genetics,* 54: 1261–1277.

MURRAY, J. & CLARKE, B., 1976a, Supergenes in polymorphic land snails I. *Partula taeniata. Heredity,* 37: 253–269.

MURRAY, J. & CLARKE, B., 1976b, Supergenes in polymorphic land snails II. *Partula suturalis. Heredity,* 37: 271–282.

NEWKIRK, G. F. & DOYLE, R. W., 1975, Genetic analysis of shell-shape variation in *Littorina saxatilis* on an environmental cline. *Marine Biology,* 30: 227–237.

PALMER, A. R., 1980, *A comparative and experimental study of feeding and growth in thaidid gastropods.* Ph.D. dissertation, University of Washington, Seattle, Washington, 320 p.

REIMCHEN, T. E., 1979, Substratum heterogeneity, crypsis, and colour polymorphism in an intertidal snail (*Littorina mariae*). *Canadian Journal of Zoology,* 57: 1070–1085.

SCHOPF, T. J. M., 1981, Punctuated equilibrium and evolutionary stasis. *Paleobiology,* 7: 156–166.

SEBENS, K. S., 1977, Habitat suitability, reproductive ecology, and plasticity of body size in two sea anemones, *Anthopleura elegantissima* and *A. xanthogrammica.* Ph.D. dissertation, University of Washington, Seattle, 257 p.

SHUTO, T., 1974, Larval ecology of prosobranch gastropods and its bearing on biogeography and paleontology. *Lethaia,* 7: 239–256.

SLATKIN, M., 1981, Estimating levels of gene flow in natural populations. *Genetics,* 99: 323–335.

SPIGHT, T. M., 1973, Ontogeny, environment, and shape of a marine snail *Thais lamellosa* Gmelin. *Journal of Experimental Marine Biology and Ecology,* 13: 215–228.

SPIGHT, T. M., 1976, Colors and patterns of an intertidal snail, *Thais lamellosa. Researches on Population Ecology,* 17: 176–190.

STRUHSAKER, J. W., 1968, Selection mechanisms associated with intraspecific shell variation in *Littorina picta* (Prosobranchia: Mesogastropoda). *Evolution,* 22: 459–480.

THORSON, G., 1950, Reproduction and larval ecology of marine bottom invertebrates. *Biological Reviews,* 25: 1–45.

UNDERWOOD, A. J. & CREESE, R. G., 1976, Observation on the biology of the trochid gastropod *Austrocochlea constricta* (Lamarck) (Prosobranchia). II. The effects of available food on shell-banding pattern. *Journal of Experimental Marine Biology and Ecology,* 32: 229–240.

VALENTINE, J. W., 1966, Numerical analysis of marine molluscan ranges on the extratropical northeastern Pacific shelf. *Limnology and Oceanography,* 11: 198–211.

VERMEIJ, G. J., 1978, *Biogeography and adaptation; patterns of marine life.* Harvard University, Cambridge, Mass., xi + 332 p.

ZACH, R., 1979, Shell dropping: decision-making and optimal foraging in northwestern crows. *Behavior,* 68: 106–117.