Zoological Studies **47**(1): 17-24 (2008)

Zoological Studies

Low Levels of Genetic Differentiation among Populations of the Coral-Inhabiting Snail *Coralliophila violacea* (Gastropoda: Coralliophilidae) in Regions of the Kuroshio and South China Sea

Ta-Yu Lin and Li-Lian Liu*

Institute of Marine Biology and Asia-Pacific Ocean Research Center - Kuroshio Research Group, National Sun Yat-sen University, Kaohsiung 804, Taiwan

(Accepted July 30, 2007)

Ta-Yu Lin and Li-Lian Liu (2008) Low levels of genetic differentiation among populations of the coral-inhabiting snail *Coralliophila violacea* (Gastropoda: Coralliophilidae) in regions of the Kuroshio and South China Sea. *Zoological Studies* **47**(1): 17-24. The coral-inhabiting snail, *Coralliophila violacea*, is a common species in Indo-Pacific coral reefs and usually aggregates on the surfaces of living massive *Poritis* corals. A previous study indicated a low genetic diversity (Nei's genetic distance of < 0.003) for *C. violacea* of southern Taiwan (Lin 1992). Herein, we attempted to determine whether the low genetic differentiation extends to the South China Sea (SCS) by examining allozyme variations at 6 polymorphic loci. Snails were sampled from the Kuroshio region around Taiwan and the SCS which are 1500 km apart. The mean observed heterozygosity among the 7 populations varied from 0.155 to 0.293, with all indicating heterozygote deficiencies. We detected small but significant genetic differentiation among all populations (mean F_{ST} of 0.078); however, genetic distances (Nei's D) between populations were relatively low, ranging from 0 to 0.093. There was a positive trend, although insignificant, between the geographic distance and Nei's genetic distance (Mantel test, Z = 575.7, r = 0.66, p = 0.13). This pattern was confirmed by a UPGMA cluster analysis which showed that geographical-closed populations did not cluster together. The Kuroshio intrusion, high larval dispersal capability, and the availability of host poritid corals may be responsible for these heterogeneities. http://zoolstud.sinica.edu.tw/Journals/47.1/17.pdf

Key words: *Coralliophila violacea*, Allozyme, Population genetics, Kuroshio, South China Sea.

The coral-inhabiting snail, *Coralliophila violacea* Kiener (Gastropoda: Coralliophilidae), is a common coral reef species in the Indo-Pacific. Coralliophilid snails usually aggregate together on the surface of living corals by forming patches of up to 45 snails (Robertson 1980, Brawley and Adey 1982, Baums et al. 2003, Chen et al. 2004), except for *C. stearnsi* which lives on the surface of the sea anemone, *Anthopleura japonica* (Habe 1965). The degree of host specificity varies within the genus *Coralliophila*. In the Caribbean, *C. abbreviata* and *C. caribaea* are found on various genera and families of coral hosts (Ward 1965, Hayes 1990). In contrast, *C. violacea* usually only inhabits massive corals such as *Porites* and *Goniopora* (Poritidae) (Soong and Chen 1991). These massive poritids are relatively common but not the dominant coral species in Taiwan and adjacent islands (Yang and Dai 1982, Dai 1993, Dai et al. 1995, Dai and Fan 1996).

It is known that gene flow between populations of marine organisms can be achieved during different life history stages. Because of the low mobility and the low host searching ability of adult snails (Fujioka and Yamazato 1983), gene flow in *C. violacea* is believed to occur primarily via larval dispersal. Although the reproductive season is unknown for *C. violacea*, females carrying egg capsules in their mantle cavity can be observed year round (Soong and Chen 1991, Lin and Liu 1995). Hatched veliger larvae remain actively swimming and strongly photopositive for at least 1

*To whom correspondence and reprint request should be addressed. Tel: 886-7-5255108. Fax: 886-7-5255100. E-mail:lilian@faculty.nsysu.edu.tw

wk in the laboratory, indicating the potential for long-distance dispersal in water column.

Lin (1992) previously found low levels of genetic differentiation in *C. violacea* among southern Taiwanese populations, i.e., Hsiaoliuchiu (HLC), Kenting (KT), Taitung, and Green I. The geographic distances among those populations were less than 200 km, and their Nei's genetic distances (D) (Nei, 1978) ranged from 0 to 0.003. In addition, among different coral colonies from HLC, the genetic distances of *C. violacea* varied in the range of 0-0.03. These findings suggest significant levels of gene flow among and within populations of *C. violacea* in southern Taiwan; however, it is not known whether populations from the east and west coasts of Taiwan are genetically connected. Herein, we used allozyme markers to assess levels of genetic differentiation among populations around Taiwan and in the South China Sea (SCS).

The SCS is the largest marginal sea in Southeast Asia. It is generally regarded as joining the Pacific Ocean through the Luzon Strait between Taiwan and Luzon I., the Philippines (Fig. 1). Its seasonal circulation is mostly affected by monsoon winds, and the northern SCS circulation is also related to water exchanges between the SCS and the East China Sea through the Taiwan Strait and between the SCS and the Kuroshio through the Luzon Strait (Fig. 2) (Hu et al. 2000). Nothing is known about the population structure of *C. violacea* in this region. An investigation of its population structure would provide important information on patterns of differentiation of the species in this region and the potential for larval dispersal in relation to ocean current circulation. Therefore, the present study was undertaken to evaluate the genetic structure of *C. violacea* populations sampled over the regions of the Kuroshio and the SCS, by examining allozyme variations at 6 polymorphic loci.

MATERIALS AND METHODS

Coralliophila violacea was sampled from the Kuroshio region around Taiwan in 1991, including Mau-Oah (MO), Penghu (PH), Hsiaoliuchiu (HLC), and Kenting (KT), and from the SCS region in 1994, including Dongsha I. (DS) and Taiping (TP, part of the Nansha Is.) (Fig. 1). The surveyed region extended 1500 km in distance (from 112°55'E and 25°10'N to 114°22'E and 10°22'N).

Coralliophila violacea with an aperture length of 15-20 mm was collected from at least 10 different coral colonies at each sampling site at depths of 0.5-8.0 m by either scuba diving or snorkeling. Adjacent sampled coral colonies were at least 3 m apart. During the sampling period, it was found that most *C. violacea* inhabited the surface of *Porites* spp., except at MO where snails on the surface of *Goniopora* sp. were also common. Thus, at MO, snails from *Porites* spp. and *Goniopora* sp. were treated as different groups which were respectively designated MO-PO and MO-GO.

Collected snails were preserved in dry ice in the field. They were deep-frozen at -70°C upon returning to the laboratory until being dissected. For allozyme analysis, the whole tissue was homogenized in a Tekmar Tissumizer with an equal volume of 10 mM Tris-HCl buffer (pH 7.0) containing 1% Triton X-100. Homogenates were centrifuged at 5000*g* for 10 min at 4°C, and the supernatant fractions were stored at -70°C until

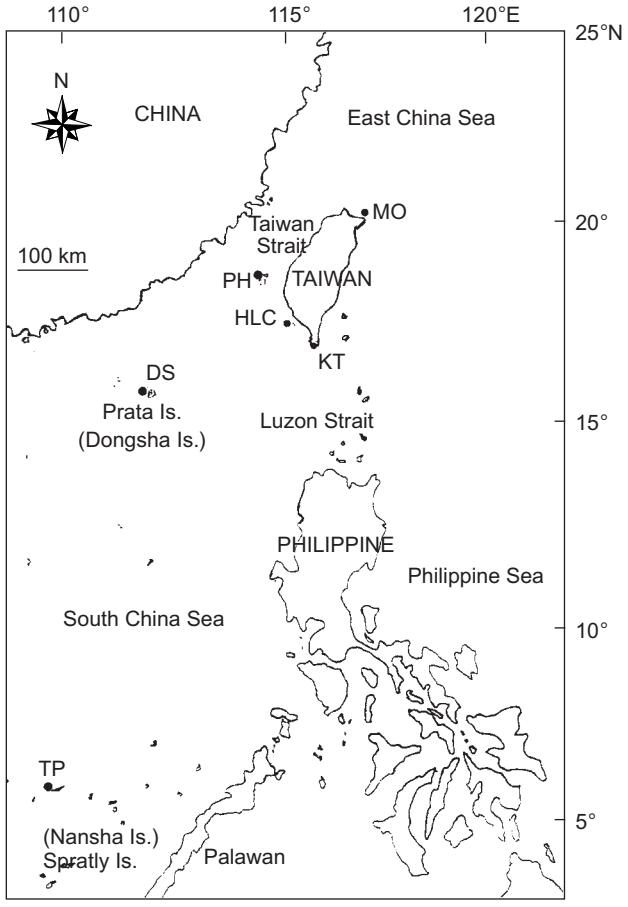

Fig. 1. Map showing collection sites of *Coralliophila violacea*. MO, Mau-Oah; PH, Penghu; HLC, Hsiaoliuchiu; KT, Kenting; DS, Dongsha; TP, Taiping.

analyzed by electrophoresis.

The following enzyme systems were screened using electrophoretic methods of Murphy et al. (1990). Allozymes were esterase (*Est*-1,2, EC 3.1.1.1), isocitrate dehydrogenase (*Idh*, EC 1.1.1.42), leucine aminopeptidase (*Lap*-1,2, EC 3.4.11 or 13), and phosphoglucomutase (*Pgm*, EC 2.7.5.1). Multiple loci encoding the same enzyme (isozymes) were designated by consecutive numbers, with 1 denoting the slowest migrating isozyme. Alleles within each locus were scored by designating the most common allele as 100. All other alleles were numbered according to their relative anodal distances from the reference allele.

Calculations of basic genetic parameters (Hardy-Weinberg test, genetic distances, cluster, and *F*-statistics) were performed with BIOSYS-I (Swofford and Selander 1989). The significance of F_{IS} (a measure of inbreeding within populations) and F_{ST} (a measure of genetic differentiation between populations) was tested using the X^2 statistic as described in Waples (1987). Non-biased genetic distances (Ds) (Nei 1978) were computed for all pairwise comparisons, and for all loci, and the resulting matrix was used to produce a unweighted pair group method with arithmetic mean (UPGMA) dendrogram.

To test for evidence of isolation by distance, a Mantel test was performed on geographic distances (km) and Nei's genetic distances. The significance of Mantel's Z test statistic was directly based on the distribution of 30,000 randomizations (Mantel 1967), using IBDWS (Isolation By Distance Web Service, vers. 3.11) (http://ibdws.sdsu.edu/~ibdws/distances.html).

RESULTS

Allelic frequencies at each locus for each population of *C. violacea* are given in table 1. Using the commonest allele at ≤ 0.95 as the criterion for polymorphism, all 6 loci were polymorphic. Significant variations in allelic frequencies in some populations for the *Est*2 and *Lap*1 loci were observed. The *Est*2-*100* allele was dominant in the TP population, while for all other populations, the *Est*2-*89* allele was predominant. At the *Lap*1 locus, allele *Lap*1-*127* was dominant in the PH and KT populations, while in the other 5 populations, the *Lap*1-*100* allele was predominant. The mean number of alleles per locus was 2.2-2.7, and the observed mean heterozygosity of all loci in each population ranged from 0.155 to 0.293 (Table

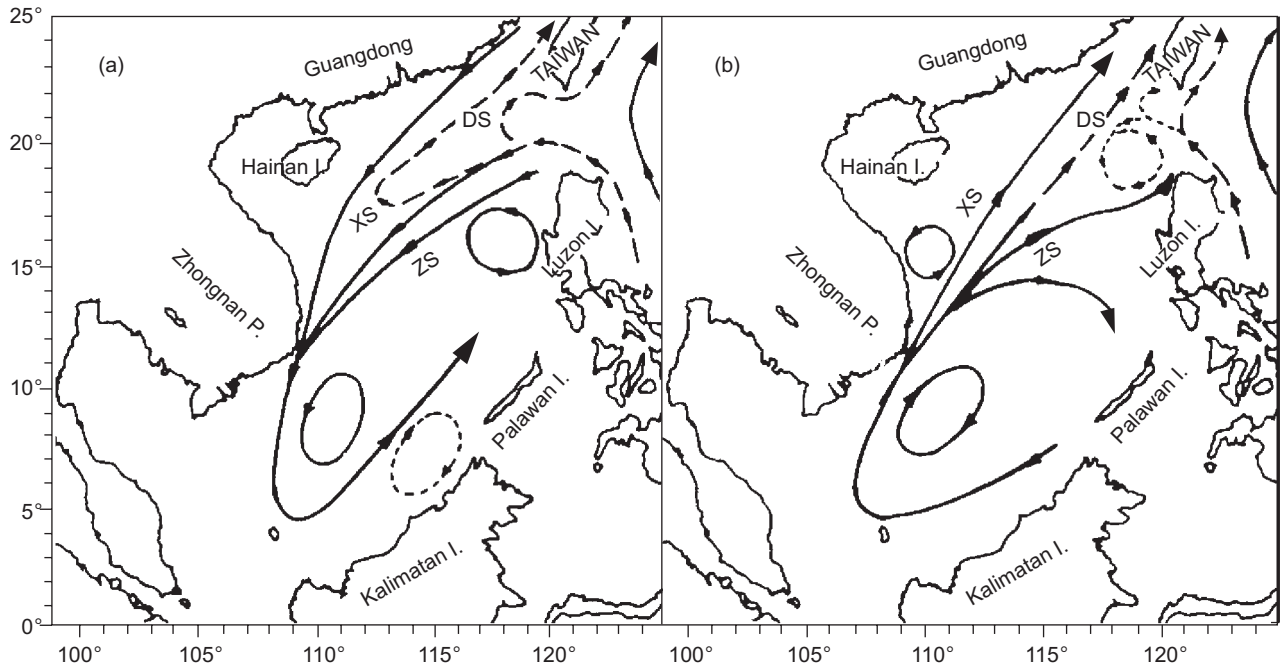

Fig. 2. Overall upper-layer mean circulation patterns in the South China Sea (Hu et al. 2000). (a) Winter; (b) summer. The long dashed arrows schematically illustrate the South China Sea Warm Current and the Kuroshio intrusion. The short dashed arrows indicate unstable intrusions and eddies in need of further confirmation. DS, Dongsha Island; XS, Xisha Islands; ZS, Zhongsha Islands.

2).

The mean F_{IS}, a measure of the deviation from random mating within the 7 populations, was 0.181, and ranged from -0.051 (*PGM*) to 0.527 (*EST*2) (Table 3). Three of the 6 polymorphic loci deviated from 0, suggesting that these populations might not have fully random mating. The significant mean F_{ST} value (0.078) demonstrated the presence of genetic differentiation among populations, with all loci except *PGM* contributing to its significance.

Nei's genetic distances (Ds) ranged from 0 to 0.093 between populations of *C. violacea* (Table 4). The highest genetic distance was found between the TP and PH populations (D = 0.093). A UPGMA cluster analysis was performed on Nei's genetic distance values (Fig. 3). Snails collected from corals of *Goniopora* sp. (MO-GO) and *Porites* spp. (MO-PO) clustered in the same group. The TP population was separated from other populations by a distance of 0.065.

Taking into account all 7 populations, there was a positive trend between geographic distance and Nei's genetic distance (Mantel's test, Z = 575.7, r = 0.66, p = 0.13) (Fig. 4, Table 5). If any one of the analyzed populations except for the TP population was excluded, the positive trend was still observed, with p values ranging from 0.09 to 0.16. When the TP population was excluded from the analysis, the isolation by distance pattern was

Table 1. Allelic frequencies of 6 loci in 7 populations of *Coralliophila violacea*. *n*, sample size. MO-GO, *C. violacea* on *Goniopora* sp. at Mau-Oah; MO-PO, *C. violacea* on *Poritis* spp. at Mau-Oah; PH, Penghu; HLC, Hsiaoliuchiu; KT, Kenting; DS, Dongsha; TP, Taiping

Locus	Population						
	MO-GO	MO-PO	PH	HLC	KT	DS	TP
*EST*1							
(*n*)	45	64	45	22	27	42	48
100	0.900	0.891	0.800	0.909	0.963	0.929	0.969
93	0.100	0.109	0.200	0.091	0.037	0.071	0.031
*EST*2							
(*n*)	39	62	32	22	27	37	39
100	0.346	0.185	0.344	0.023	0.222	0.284	0.628
89	0.641	0.806	0.641	0.932	0.759	0.716	0.372
67	0.013	0.008	0.016	0.045	0.019	-	-
IDH							
(*n*)	43	66	44	19	27	41	43
100	0.872	0.856	0.909	0.974	0.778	0.939	0.977
75	0.128	0.144	0.091	0.026	0.222	0.061	0.023
*LAP*1							
(*n*)	33	49	26	20	19	39	39
150	0.167	0.235	0.308	-	0.184	0.244	0.103
127	0.227	0.204	0.442	0.150	0.342	0.141	0.038
115	0.288	0.204	0.192	0.325	0.211	0.205	0.179
100	0.318	0.347	0.058	0.525	0.263	0.41	0.679
75	-	0.010	-	-	-	-	-
*LAP*2							
(*n*)	44	58	41	17	25	31	42
143	-	-	-	-	-	0.032	0.060
125	-	-	0.024	-	-	-	0.060
100	0.864	0.879	0.854	1.000	0.960	0.839	0.798
43	0.136	0.121	0.122	-	0.040	0.129	0.083
PGM							
(*n*)	45	66	44	22	27	42	47
100	0.978	0.932	0.955	0.955	1.000	0.964	1.000
90	0.022	0.068	0.045	0.045	-	0.036	-

no longer maintained (Z = 65.0, r = -0.44, p = 0.97), indicating a highly significant contribution of the TP population in forming this trend. In general, the grouping patterns of genetic data did not correspond to their geographical separations within the range of 700 km (Tables 4, 5, Figs. 3, 4). For example, the DS population from the SCS was clustered with MO populations instead of with KT and HLC populations. These results indicate that isolation by distance may be a factor only in the presence of the TP population which is located in the SCS region.

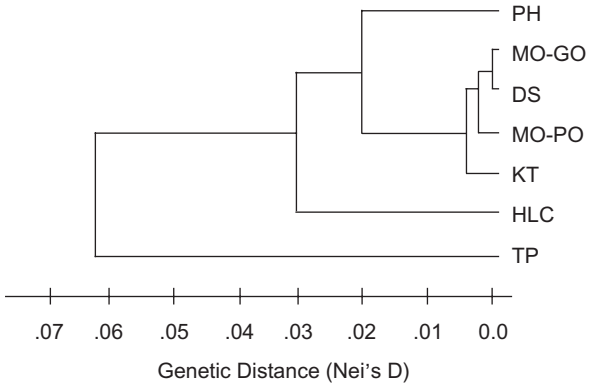

Fig. 3. UPGMA dendrogram showing genetic relationships among populations of *Coralliophila violacea* based on Nei's unbiased genetic distances (D). The cophenetic correlation of the dendrogram was 0.855; locality abbreviations are given in table 1.

DISCUSSION

The central finding of this study is that populations of *C. violacea* in the Kuroshio and SCS regions are characterized by low levels of genetic differentiation, suggesting high levels of gene flow among widely separated geographic populations. Estimates of genetic differentiation, while significant, were low (mean F_{ST} = 0.078), and we detected no consistent pattern of neighboring populations clustering together (Fig. 3). The high larval dispersal capability, the availability of host poritid corals, and the circulation patterns of ocean currents may play crucial roles in forming these heterogeneities.

Table 3. Estimates of genetic differentiation in 7 populations of *Coralliophila violacea*. F_{IS}, measure of standardized genetic variance within populations; F_{IT}, measure of the total genetic variance; F_{ST}, measure of the standardized genetic variance between populations. NS; $p > 0.05$; ** $p < 0.01$

Locus	FIS	FIT	FST
EST1	0.305**	0.327	0.033**
EST2	0.527**	0.588	0.130**
IDH	0.346**	0.377	0.049**
LAP1	-0.028NS	0.057	0.083**
LAP2	0.061NS	0.095	0.036**
PGM	-0.051NS	-0.032	0.018NS
Mean	0.181**	0.245	0.078**

Table 2. Genetic variability measures in 7 populations of *Coralliophila violacea*. The expected heterozygosities were calculated using Nei's unbiased estimate (Nei 1978) of heterozygosity under conditions of Hardy-Weinberg equilibrium. [a]Locus considered polymorphic if the relative frequency of the most common allele does not exceed 0.95; locality abbreviations are given in table 1

Population	Mean sample size per locus (± SE)	Mean no. of alleles per locus (± SE)	Percentage of polymorphic loci[a] (%)	Mean heterozygosity (± SE)	
				Direct count	Expected
MO-GO	41.5 ± 1.9	2.5 ± 0.3	83.3	0.293 ± 0.112	0.319 ± 0.103
MO-PO	60.8 ± 2.7	2.7 ± 0.5	100.0	0.264 ± 0.114	0.309 ± 0.092
PH	38.7 ± 3.2	2.7 ± 0.3	83.3	0.257 ± 0.065	0.333 ± 0.089
HLC	20.3 ± 0.8	2.2 ± 0.3	50.0	0.178 ± 0.106	0.176 ± 0.090
KT	25.3 ± 1.3	2.3 ± 0.4	50.0	0.155 ± 0.117	0.273 ± 0.116
DS	38.7 ± 1.7	2.5 ± 0.3	83.3	0.259 ± 0.096	0.289 ± 0.100
TP	43.0 ± 1.6	2.5 ± 0.5	50.0	0.157 ± 0.077	0.239 ± 0.094

Marine organisms exhibit great variations in reproductive modes, larval types, and other life-history traits that may have major evolutionary consequences. Species with larvae which disperse over long distances are often associated with lower levels of genetic subdivision and wider geographical ranges than those with low dispersal capabilities such as brooders (Hellberg, 1996). But actual dispersal is often restricted by habitat, local ocean conditions, historical events, etc. (Palumbi et al. 1997). Thus partially isolated populations may commonly occur in marine systems. For example, genetic differentiation was observed among populations of the giant clam, *Tridacna derasa*, from the Great Barrier Reef, Fiji, and the Philippines (F_{IS} = 0.041, F_{ST} = 0.098) (Macaranas et al. 1992). It is thought that historical isolation and present-day oceanographic current patterns are responsible for such genetic differentiation. In the broadcast spawning coral, *Mycedium elephantotus*, genetic differentiation occurred within a geographical distance of < 200 km in Taiwan (Yu et al. 1999). Its F_{IS} and F_{ST} among 7 polymorphic loci ranged from -0.115 to 0.901 and 0.018 to 0.786, respectively. Such genetic differentiation was not related to geographic distance but was likely driven by isolation due to ocean currents.

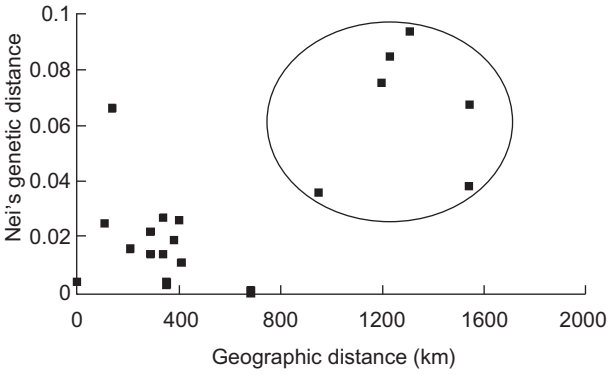

Fig. 4. Mantel test of correlations between genetic and geographic distances of *Coralliophila violacea*. ○, TP population; Z = 575.7, r = 0.66, p = 0.13.

Our results show that a low level of genetic variation was found both within and among populations of *C. violacea*. Moreover, the within-population component was larger than the amount of differentiation among populations (F_{IS} = 0.181 greater than F_{ST} = 0.078) (Table 3). This pattern is consistent with an earlier study by Lin (1992) in southern Taiwan in which the F_{IS} and F_{ST} values were 0.021 and 0.002 among 8 populations. Although the reproductive season of *C. violacea* is unknown, females carrying egg masses in their mantle cavity have been observed year round (Soong and Chen 1991, Lin and Liu 1995). Its planktonic larval stage lasts for at least 1 wk, indicating the potential for high gene flow among populations. Therefore, inbreeding might not be the most likely explanation for such differentiation. It is suggested that the high host specificity on poritid corals resulting in habitat discontinuity in space may be responsible for the population structure. This coral-inhabiting snail has high host specificity and forms patches (mostly with 2-31 individuals per patch) on the surfaces of poritid corals (Soong and Chen 1991). Adult snails have very low mobility, as shown by leaving scars on the coral surface, which hinders genetic exchange through sexual reproduction among spatially separated populations by their host corals. Theoretically, this can lead to effective isolation at very small scales.

Although the genetic structure of many marine species has been studied in the Indo-Pacific, reports on coral reef invertebrates with pelagic larvae around Taiwan and the SCS are still scarce. The only published genetic work on a

Table 4. Nei's unbiased genetic distance (below the diagonal) (Nei 1978) and the geographical distance (km) between populations of *Coralliophila violacea*. Locality abbreviations are given in table 1

Population	MO-GO	MO-PO	PH	HLC	KT	DS	TP
MO-GO		0	290	340	350	680	1540
MO-PO	0.004		290	340	350	680	1540
PH	0.014	0.022		140	210	400	1310
HLC	0.027	0.014	0.066		110	380	1230
KT	0.004	0.003	0.016	0.025		410	1195
DS	0.000	0.001	0.026	0.019	0.011		950
TP	0.038	0.067	0.093	0.084	0.075	0.036	

scleractinian coral, *M. elephantotus*, describes genetic differentiation among populations of PH and northern and southern Taiwan, for which Nei's genetic distances ranged 0-0.293 (Yu et al. 1999). In *C. violacea*, genetic distances ranged 0-0.093, indicating low levels of genetic difference among distant populations. Also, minor genetic differentiation was found (D = 0.004) between snails from *Porites* spp. and *Goniopora* sp. at MO. These results are consistent with a study by Lin (1992), which found little genetic differentiation (Nei's D < 0.003) among populations of *C. violacea* from southern Taiwan.

Based on the small genetic distances, it is suggested that gene flow is maintained within our sampling area. However, low levels of genetic differentiation among populations detected were not in accordance with their geographical separation (Figs. 3, 4). For instance, the genetic distance between KT and HLC (D = 0.025; 110 km apart) was greater than that between KT and MO (D = 0.003-0.004; 350 km apart), although the former 2 populations are closer geographically. *Coralliophila violacea* produces planktonic larvae year round, and seasonal changes in the directions of ocean currents suggest that populations may be genetically connected at times.

The surface circulation around Taiwan is mainly influenced by 3 major water masses, the Kuroshio, the SCS warm current, and the China Coastal current (Chern and Wang 1992). The Kuroshio comes from seas northeast of the Philippines and runs northward along the east coast of Taiwan, then enters the East China Sea. The Kuroshio intrusion flows westward passing through the Luzon Strait then entering the northern SCS (Fig. 2). In the SCS, the SCS warm current exists year round along the shelf off the Guangdong coast of southern China, and its extension flows to the Taiwan Strait (Hu et al. 2000). These circulation patterns in the northern SCS suggest that larvae may be dispersed between the DS and Kuroshio regions. Based on the currents in the SCS (reviewed by Hu et al 2000), the maximum Kuroshio intrusion occurs in winter and reaches at least seas near the Dongsha I. The clustering of MO, KT, and DS together (Fig. 3) indicates consistency between the genetic structure of *C. violacea* and the pattern of the Kuroshio intrusion. Meanwhile, the exchange of genetic materials among populations may predominantly occur during the winter season.

However, a study of the distributional patterns of scleractinian corals of *Acropora* and Faviidae in Taiwan indicated that the DS population was separated from the remaining populations of Taiwan, e.g., KT and PH (Chen 1999). The distribution of corals around Taiwan is divided into Kuroshio-influenced and SCS-influenced provinces. In the SCS-influenced province, the SCS warm current dominates the Taiwan Strait during the corals' spawning season (late spring to summer) which provides a northbound gene flow from PH to northern Taiwan, while the Kuroshio-influenced province covers southern and eastern Taiwan. This pattern was also observed in a study of genetic differentiation among populations of the coral, *M. elephantotus* (Yu et al. 1999).

An obvious discrepancy between Chen's (1999) study and ours is the relationship between the DS population and other populations of Taiwan. In our study, the DS population and populations of Taiwan were closely related which contrasts with a study by Chen (1999) on *Acropora* and Faviidae corals. It is known that *C. violacea* females carry egg capsules year round (Soong and Chen 1991, Lin and Liu 1995), and spawning in scleractinian corals occurs only in late spring to summer (Chen 1999, Yu et al. 1999). Obviously, additional studies on the population density, and larval longevity and behaviors are needed to draw sounder conclusions.

Table 5. Results of the Mantel's Z test statistic of *Coralliophila violacea*. *r*, Mantel correlation coefficient; *p*, significance level

Variable	Z value	*r* value	*p* value
All 7 populations included	575.7	0.66	0.13
MO-PO excluded	459.6	0.60	0.14
PH excluded	420.4	0.75	0.12
HLC excluded	438.1	0.77	0.09
KT excluded	473.0	0.60	0.15
DS excluded	518.7	0.72	0.16
TP excluded	65.0	-0.44	0.97

Acknowledgments: We thank Drs. L. S. Fang and K. Soong for help with collecting snails. We are grateful to several anonymous reviewers for their constructive comments which substantially improved the manuscript. This study was supported by the National Science Council, R.O.C. (NSC95-2621-Z-110-004), the Bureau of Animal and Plant Health Inspection and Quarantine, Council of Agriculture of Taiwan and the Asia-Pacific Ocean Research Center-Kuroshio

Research Group, National Sun Yat-sen University supported by the Ministry of Education, Taiwan. This paper is partially based on a thesis submitted by Ta-Yu Lin in partial fulfillment of the requirements for a master's degree in 1992 at National Sun Yat-sen University.

REFERENCES

Baums IB, MW Miller, AM Szmant. 2003. Ecology of a corallivorous gastropod, *Coralliophila abbreviata*, on two scleractinian hosts. I: Population structure of snails and corals. Mar. Biol. **142:** 1083-1091.

Brawley SH, WH Adey. 1982. *Coralliophila abbreviata*: a significant corallivore. Bull. Mar. Sci. **32:** 595-599.

Chen CA. 1999. Analysis of scleractinian distribution in Taiwan indicating a pattern congruent with sea surface temperatures and currents: examples from *Acropora* and Faviidae corals. Zool. Stud. **38:** 119-129.

Chen MH, K Soong, ML Tsai. 2004. Host effect on size structure and timing of sex change in the coral-inhabiting snail *Coralliophila violacea*. Mar. Biol. **144:** 287-293.

Chern CS, J Wang. 1992. The influence of Taiwan Strait waters on the circulation of the southern East China Sea. La Mer **30:** 223-228.

Dai CF. 1993. Patterns of coral distribution and benthic space partitioning on the fringing reefs of southern Taiwan. Mar. Ecol. **14:** 185-204.

Dai CF, TY Fan. 1996. Coral fauna of Taiping island (Itu Aba island) in the Spratlys of the South China sea. Atoll Res. Bull. **436:** 1-21.

Dai CF, TY Fan, CS Wu. 1995. Coral fauna of Tungsha Tao (Pratas Islands). Acta Oceanogr. Taiwan. **34:** 1-16.

Fujioka Y, K Yamazato. 1983. Host selection of some Okinawa coral associated gastropods belonging to the genera *Drupella*, *Coralliophila* and *Quoyula*. Galaxea **2:** 59-73.

Habe T. 1965. Molluscs. *In* K Okadk, ed. New illustrated encyclopedia of the fauna of Japan 2. Tokyo, Japan: Hokuryu-Kan Publ. (in Japanese)

Hayes JA. 1990. Distribution, movement and impact of the corallivorous gastropod *Coralliophila abbreviata* (Lamarck) on a Panamanian patch reef. J. Exp. Mar. Biol. Ecol. **142:** 25-42.

Hellberg ME. 1996 Dependence of gene flow on geographic distance in two solitary corals with different larval dispersal capabilities. Evolution **50:** 1167-1175.

Hu J, H Kawamura, H Hong, Y Qi. 2000. A review on the currents in the South China Sea: seasonal circulation, South China Sea Warm Current and Kuroshio intrusion. J. Oceanogr. **56:** 607-624.

Lin TY. 1992. The study of population genetic structure of coral-inhabiting snail, *Coralliophila violacea*. Master's thesis, National Sun Yat-sen University, Kaohsiung, Taiwan, 50 pp.

Lin TY, PJ Liu. 1995. Fecundity of female coral-inhabiting snails, *Coralliophila violacea* (Gastropoda: Coralliophilidae). Veliger **38:** 319-322.

Macaranas JM, CA Ablan, MJR Pante, JAH Benzie, ST Williams. 1992 Genetic structure of giant clam (*Tridacna derasa*) populations from reefs in the Indo-Pacific. Mar. Biol. **113:** 231-238.

Mantel N. 1967. The detection of disease clustering and a generalized regression approach. Cancer Res. **27:** 209-220.

Murphy RW, JW Sites, DG Buth, CH Haufler. 1990. Proteins. I: Isozyme electrophoresis. *In* DM Hills, C Moritz, eds. Molecular systematics. Sunderland, MA: Sinauer Press, pp 45-126.

Nei M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics **89:** 583-590.

Palumbi SR, G Grabowsky, T Duda, L Geyer, N Tachino. 1997. Speciation and population genetic structure in tropical Pacific sea urchins. Evolution **51:** 1506-1517.

Robertson R. 1980. *Epitonium millecostatum* and *Coralliophila clathrata*: two prosobranch gastropods symbiotic with Indo-Pacific *Palythoa* (Coelenterata: Zoanthidae). Pac. Sci. **34:** 1-17.

Soong K, JL Chen. 1991. Population structure and sex-change in the coral-inhabiting snail *Coralliophila violacea* at Hsiao-liu-chiu, Taiwan. Mar. Biol. **111:** 81-86.

Swofford DL, RK Selander. 1989. BIOSIS-I: a FORTRAN program for the analysis of allelic variation in population genetic and biochemical systematic. University of Illinois at Urbana-Champaign Urbana, IL.

Waples RS. 1987. A multispecies approach to the analysis of gene flow in marine shore fishes. Evolution **41:** 385-400.

Ward J. 1965. The digestive tract and its relation to feeding habits in the stenoglossan prosobranch *Coralliophila abbreviata* (Lamarck). Can. J. Zool. **43:** 447-463.

Yang RT, CF Dai. 1982. Coral communities in Yen-liao Bay, Taiwan. Acta Oceanogr. Taiwan **13:** 167-180.

Yu JK, HY Wang, SC Lee, CF Dai. 1999. Genetic structure of a scleractinian coral, *Mycedium elephantotus*, in Taiwan. Mar. Biol. **133:** 21-28.