Abstract.—Allozymes were used to examine spatial and temporal components of genetic variation among populations of queen conch in the Florida Keys and Bimini over a 4-year period. Spatial and temporal genetic variation were both significant ($P<0.001$) despite high levels of genetic similarity among samples (mean Nei's I, 0.994). However, no consistent pattern of variation was observed. The gene diversity among localities (G_{LT} 0.50%) did not differ significantly ($P>0.05$) from the diversity among years or samples within localities (G_{SL} 0.60%). In addition, Florida Keys and Bimini populations were very similar genetically to those studied previously in the Caribbean Sea and Bermuda (mean Nei's I, 0.988). In general, populations of queen conch appear to be structured as a mosaic of spatial and temporal genetic patchiness within a continuum of high genetic similarity. This genetic similarity is presumably maintained by larval drift and gene flow. However, the observed patterns of genetic variation suggest a dynamic population structure. This structure may reflect presettlement stochastic events and processes in the marine environment.

Genetic patchiness among populations of queen conch *Strombus gigas* in the Florida Keys and Bimini*

Donald E. Campton
Department of Fisheries and Aquaculture, University of Florida
7922 NW 71st Street, Gainesville, Florida 32606-0300

Carl J. Berg Jr.
Florida Marine Research Institute, Florida Department of Natural Resources
13365 Overseas Highway, Marathon, Florida 33050
Current address: P.O. Box 769, Kilauea, Hawaii 90754

Lynn M. Robison
Department of Fisheries and Aquaculture, University of Florida
7922 NW 71st Street, Gainesville, Florida 32606-0300
Current address: Department of Fisheries and Allied Aquacultures
Auburn University, Auburn, Alabama 36849

Robert A. Glazer
Florida Marine Research Institute, Florida Department of Natural Resources
13365 Overseas Highway, Marathon, Florida 33050

The queen conch *Strombus gigas* is a large marine gastropod of significant economic importance to the Caribbean Sea area (reviewed by Berg and Olsen 1989). The native range of the species extends from south Florida to Venezuela and eastward from Central America to the Bahama and West Indies Islands. An isolated population also inhabits the coastal waters of Bermuda. The species has been heavily exploited in commercial, recreational, and subsistance fisheries throughout its geographic range. Many populations are considered depleted or overfished.

The life history of queen conch suggests the potential for extensive gene flow through larval dispersal (Scheltema 1971, 1986). Laboratory studies indicate that larvae maintain the planktonic stage for 12–35 days ($\bar{x}$ 21 days) before settling and metamorphosis (Ballantine and Appledoorn 1983, Davis and Hesse 1983). Larvae entrained in swift, Caribbean currents (1–3 km/h) could thus be transported significant distances (Kinder et al. 1985). However, dispersal and recruitment patterns of *S. gigas* during the planktonic stage are largely unknown. Effective management and rehabilitation of the species throughout its geographic range necessitate an understanding of population structure, patterns of gene flow, and genetic relationships.

In a recent allozyme study, Mitton et al. (1989) found a high level of genetic similarity among populations of queen conch from eight localities throughout the Caribbean Sea. However, significant spatial heterogeneity in allele frequencies indicated that the sampled populations were not totally panmictic. In addition, allele frequencies for the geographically disjunct population of Bermuda were distinctive at one locus.

Manuscript accepted 4 March 1992.
Fishery Bulletin, U.S. 90:250–259 (1992).

* Journal Series R-01534, Florida Agricultural Experiment Station.

In the study described here, allozymes were used to examine the genetic structure of queen conch populations in the Florida Keys and Bimini. We collected conch from the same localities in multiple years to compare spatial and temporal components of genetic variation. Testing the relative significance of those two components was a major objective of our study.

Materials and methods

Sampled populations

Queen conch were collected between 1987 and 1990 from four localities in the Florida Keys and from Bimini, a linear distance of approximately 350 km (Table 1, Fig. 1). Samples of conch were obtained in multiple years from Ballast Key, Coffins Patch, and Craig Key. Single samples were obtained from Key Biscayne and Bimini. All animals were collected by scuba diving or snorkeling.

The shell length, or major axis, of each conch was measured with calipers to the nearest mm. Based on size distributions, the Coffins Patch population (or aggregation) appeared to be a single year-class or cohort that we sampled in three consecutive years (Table 1). All other populations represented mixtures of year-classes with new recruits added each year.

Tissues

Conch collected in 1987 (three samples) were processed according to the methods of Mitton et al. (1989): Only the distal tip of the digestive gland, including gonad and associated connective tissue, was retained for enzyme extraction. We were not able to resolve some of the enzymes or presumptive loci reported by Mitton et al. (1989) but were able to resolve some enzymes and loci not examined previously. Consequently, from each of 12 conch collected from Ballast Key in February, 1988 (Table 1), we dissected six tissues for further screening of enzymes and loci: (1) foot muscle, (2) proboscis with radula, (3) eyes and eyestalks, (4) crystalline style, (5) mantle tissue, and (6) distal tip of the digestive gland (Little 1965). Thirty-eight enzymes

Table 1

Means ± standard errors (SE) and ranges of shell length for samples of queen conch *Strombus gigas* collected from four localities in the Florida Keys and Bimini, 1987-90.

			Length (mm)	
Locality	Year	*N*	Mean ± SE	Range
Ballast Key	1987	56	167 ± 6.2	96-241
	1988[a]	12	125 ± 5.6	91-157
	1988[b]	30	135 ± 4.2	69-167
Coffins Patch	1988	100	58 ± 0.4	46-71
	1989	102	98 ± 0.6	87-112
	1990	100	142 ± 0.9	117-170
Craig Key	1987	105	177 ± 2.5	127-267
	1989	71	225 ± 3.5	137-257
	1990	92	187 ± 3.5	125-252
Key Biscayne	1987	79	155 ± 3.5	99-216
Bimini	1989	96	194 ± 2.0	127-236

[a] February collection.
[b] April collection.

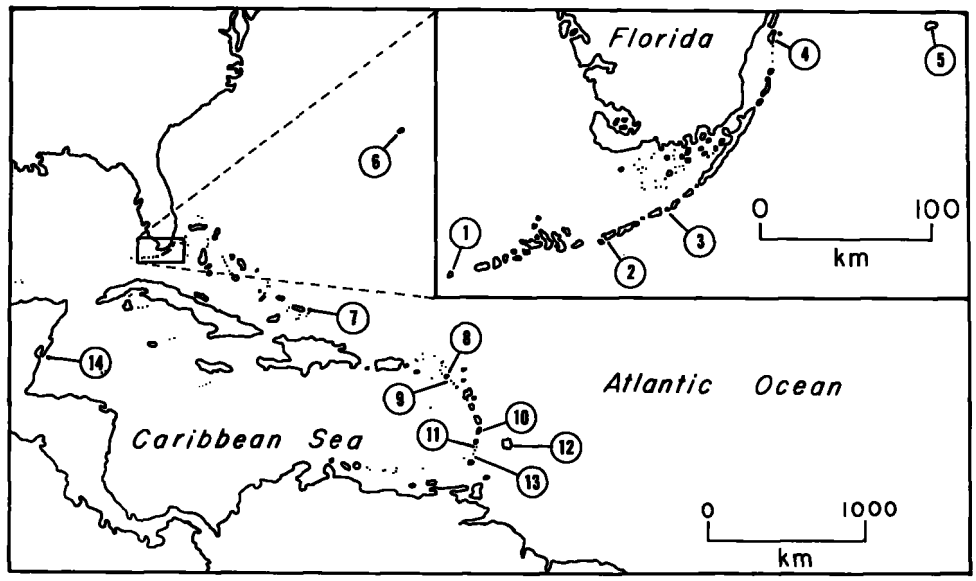

Figure 1

Localities from which queen conch *Strombus gigas* were collected. For the study described here, conch were collected from (1) Ballast Key, (2) Coffins Patch, (3) Craig Key, (4) Key Biscayne, and (5) Bimini. Localities 6-14 are from Mitton et al. (1989): (6) Bermuda, 1 site; (7) Turks and Caicos Islands, 4 sites; (8) St. Kitts, 2 sites; (9) Nevis, 1 site; (10) St. Lucia, 2 sites; (11) Bequia, 1 site; (12) Barbados, 1 site; (13) Grenadines, 3 sites; and (14) Belize, 2 samples, 1 each of the normal and melanic forms.

were assayed in each tissue using a variety of electrophoresis buffers.

On the basis of the aforementioned analyses, three tissues were retained from all conch collected subsequently in 1988–90: (1) foot muscle, (2) proboscis with radula, and (3) digestive gland with gonad. The three tissues were dissected from each individual, placed in separate cryotubes or plastic bags, and frozen in the field with liquid nitrogen or dry ice. All tissues were stored at −80°C until prepared for enzyme extraction.

Table 2

Enzymes and loci resolved in queen conch *Strombus gigas*. Tissues are digestive gland (D), foot muscle (F), and proboscis (P).

Enzyme	Enzyme number	Locus	Tissue	Optimum buffer[a]
Aspartate aminotransferase	2.6.1.1	*AAT-1**	D,P	TC
		*AAT-2**	F,P	TC
Argenine kinase	2.7.3.3	*ARGK**	F	TC
Dipeptidase[b] (substrates: Leu-Ala, Leu-Tyr)	3.4.13.11	[b]*DPEP-1**	D,F,P	TLBC-2,TC
		*DPEP-2**	D,F,P	TLBC-1
		*DPEP-3**	D,F,P	TLBC-1
Glucose-6-phosphate dehydrogenase	1.1.1.49	*G6PDH**	D	TLBC-2
Glucose-6-phosphate isomerase	5.3.1.9	*GPI**	D,F,P	TC
Isocitrate dehydrogenase ($NADP^+$)	1.1.1.42	*IDHP-1**	D,F,P	AC
		*IDHP-2**	D,F,P	AC
Malate dehydrogenase[b]	1.1.1.37	*MDH-1**	F,P	AC
		[b]*MDH-2**	D,P	AC
Octopine dehydrogenase	1.5.1.11	*ODH**	F,P	TLBC-1
Phosphoglucomutase[b]	5.4.2.2	[b]*PGM-1**	D,F,P	TC
		[b]*PGM-2**	D,F,P	TC
		*PGM-3**	F	TC
Phosphogluconate dehydrogenase[b]	1.1.1.44	[b]*PGDH**	F,P	AC
Tripeptide aminopeptidase (substrate: Leu-Gly-Gly)	3.4.11.4	*TPEP-1**	D,F,P	TLBC-1
		*TPEP-2**	D,F,P	TLBC-1

[a] AC: 0.04 M citric acid adjusted to pH 7.5 with N-(3-aminopropyl) morpholine (Clayton and Tretiak 1972); TBE: Tris-borate-EDTA, pH 8.6 (Boyer et al. 1963); TC: TC buffer of Siciliano and Shaw 1976; TLBC-1: LiOH buffer of Ridgway et al. (1970); TLBC-2: LiOH buffer of Selander et al. (1971).
[b] Enzymes and loci assayed also by Mitton et al. (1989).

Electrophoresis

Allozymes were detected by horizontal starch-gel electrophoresis following the procedures of Aebersold et al. (1987). Enzymes were extracted by homogenizing each tissue separately in 0.5–1.0 volumes of 0.05M PIPES, 0.05% Triton X-100, and 0.2mM pyridoxal-5′-phosphate (adjusted to pH 6.8 with 1.0M NaOH). Gels were prepared with a 12.5% mixture (wt:vol) of Connaught starch (Fisher Sci. Co.) and one of five buffer solutions (Table 2). Histochemical staining of gels followed standard procedures (Morizot and Schmidt 1990). Gels were stained by agar overlay for all enzymes except AAT.

Presumptive loci and alleles were designated by the nomenclature system outlined by Shaklee et al. (1990), except peptidase loci were identified by their di- or tripeptide acronyms (DPEP, TPEP). Multiple loci of a particular enzyme were designated numerically (1, 2, etc.) from fastest to slowest anodic mobility. Alleles of a particular locus were designated by their relative, anodic mobilities (most frequent allele = **100*).

Statistics

Genotypic proportions at each locus were tested for goodness-of-fit to Hardy-Weinberg expectations using the likelihood-ratio test or G-statistic (Sokal and Rohlf 1981). Allele frequencies at each locus were tested for homogeneity among samples by contingency table (samples × alleles) G-tests (Sokal and Rohlf 1981). This total G-statistic, or likelihood ratio, was then partitioned into hierarchical components representing temporal and spatial components of genetic variation within and among localities, respectively (e.g., Smouse and Ward 1978). An approximate F-ratio was then constructed as (G among localities/df)/(G among years within localities/df) to test whether the genetic heterogeneity among localities was significantly greater than the heterogeneity among years within localities. The total gene diversity (Nei 1973) was similarly partitioned into within- and among-locality components following the algorithm of Chakraborty et al. (1982). In all tests of statistical significance, significance probabilities were adjusted for the number of tests (loci) evaluated simultaneously (Rice 1989).

Nei's (1972) index of gene identity was calculated between all population samples. The genetic similarities among all populations, including those sampled by Mitton et al. (1989), were represented graphically in a UPGMA dendrogram (Sneath and Sokal 1973). The 1987 sample from Ballast Key was excluded from these latter analyses because of small sample size (n 12).

Table 3

Allele frequencies for samples of queen conch *Strombus gigas* from the Florida Keys (4 sites) and Bimini. "ND" indicates no data for that locus.

		Ballast Key			Coffins Patch			Craig Key			Key Biscayne	Bimini
Locus	Alleles	1987	1988[a]	1988[b]	1988	1989	1990	1987	1989	1990	1987	1990
*AAT-1**	*100*	0.713	1.00	0.62	0.723	0.755	0.696	0.663	0.671	0.678	0.648	0.591
	120	0.287	—	0.38	0.277	0.245	0.304	0.338	0.329	0.322	0.352	0.403
	130	—	—	—	—	—	—	—	—	—	—	0.005
*AAT-2**	*100*	ND	1.00	1.00	0.975	0.980	0.955	ND	0.993	0.973	ND	0.973
	150		—	—	0.025	0.020	0.045		0.007	0.022		0.016
	81		—	—	—	—	—		—	—		0.011
	180		—	—	—	—	—		—	0.005		—
*DPEP-1**	*100*	0.472	0.42	0.57	0.536	0.536	0.460	0.567	0.521	0.522	0.513	0.565
	108	0.528	0.58	0.43	0.464	0.464	0.540	0.433	0.479	0.478	0.487	0.435
*GPI**	*100*	0.929	1.00	0.98	1.000	0.990	1.000	0.985	1.000	0.995	0.994	0.995
	117	0.071	—	0.02	—	—	—	0.015	—	0.005	0.006	0.005
	78	—	—	—	—	0.010	—	—	—	—	—	—
*IDH-2**	*100*	ND	1.00	1.00	1.000	0.975	0.976	1.000	0.979	0.956	1.000	0.978
	82		—	—	—	0.025	0.024	—	0.021	0.044	—	0.022
*MDH-1**	*100*	ND	1.00	1.00	1.000	0.951	0.960	ND	0.944	0.944	ND	0.982
	120		—	—	—	0.049	0.040		0.056	0.056		0.018
*MDH-2**	*100*	0.794	1.00	1.00	1.000	1.000	1.000	0.955	1.000	1.000	1.000	1.000
	138	0.206	—	—	—	—	—	0.005	—	—	—	—
*ODH**	*100*	ND	1.00	1.00	0.990	0.990	1.000	ND	0.993	0.995	ND	0.995
	68		—	—	0.005	0.010	—		0.007	0.005		0.005
	134		—	—	0.005	—	—		—	—		—
*PGM-1**	*100*	0.723	0.83	0.62	0.665	0.706	0.645	0.737	0.697	0.658	0.709	0.660
	111	0.250	0.17	0.38	0.335	0.279	0.350	0.263	0.275	0.342	0.291	0.340
	89	0.027	—	—	—	0.015	0.005	—	0.028	—	—	—
*PGDH**	*100*	ND	0.59	0.63	0.686	0.721	0.695	ND	0.641	0.696	ND	0.681
	150		0.41	0.37	0.314	0.279	0.305		0.359	0.293		0.319
	200		—	—	—	—	—		—	0.011		—

[a] Data for these conch (February collection) were excluded from the statistical analyses because of small sample size.
[b] April collection.

Results

Nineteen presumptive loci encoding 11 enzymes were resolved electrophoretically (Table 2). Ten loci were polymorphic and were used exclusively in the population analyses (Table 3).

Florida Keys and Bimini populations

Allele frequencies for samples of queen conch from the Florida Keys and Bimini were very similar (Table 3). The gene identity between samples, averaged over the ten polymorphic loci, ranged from 0.978 to 0.999 and averaged 0.994 for all pairwise comparisons. Most alleles were present in all samples, but some rare ($P<0.01$) alleles were detected as only one or two heterozygotes (e.g., *AAT-1*130*). An exception to this latter generalization was the presence of the *MDH-2*138* allele at a frequency of 0.206 (35 **100/100*, 11 **100/138*, and 5 **138/138*) among 51 scored individuals collected from Ballast Key in 1987. Only one heterozygote for this allele was observed elsewhere during the study.

Genotypes conformed ($P>0.05$) to Hardy-Weinberg proportions at all loci except *DPEP-1**. At this latter locus, significant ($P<0.01$) deficits of heterozygotes were detected in 7 of 10 samples. Overall, 285, 279, and 244 individuals had the **100/100*, **100/108*, and **108/108* genotypes, respectively, at *DPEP-1**. This overall deficit of heterozygotes occurred despite similar ($P>0.05$) allele frequencies among samples (Table 3).

Spatial and temporal variation in allele frequencies accounted for minor but approximately equal amounts of gene diversity. The total gene diversity (H_T) averaged 0.202 for the ten polymorphic loci. Of this total, 0.60% and 0.50% were due to temporal and spatial variation within and among localities, respectively

Table 4

Hierarchical likelihood-ratio tests (G-statistics) for homogeneity of allele frequencies among samples of queen conch *Strombus gigas* from the Florida Keys and Bimini. Degrees of freedom are in parentheses.

Source of variation	*AAT-1**	*AAT-2**	*DPEP-1**	*GPI**	*IDH-2**	*MDH-1**
Total	19.68(18)	20.03(18)	7.84(9)	43.22(18)**	21.09(8)*	24.51(6)**
Among localities	16.26(8)	15.21(9)	2.42(4)	32.66(8)*	9.48(4)	9.57(3)
Within localities	3.42(5)	4.82(4)	5.42(5)	10.57(5)	11.61(4)	14.95(3)*
Ballast Key	1.62(1)	—	1.38(1)	2.81(1)	—	—
Coffins Patch	1.71(2)	2.37(2)	3.04(2)	4.36(2)	4.41(2)	14.94(2)**
Craig Key	0.09(2)	2.45(2)	1.00(2)	3.40(2)	7.20(2)	0.01(1)
(Approx. F-ratio[a])	2.97(8,5)	1.40(9,4)	0.56(4,5)	1.93(8,5)	0.82(4,4)	0.64(3,3)

Source of variation	*MDH-2**	*ODH**	*PGM-1**	*PGDH**	Total
Total	116.83(9)***	7.03(12)	34.13(18)	10.97(12)	305.33(128)***
Among localities	95.42(4)***	2.02(6)	8.79(8)	6.65(6)	198.48(60)***
Within localities	21.41(3)***	5.00(5)	25.34(10)*	4.32(4)	106.86(48)***
Ballast Key	19.54(1)***	—	5.49(2)	—	30.84(6)***
Coffins Patch	—	4.97(4)	6.58(4)	0.61(2)	42.99(22)**
Craig Key	1.87(2)	0.03(1)	13.27(4)	3.71(2)	33.03(20)*
(Approx. F-ratio[a])	3.34(4,3)	0.37(6,5)	0.43(8,10)	1.03(6,4)	1.49(60,48)

[a] Approximate F-ratio = (G among localities/df)/(G within localities/df).
*$P<0.05$; **$P<0.01$; ***$P<0.001$; after adjustment for number of tests (Rice 1989).

(G_{SL} 0.0060, G_{LT} 0.0050). The remaining 98.9% (H_S/H_T) was due to within-sample heterozygosity.

Allele-frequency heterogeneity among samples was significant ($P<0.05$) at several loci and was due to both spatial and temporal components of variation (Table 4). Temporal variation at Ballast Key ($P<0.001$) and Coffins Patch ($P<0.01$) was due primarily to variation at *MDH-2** and *MDH-1**, respectively. On the other hand, the heterogeneity among years at Craig Key ($P<0.05$) was due primarily to the cumulative effects of variation at *IDH-2** and *PGM-1**. Significant allele-frequency variation also existed among localities, but this latter variation did not exceed the temporal variation within localities as measured by F-ratio comparisons ($P>0.05$) at each locus.

Comparisons with Caribbean Sea and Bermuda populations

Allele frequencies at *DPEP-1**, *MDH-2**, *PGM-1**, and *PGDH** for the Florida Keys and Bimini populations of *S. gigas* can be compared directly with those for populations sampled by Mitton et al. (1989). In that previous study, queen conch were collected from 16 sampling sites representing eight major localities throughout the Caribbean Sea area (Fig. 1). In addition, conch were collected from one site in Bermuda.

Patterns of genetic variation among populations in the Caribbean Sea and Bermuda were similar to those for populations in the Florida Keys and Bimini (Table 5). Total gene diversities (H_T) for the two groups of populations were essentially equal (0.355 and 0.354, respectively). However, the diversity within and among localities was somewhat greater for Caribbean Sea and Bermuda populations (G_{LT} 1.69%, G_{SL} 1.14%) than for populations from the Florida Keys and Bimini (G_{LT} 0.39%, G_{SL} 0.68%). This latter result might be expected considering the relative geographic scales over which populations were sampled in the two studies (Fig. 1). In this context, summing G_{LT} and G_{SL} for Florida Keys and Bimini populations yields a percentage of gene diversity (1.07%) that is approximately equal to G_{SL} (sites within localities) for the Caribbean Sea and Bermuda populations (1.14%).

A dendrogram based on Nei's index of gene identity clearly reflected the high genetic similarity among populations of *S. gigas* (Fig. 2). The average gene identity (based on the four aforementioned loci) among populations sampled by Mitton et al. (1989) was 0.984, among those sampled here was 0.993, and between populations (samples) of the two studies was 0.988. Twenty-three of these populations clustered together at the 0.99 level or above. The Bermuda population and the 1987 Ballast Key population (sample) formed a separate subcluster, due primarily to divergent allele frequencies at *MDH-2**. The Vieux Fort (St. Lucia) and Six Hill Cay (Turks and Caicos Islands) populations also clustered separately, due primarily to slightly divergent

Table 5

Percentages of total gene diversity (H_T) among localities (G_{LT}), among samples and sites within localities (G_{SL}), and within samples and sites (H_S/H_T) for populations of queen conch *Strombus gigas* from the Florida Keys and Bimini (this study) and from the Caribbean Sea and Bermuda (Mitton et al. 1989). Data represent the means for *DPEP-1**, *MDH-2**, *PGM-1**, *PGDH**.

		Gene diversity (%)		
Populations	H_T	G_{LT}	G_{SL}	H_S/H_T
Florida Keys and Bimini	0.354	0.39	0.68	98.94
Caribbean Sea and Bermuda	0.355	1.69	1.14	97.17
All populations	0.354	1.24	1.01	97.75

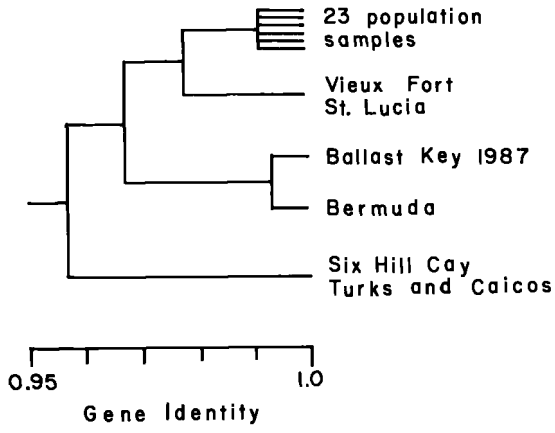

Figure 2

UPGMA dendrogram of genetic similarities among population samples of queen conch *Strombus gigas* based on allele frequencies at *DPEP-1**, *MDH-2**, *PGDH**, and *PGM-1**, and Nei's (1972) index of genetic identity.

allele frequencies at *PGDH** and *DPEP-1**, respectively (Mitton et al. 1989).

In summary, populations of *S. gigas* are very similar genetically and do not appear to be structured geographically. However, those populations cannot be considered totally panmictic.

Discussion

Population structure

Benthic marine invertebrates with planktonic larvae often exhibit spatial and temporal genetic variation similar to that described here for *S. gigas*. For example, Watts et al. (1990) found significant allele-frequency variation among three populations of sea urchin *Echinometra mathaei* separated by only 4km. Moreover, that heterogeneity over a 4km distance was approximately equal to the genetic heterogeneity among populations separated by over 1300km. Those investigators also detected significant allele-frequency variation among year-classes within each of the three microspatial sample sites. Similar patterns of heterogeneity were reported for the limpet *Siphonaria jeanae* (Johnson and Black 1982, 1984ab) and seastar *Acanthaster planei* (Nash et al. 1988, Nishida and Lucas 1988).

Significant microspatial genetic heterogeneity, despite high macrospatial genetic similarity, has been termed "genetic patchiness" (e.g., Johnson and Black 1984b). Such genetic patchiness could be due to either postsettlement natural selection or genetic heterogeneity among groups of recruits that are spatially or temporally separated (Watts et al. 1990). Under both hypotheses, planktonic dispersal is believed to maintain high genetic similarity among populations over broad geographic areas. However, under postsettlement natural selection, one would expect genetic variation among localities to be greater than the temporal variation within localities because of local adaptation. Conversely, under the model of presettlement genetic heterogeneity, spatial and temporal components of genetic variation are expected to be equal because the population structure would result from presettlement events that were independent of the specific localities at which settlement occurred. Under this latter model, spatial heterogeneity among localities would simply reflect the temporal heterogeneity within localities.

Results obtained here for *S. gigas* are most consistent with the presettlement hypothesis of genetic patchiness. Populations of queen conch throughout their geographic range are very similar genetically, yet spatial and temporal components of genetic variation appear significant and approximately equal. Mitton et al. (1989) obtained similar results for macrospatial (among-locality) and microspatial (within-locality) components of genetic variation. These results suggest a dynamic population structure in which allele-frequency heterogeneity may exist among groups of recruits that settle in different years at the same locality or at different localities in the same year. Johnson and Black (1982, 1984ab) and Watts et al. (1990) reached similar conclusions regarding genetic patchiness among populations of limpet and sea urchin, respectively.

Several mechanisms can be invoked to explain genetic patchiness due to presettlement events. Johnson and Black (1984ab) and Watts et al. (1990) suggest that

selective mortality prior to settlement, possibly reflecting stochastic variation in the marine environment (e.g., water temperature, salinity), may be responsible for the "chaotic genetic patchiness" that they observed. Alternatively, temporal variation in the source of recruits for each locality and/or genetic drift resulting from a finite number of breeders could also generate random genetic patchiness on both temporal and spatial scales (e.g., Waples 1989). None of these aforementioned hypotheses can be excluded with the available data.

The effective number of breeders (N_e) contributing to a cohort of larvae that settle together at a particular location is unknown for *S. gigas*. Males and females breed in aggregations at characteristic locations over a 6–9 month period, and each female may produce several egg masses of approximately 310,000–750,000 eggs each during the breeding season (Robertson 1959, Randall 1964, Weil and Laughlin 1984, Berg and Olson 1989). Several females within an aggregation may lay their egg masses simultaneously, and because the rate of embryonic development is temperature-related, hordes of larvae are released synchronously. These larvae can thus be entrained together into the water column and affected simultaneously by marine and oceanic processes. Consequently, hordes of larvae from a finite number of parents could potentially be presented simultaneously to a substrate that would induce settlement and metamorphosis.

Recently, Bucklin et al. (1989) and Bucklin (1991) obtained evidence that ocean currents and related processes (e.g., upwellings, eddies, offshore jets) can spatially and temporally maintain genetically discrete cohorts of zooplankton in the marine environment. For example, Bucklin et al. (1989) concluded that such processes "prevented homogenization of the plankton assemblages during transport" and that "plankton populations in complex flow fields may show patchiness in biological, biochemical, and/or genetic character at small time/space scales." Their results suggest that similar processes could affect significantly the distribution of pelagic larvae following their release into the water column.

The source of *S. gigas* recruits for the Florida Keys is unknown. The Florida Current, which sweeps eastward past the Florida Keys and subsequently forms the Gulf Stream, is created by the massive flow of warm water northward from the Caribbean Sea through the Yucatan Channel. This current could entrain large numbers of larvae from numerous locations prior to flowing eastward past the Florida Keys (Mitton et al. 1989). Stochastic variations in water currents, surface winds, and meteorological events (e.g., tropical storms) could thus affect significantly the source of *S. gigas* recruits for any particular locality. During the course of our study, we attempted to gain permission to collect conch from Cuba and Yucatan, Mexico—two possible sources of recruits for the Florida Keys—but were unable to do so.

One potential shortcoming of our study was that the temporal effects of recruitment were confounded with other population processes; that is, temporal genetic variation was measured among mixed aggregations of conch sampled in different years at the same locality and not among separate year-classes or cohorts. With the exception of the Coffins Patch population or aggregation (see below), all samples consisted of mixed age- and size-classes with new recruits added each year. In addition, some of the temporal genetic variation may have been due to migration of juveniles and adults into and out of the study areas (Hesse 1979, Weil and Laughlin 1984, Stoner et al. 1988, Stoner 1989). Consequently, we cannot separate the temporal effects of recruitment from other population processes. However, our goal was not to estimate temporal genetic variation among cohorts or year-classes *per se*, but rather to provide a measure of within-population (i.e., within-locality) variation by which the significance of genetic variation among localities could be evaluated. Population processes causing temporal genetic variation within localities would similarly affect the genetic variation among localities. Some measure of temporal variation was thus needed before the microevolutionary significance of genetic variation among localities could be ascertained. Alternatively, some form of stratified sampling of year- and/or size-classes would be required to separate recruitment or year-class effects from other potential sources of temporal genetic variation.

Possible evidence that recruitment, migration, or similar population processes may significantly affect the population structure of *S. gigas* was the presence of the *MDH-2*(138)* allele at a frequency of 0.206 in the 1987 sample from Ballast Key but the near absence of this allele in the 1988 sample and elsewhere during our study. Mitton et al. (1989) similarly reported, for the Bermuda population, a frequency of 0.30 for a "fast" *MDH-2** allele that was also rare elsewhere. However, the Bermuda population is believed to be self-sustaining with little planktonic recruitment from the Gulf Stream or elsewhere (Mitton et al. 1989). Conversely, Ballast Key is situated within the Florida Current and is the most upstream locality from which we collected conch for the present study. Two distinct aggregations of *S. gigas* may have been sampled at Ballast Key in 1987 and 1988, respectively.

Anomalous results

Coffins Patch Size distributions suggest that the Coffins Patch population was most likely a single year-class

or cohort that we sampled in three consecutive years (1988–90). This population or cohort presumably resulted from a large recruitment event during the summer and fall of 1987. We estimated that the 1987 aggregation at Coffins Patch consisted of at least 250,000 animals covering an area of approximately 30 hectares (Berg and Glazer, unpubl.).

Although the Coffins Patch aggregation appeared to be a single cohort, we detected a significant allele-frequency variation among years (1988–90) at *MDH-1**. This difference was due to the absence of the *MDH-1* (120)* allele in the 1988 sample (n 100) versus the presence of eight **100/120* heterozygotes in both the 1989 (n 102) and 1990 (n 100) samples. The 1989 sample also had one **120/120* homozygote. Sampling error does not adequately explain those results because the probability of obtaining all **100/100* homozygotes in the 1988 sample was only $(0.955^2)^{100} = 0.0001$ (assuming the true frequency of the **120* allele was 0.045 [mean of 1989 and 1990 samples] and random mating). Similarly, differential mortality among genotypes does not adequately explain those results unless heterozygotes were initially very rare and the subsequent mortality of **100/100* homozygotes was extremely high.

Alternatively, recruitment to the Coffins Patch area in 1987 may have been from more than one source population. This could have resulted in an aggregation that was not distributed randomly. Subsequent mixing and/or possible immigration of juveniles (e.g., Stoner 1989) could thus explain changes in allele frequencies between 1988 and 1989. None of these hypotheses can be excluded with the available data.

Regardless of actual mechanism, the presence of only one highly abundant year-class at Coffins Patch over a 3-year period indicates that recruitment to specific localities in the Florida Keys can be highly variable and unpredictable. This observation thus supports the interpretation that genetic patchiness may simply reflect stochastic events prior to settlement.

DPEP-1* We observed a consistent deficit of heterozygotes (with respect to Hardy-Weinberg expectations) at *DPEP-1** but not at other loci. Similar deficits of heterozygotes have been reported often for marine mollusks (reviewed by Gaffney et al. 1990). Such deficits are frequently associated with positive correlations between body size and individual heterozygosity. We also observed a positive correlation between body size and heterozygosity, but genotypic variation at *DPEP-1** did not contribute to that correlation. These results will be described in detail elsewhere (Campton et al. In press).

PGM-2* One possible point of inconsistency between the study described here and that of Mitton et al. (1989) concerns data for *PGM-2**. Mitton et al. (1989) presented only limited data for this latter locus (9 of 17 populations), but those investigators consistently observed a high frequency (0.57–0.69) polymorphism for a "slow" allele. In contrast, we found *PGM-2** to be fixed for a single allele. Only *PGM-1** and *PGM-2** are expressed in digestive gland tissue, which was the only tissue assayed by Mitton et al (1989). However, we also scored PGM in foot muscle which clearly revealed a third, more cathodal locus (*PGM-3**). We also observed three distinct loci in foot tissue of a second conch species, *S. costatus*.

At least three possibilities could thus account for the apparent difference between our results and those of Mitton et al. (1989) at *PGM-2**: (1) our inability to resolve the variant electromorph at *PGM-2**, (2) the partial expression of the *PGM-3** locus in digestive gland tissue (e.g., Allendorf et al. 1983) of individuals sampled by Mitton et al. (1989), thus giving false readings of heterozygotes at *PGM-2**, or (3) the reported allele-frequency difference between the two groups of populations are indeed real. Of the three possibilities, we believe explanations (1) and (2) are the most likely because of the high consistency of our allele frequencies with those of Mitton et al. (1989) at all other loci. Consequently, we believe that this apparent discrepancy at *PGM-2** most likely reflects laboratory-specific adaptations of basic electrophoretic procedures. In this context, we were able to resolve several loci not resolved by Mitton et al. (1989) and vice-versa.

Conclusions

The major finding of our study was the existence of spatial and temporal genetic patchiness among populations of queen conch in the Florida Keys and Bimini. We suggest that such genetic patchiness most likely results from presettlement stochastic events and processes in the marine environment. Nevertheless, these populations are all very similar genetically, presumably reflecting high levels of gene flow due to larval drift. These interpretations are consistent with the results of Mitton et al. (1989) and also explain similar patterns of "chaotic genetic patchiness" in other taxa of marine invertebrates.

Acknowledgments

We thank R. Estling, A. Kirkley, and W. Schumacher for their assistance in the laboratory.

Citations

Aebersold, P.B., G.A. Winans, D.J. Teel, G.B. Milner, and F.M. Utter
1987 Manual for starch gel electrophoresis: A method for the detection of genetic variation. NOAA Tech. Rep. NMFS 61, 19 p.

Allendorf, F.W., R.F. Leary, and K.L. Knudsen
1983 Structural and regulatory variation of phosphoglucomutase in rainbow trout. Isozymes Curr. Top. Biol. Med. Res. 9:123–142.

Ballantine, D.L., and R.S. Appeldoorn
1983 Queen conch culture and future prospects in Puerto Rico. Proc. Gulf Caribb. Fish. Inst. 35:57–63.

Berg, C.J. Jr., and D.A. Olsen
1989 Conservation and management of queen conch (*Strombus gigas*) fisheries in the Caribbean. *In* Caddy, J.F. (ed.), Marine invertebrate fisheries: Their assessment and management, p. 421–442. John Wiley, NY.

Boyer, S.H., D.C. Fainer, and E.J. Watson-Williams
1963 Lactate dehydrogenase variant from human blood: Evidence for molecular subunits. Science (Wash. DC) 141: 642–643.

Bucklin, A., M.M. Rienecker, and C.N.K. Mooers
1989 Genetic tracers of zooplankton transport in coastal filaments off northern California. J. Geophys. Res. 94(C6: 8277–8288.

Bucklin, A.
1991 Population genetic responses of the planktonic copepod *Metridia pacifica* to a coastal eddy in the California Current. J. Geophys. Res. 96(C8):14,799–14,808.

Campton, D.E., C.J. Berg Jr., L.M. Robison, and R.A. Glazer
In press Deficits of heterozygotes and correlation between size and heterozygosity in the marine mollusk, *Strombus gigas* (Gastropoda: Strombidae). Evolution.

Chakraborty, R., M. Haag, N. Ryman, and G. Stahl
1982 Hierarchical gene diversity analysis and its application to brown trout populations. Hereditas 97:17–21.

Clayton, J.W., and D.N. Tretiak
1972 Amine-citrate buffers for pH control in starch gel electrophoresis. J. Fish. Res. Board Can. 29:1169–1172.

Davis, M., and C. Hesse
1983 Third world level conch mariculture in the Turks and Caicos Islands. Proc. Gulf Caribb. Fish Inst. 35:73–82.

Gaffney, P.M., T.M. Scott, R.K. Koehn, and W.J. Diehl
1990 Interrelationships of heterozygosity, growth rate and heterozygote deficiencies in the coot clam, *Mulinia lateralis*. Genetics 124:687–699.

Hesse, K.O.
1979 Movement and migration of the queen conch, *Strombus gigas*, in the Turks and Caicos Islands. Bull. Mar. Sci. 29: 303–311.

Johnson, M.S., and R. Black
1982 Chaotic genetic patchiness in an intertidal limpet, *Siphonaria* sp. Mar. Biol. (Berl.) 70:157–164.
1984a The Wahlund effect and the geographical scale of variation in the intertidal limpet *Siphonaria* sp. Mar. Biol. (Berl.) 79:295–302.
1984b Pattern beneath the chaos: The effect of recruitment on genetic patchiness in an intertidal limpet. Evolution 38: 1371–1383.

Kinder, T.H., G.W. Hebrun, and A.W. Green
1985 Some aspects of the Caribbean circulation. Mar. Geol. 68:25–52.

Little, C.
1965 Notes on the anatomy of the queen conch, *Strombus gigas*. Bull Mar. Sci. 15:338–358.

Mitton, J.B., C.J. Berg Jr., and K.S. Orr
1989 Population structure, larval dispersal, and gene flow in the queen conch, *Strombus gigas*, of the Caribbean. Biol. Bull. (Woods Hole) 177:356–362.

Morizot, D.C., and M.E. Schmidt
1990 Starch gel electrophoresis and histochemical visualization of proteins. *In* Whitmore, D.H. (ed.), Electrophoretic and isoelectric focusing techniques in fisheries management, p. 23–80. CRC Press, Boca Raton.

Nash, W.J., M. Goddard, and J.S. Lucas
1988 Population genetic studies of the crown-of-thorns starfish, *Acanthaster planci* (L.), in the Great Barrier reef region. Coral Reefs 7:11–18.

Nei, M.
1972 Genetic distance between populations. Am. Nat. 106: 283–292.
1973 Analysis of gene diversity in subdivided populations. Proc. Natl. Acad. Sci. USA 70:3321–3323.

Nishida, M., and J.S. Lucas
1988 Genetic differences between geographic populations of the crown-of-thorns starfish throughout the Pacific region. Mar. Biol. (Berl.) 98:359–368.

Randall, J.E.
1964 Contributions to the biology of the queen conch, *Strombus gigas*. Bull. Mar. Sci. 14:246–295.

Rice, W.R.
1989 Analyzing tables of statistical tests. Evolution 43: 223–225.

Ridgway, G.J., S.W. Sherburne, and R.D. Lewis
1970 Polymorphisms in the esterases of Atlantic herring. Trans. Am. Fish. Soc. 99:147–151.

Robertson, R.
1959 Observations on the spawn and veligers of conchs (*Strombus*) in the Bahamas. Proc. Malacol. Soc. Lond. 33:164–171.

Scheltema, R.S.
1971 Larval dispersal as a means of genetic exchange between geographically separated populations of shallow-water benthic marine gastropods. Biol Bull. (Woods Hole) 140:284–322.
1986 On dispersal and planktonic larvae of benthic invertebrates: An eclectic overview and summary of problems. Bull. Mar. Sci. 39:241–256.

Selander, R.K., M.H. Smith, S.H. Yang, W.E. Johnson, and J.B. Gentry
1971 Biochemical polymorphism and systematics in the genus *Peromyscus*. I. Variation in the old field mouse (*Peromyscus polionotus*). Studies in Genetics VI. Univ. Texas Publ. 7103: 49–90.

Shaklee, J.B., F.W. Allendorf, D.C. Morizot, and G.S. Whitt
1990 Gene nomenclature for protein-coding loci in fish. Trans. Am. Fish. Soc. 119:2–15.

Siciliano, M.J., and C.R. Shaw
1976 Separation and visualization of enzymes on gels. *In* Smith, I. (ed.), Chromatographic and electrophoretic techniques. Vol. II, Zone electrophoresis (4th ed.), p. 185–209. Year Book Med. Publ., Chicago.

Smouse, P.E., and R.H. Ward
1978 A comparison of the genetic infrastructure of the Ye'cuana and the Yanomama: A likelihood analysis of genotypic variation among populations. Genetics 88:611–631.

Sneath, P.H.A., and R.R. Sokal
1973 Numerical taxonomy. W.H. Freeman, San Francisco.

Sokal, R.R., and F.J. Rohlf
1981 Biometry. W.H. Freeman, San Francisco.
Stoner, A.W.
1989 Winter mass migration of juvenile queen conch *Strombus gigas* and their influence on the benthic environment. Mar. Ecol. Prog. Ser. 56:99–104.
Stoner, A.W., R.N. Lipcius, L.S. Marshall Jr., and A.T. Bardales
1988 Synchronous emergence and mass migration in juvenile queen conch. Mar. Ecol. Prog. Ser. 49:51–55.
Waples, R.S.
1989 Temporal variation in allele frequencies: Testing the right hypothesis. Evolution 43:1236–1251.
Watts, R.J., M.S. Johnson, and R. Black
1990 Effects of recruitment on genetic patchiness in the urchin *Echinometra mathaei* in western Australia. Mar. Biol. (Berl.) 195:145–151.
Weil, E.M., and R.G. Laughlin
1984 Biology, population dynamics, and reproduction of the queen conch *Strombus gigas* Linnaeus in the Archipielago de Los Roques National Park. J. Shellfish Res. 4:45–62.