Implications of Spiny Lobster Recruitment Patterns of the Caribbean — A Biochemical Genetic Approach

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INTRODUCTION

The major goal of most management policies for the Caribbean spiny lobster fishery is to protect gravid females and juveniles so as to maximize tonnage landed and protect reproductive potential. Presently there is considerable controversy surrounding what should be the minimum size limit. In the Florida fishery where perhaps an excess of 90% of all legal animals (76 mm carapace length) (CL) are harvested each year, arguments for increasing the legal size have been made on several bases: Larger females (>75 mm CL) produce more eggs and constitute a larger proportion of the reproductively active segment of the population than smaller females (<75 mm CL) in the Bimini, Bahamas area (Kanciruk and Herrnkind, 1978). In the Dry Tortugas, Davis (1975) found the smallest gravid female captured to be 78 mm CL. Based on the finding of their 3-year study in the heart of the Florida fishery (Key West area) Gregory et al. (1978) have suggested increasing the legal size to 85 mm CL. The impact of a small legal harvest size on reproduction potential may be even greater if larger or older females lay more than one egg mass in a single season (Creaser, 1950; Sutcliffe 1952, 1953).

On the other hand, others argue that since spawn from Florida females are probably lost to ocean currents, why impose any restrictions on the harvest of gravid females. This is based on several factors: The estimated length of the phyllosome larval period is about 6 months (Lewis, 1951). Spawning of larvae in the Florida Keys occurs predominantly on the offshore reef tracts and may be synchronized with the outgoing tide. This is based primarily on the lack of other than occasional first stage phyllosomes in bay and near shore waters (Sweat, 1968; Witham et al. 1968). The implication is that newly spawned phyllosomes quickly enter the Gulf Stream presumably to be swept away "down stream". According to Sims and Ingle (1967) late stage phyllosome and pueruli recruitment is accomplished by stock spawned south of the Yucatan channel and carried to Florida in the Gulf Stream. Larval distribution studies, drift bottle experiments (Sims and Ingle, 1967) and the studies of Austin (1972) on the distribution of phyllosomes in the Gulf of Mexico loop current tends to support this notion (Sweat, 1968; Little, 1977). Thus larval dispersal patterns and recruitment stock distribution might be

viewed as an open system or a very large transatlantic closed system if the two specimens from West Africa indicate an intermediate population (Marchal, 1968). Schematically this is shown in Figure 1.

The larvae of other *Palinurid* species are also known to have long pelagic planktonic exitances (6-10 months) and travel great distances. In several cases maximal larval transport distances can be established since no land masses lie between the nearest adult population and where larvae are found in plankton tows. Thus, *Jasus lalandii* larvae are found at distances up to 300 miles (Lazarus 1967) and *Panulirus cygnus* up to 700 miles (Chittleborough and Thomas, 1969; Phillips et al. 1978) from their respective origins. *P. gracilis, P. inflatus* and *P. penicillatus* are found up to 1500 miles from their closest adult populations (Johnson, 1971; 1974).

The voyages of the Pacific larvae are 6-10 months (the apparent developmental time) and in each case at least the first half of development correlates closely with distance from shore. The latter half of the voyage presents a more confused picture and in addition, no clear cut return route has been established for any *Palinurid* larvae. In fact, Johnson (1971; 1974) raises the possibility that most if not all larvae of *P. penicillatus, P. inflatus, P. gracilis,* and perhaps *P. interruptus* found offshore represent a loss to the population. He suggests that only those larvae caught in eddies and gyres near coasts contribute to repopulation. We call this Johnson's model (Fig. 2). The Johnson model could describe the mechanism for self-maintenance of populations throughout the range of *P. argus*. Thus, Brazilian larvae return to Brazilian populations, Honduran larvae to Honduran populations, etc. with many larvae being lost to ocean currents.

In a number of areas within the range of *P. argus* hydrological conditions are known which could give rise to local loops. For example the Antilles current and countercurrents along the eastern boundary of the Bahamas (Ingham, 1975) coupled with prevailing easterly winds could serve to minimize larval dispersal. Thus larvae spawned around Abaco might return to that area in sufficient numbers to constitute a major contribution to recruitment with little mixing of larvae spawned from Cat Island, or other areas. The converse would be true of Cat Island larvae.

Larvae released into the Florida Straits from the Florida coast might also experience loops and gyres. Not only are southerly and onshore surface currents known, but deep currents with southerly and westerly as well as the usual northerly components have been measured in the Florida straits off Miami (Kielman and Duing, 1974; P. Smith, personal communication). However, since most of these countercurrents appear to exist at depths where the temperature is quite low their significance to larval movements is questionable (Austin, 1972). On the other hand, a persistent countercurrent is known in the vicinity of Key West (Brooks and Niiler, 1975). This current, which exists from surface to bottom and from shore outward to approximately 20 km could easily provide a return loop for larvae especially if coupled with the Gulf of Mexico Loop current.

Recently Richards and Goulet (1977) have reported preliminary computer calculations from a surface drift model indicating possible paths of larval

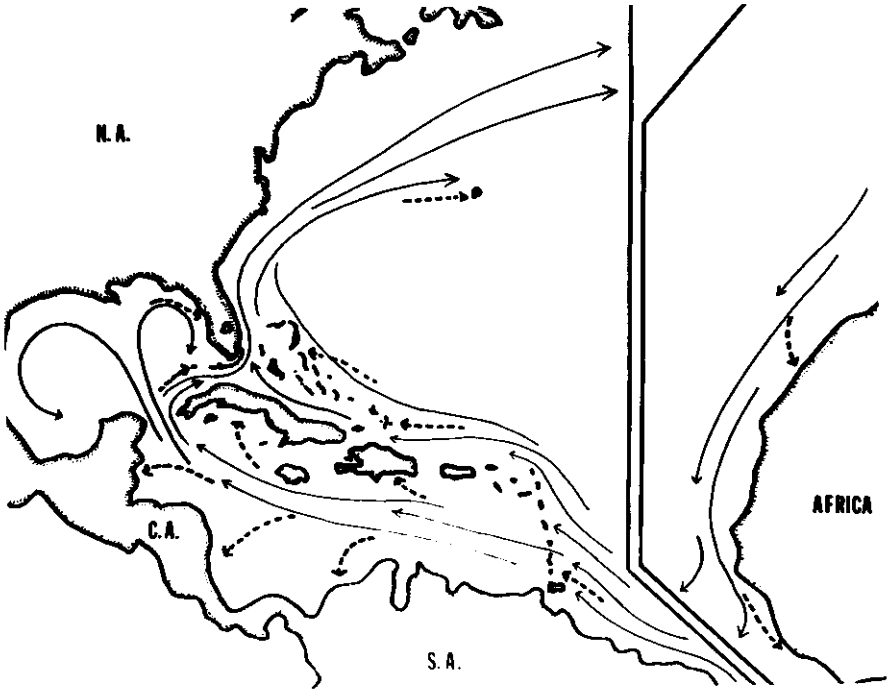

Figure 1: *"Open" system of larval recruitment.* Solid arrows indicate main current patterns somewhat exaggerated in the Caribbean Sea and Atlantic Ocean which could be involved in larval transport. Dotted arrows indicate larvae settling out of water currents at any location throughout the range of *Panulirus argus.*

recruitment and dispersal. Since their data base covers large areas and average currents, local, short term conditions were not reflected in their calculations. Nevertheless, in some cases, large scale loops were indicated. It will be interesting to see what this model generates when more detailed hydrological and meteorological data are used.

From the foregoing discussion of attempts to understand larval dispersal it is clear that no generally accepted explanation emerges from the data. However, two extreme patterns can be visualized each having different genetic and fisheries management consequences. If only an open loop or very large closed loop system exists genetic homogeneity throughout the range would be maximized. Although the environment throughout the range of a species such as *P. argus* is reasonably uniform, "micro" differences certainly exist. Large loops and long larval life (the latter perhaps dictating the former) would maximize mixing of larvae from many populations, thus randomizing the genetic makeup of incoming post larvae in any region. A great deal of genetic polymorphism might be expected as well as many larvae and possibly adult "populations" not being in "Hardy-Weinberg" equilibrium for some loci. Selection would be for plasticity to adapt to a variety of micro differences in habitat. At the other extreme short loops maximizing self-maintainance of populations could be viewed in a more classic genetic sense. Although

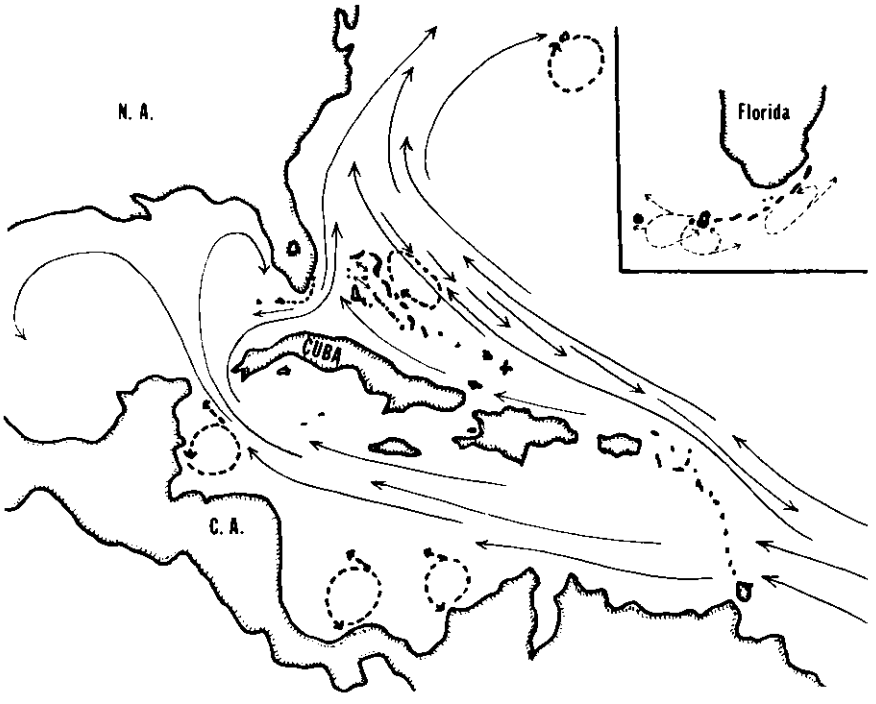

Figure 2: "Closed" System of larval recruitment. As in Figure 1, solid arrows indicate an exaggerated view of the main current patterns. Dotted arrows indicate possible gyres in which larval would be sustained in the region in which they were spawned.

exchange between adjacent populations would contribute to gene flow, distance would maximize genetic differences and reflect local genetic drift and selection pressures.

The differences in genetic consequences of the two models in their extreme form suggest an experimental approach to the larval recruitment problem. The use of biochemical-genetic techniques to determine adult and larval stock relatedness between various geographic locations. The application of biochemical population genetics has already been applied successfully in stock identification for a variety of organisms (Smith et al. 1976; Utter et al. 1976). Different breeding units within six different salmon species have been identified (May 1975; Utter et al. 1974); seatrout (Weinstein and Yerger 1976); Norwegian cod (Freydenberg et al. 1965; Moller 1968) and some species of tuna but not others have been shown to have subpopulation structure (Fujino, 1970); Pacific hake and green striped rock fish also have subpopulations; but not Pacific herring or Saury (Utter et al. 1974), while Atlantic herring are separable into two populations (Ridgeway et al. 1970). On the basis of one enzyme system populations of brown shrimp were not distinguishable (Proctor et al. 1974) nor were populations of northern lobster (Barlow and Ridgeway, 1971). However after examining 18 different enzyme

systems, Tracey et al. (1975) were able to find one enzyme (malic enzyme) that indicated population differences in the northern lobster where as 17 other enzymes showed no difference.

Biochemical genetic techniques have been applied to many other fisheries organisms, natural populations, (de Ligny, 1969) as well as a tool in mariculture (Utter and Folmar, 1978; Hedgecock et al, 1976). The application of these techniques to natural populations depends on: (1) determination of several polymorphic enzyme systems with sufficient variability to be useful in population comparison; (2) determination that variability is not due to ontogenetic, environmental or physiological parameters such as molt state, reproductive state; (3) establishing that allele frequencies in a population are stable with respect to time. Other considerations are important, but only follow when the above are established.

EXPERIMENTAL APPROACH

Rationale:—The fundamental question we are trying to answer is:

What contribution do foreign larvae make to repopulation of the Florida region and what contribution do larvae released by Florida lobsters make to the repopulation of Florida and other regions?

The following three approaches are the foundation of our research plan: (1) Analysis of genetic relatedness between various juvenile and adult populations. (2) Correlation of genetic relatedness of arriving post-larvae with each of the above adult populations. (3) Correlation of genetic relatedness of planktonic phyllosomes with various adult populations.

Presently because of the difficulties in obtaining phyllosome larvae we are concentrating on (1) and (2). If we make the working assumption that the closed loop model (Fig. 2)—is correct, we can formulate a testable hypothesis: At a particular locale, the gene frequencies of incoming post-larvae should be equal to those of adults in the region where both were captured. If the data dictate rejection of the hypothesis then recruitment of significant numbers of foreign larvae is indicated. The major exception to this would be restructuring of the adult population. This would have to occur *enmass* (Herrnkind, 1969; Herrnkind and McLean, 1971) and would be detectable in adult population genetic stability studies. Assuming this not to be the case, then analysis of gene frequencies in adult populations elsewhere should reveal the locations and extent of possible contributing parental populations.

If the hypothesis cannot be rejected, local recruitment is suggested and foreign recruitment remains unproven. However, comparison of local gene frequencies with those of other non-Florida adult populations will allow an assessment of the degree of foreign recruitment possible. Alternatives ranging from virtually total local recruitment to total foreign recruitment resulting from a mixing of larvae throughout the range of *P. argus* can be distinguished. This aspect will be dependent on comparison of many loci between various populations.

This paper will summarize data obtained thus far that have direct bearing on the recruitment question. These data are preliminary in nature since the bulk of our efforts have been directed toward experiments dealing with:

establishing polymorphic loci suitable for population surveys; determining the genetic basis for. these enzyme loci; assessing the effect of ontogenetic, environmental, seasonal, and a variety of physiological parameters on the expression and allele frequencies of the various enzyme loci studied. The results of these experiments will appear in other publications.

METHODS

Animal collection:—Adult *P. argus* were either obtained by diving or purchased from reliable fishermen. Postlarvae were collected with Witham type habitats (Witham et al. 1968; Sweat, 1968; Little, 1977)) in the Elliot Key area with the collaboration of the U.S. National Park Service (Everglades). Larvae were also obtained from the Key West area (Boca Chica to Sugarloaf Keys) by the Department of Natural Resources, State of Florida. By post larvae we mean all stages from the transparent flattened puerulus stage to the heavily pigmented rounded juvenile stage less than 10 mm CL.

Tissue Preparation:—Adults were dissected and tissues stored at –20ºC. Larvae were stored frozen. For analysis a small portion of tissue (100-300 mg) or total tail or total cephalothorax from post-larvae was homogenized in 1-5 volumes (depending on tissue) of homogenizing medium which also varied with the tissue and was either .05M Tris-HCl pH 7.5 with 10mM 2-mercaptoethanol or was the same with the addition of sucrose (0.25M). The homogenate was centrifuged for 30 minutes at 30,000 x g in a Sorvall RC-2B refrigerated centrifuge at 0ºC and the supernatant frozen and saved for electrophoretic analyses.

Elecrophoretic analysis:—For analysis of esterases, electrophoretic separation was performed on vertical polyacrylamide gels: (acrylamide 8.5% and bis-acrylamide 3%; bridge buffer .05M sodium tetraborate pH 9.2, gel buffer 0.37M Tris at pH 8.6). For peptidases electrophoresis was performed on vertical starch gels: (12% electrostarch, Electrostarch Co., Madison, Wis.), bridge buffer 0.3M boric acid, pH 8.6 and gel buffer .0037M Tris-citrate pH 7.5 with 20 mM $MgCL_2$. For peptidases in tail muscle the gel buffer was .0075M Tris-Citrate pH 7.5. Electrophoresis was performed at 4ºC for 1-3 hours in the case of polyacrylamide and 12-18 hours in the case of starch. After electrophoresis gels were sliced longitudinally and stained for esterase activity using alpha-napthylacetate as substrate (Shaw and Prasad, 1970), or peptidase activity (Harris and Hopkinson, 1976). Peptidase "B" was assayed with phenylalanyl-tyrosine as substrate and peptidase "D" with phenylalanylproline as substrate. After enzyme bands appeared, the gels were fixed, photographed and scored for the various phenotypes. The entire procedural flow is summarized in Figure 3.

RESULTS

Figure 4 is a composit photograph of the different phenotypes observed for each enzyme locus discussed in this paper. They were: esterases; EF-4 which consists of a single polypeptide enzyme with 4 alleles; EM-1, a single polypeptide enzyme with 2 alleles; EM-3, a single polypeptide enzyme with 3 alleles. The peptidases are; Pep-B a single polypeptide enzyme with 2 alleles and Pep-D a prolidase with two polypeptides per enzyme molecule and 3 alleles.

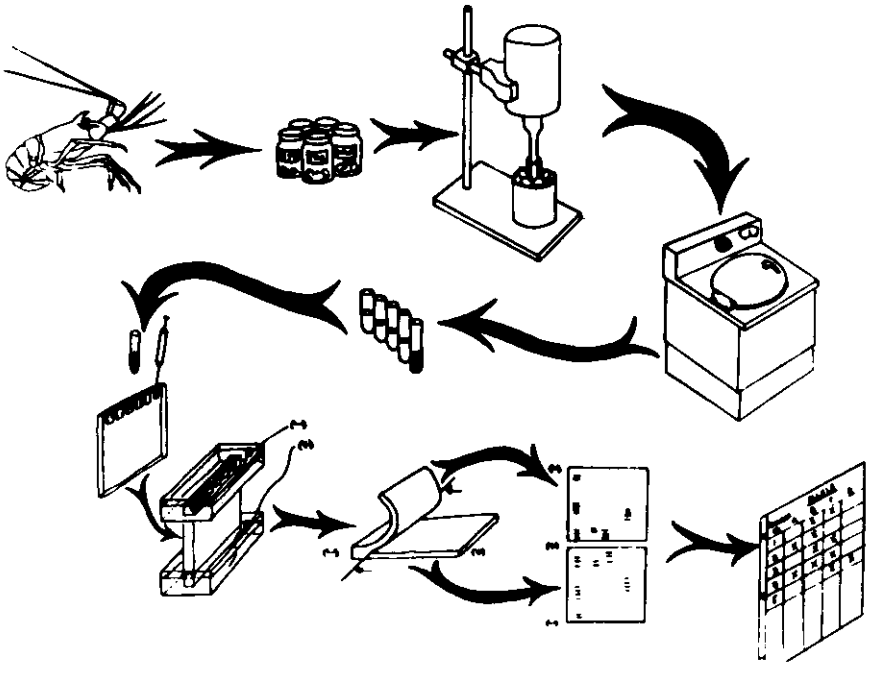

Figure 3: Schematic representation of methods used in this study. Refer to text for details.

In Table 1 is a summary of the allele frequencies for the various loci in each population for which they were analyzed. Analyses are not complete for each enzyme across all populations. Table 2 is a summary of allele frequencies for the EF-4 locus in various post larval collections. This is the only enzyme locus that has been extensively studied in post larvae. Tables 3 and 4 and Chi square contingency tables comparing EF-4 genotypic frequencies in adult populations and post larval populations respectively. In the latter table, several adult populations have been included for reference. In these calculations because of low numbers rare phenotypes were pooled. Similar Chi square contingency tables have been prepared comparing esterase EM-1 and peptidases Pep-B and D (Table 5).

DISCUSSION

At present our project is far short of being able to clearly delineate the genetic affinities and larval recruitment patterns for the many populations of *P. argus* throughout the range. The major deficiencies are: (1) at present too few populations have been collected especially from strategically located areas; and (2) insufficient enzymes per population have been analyzed. However adequate progress has been made to demonstrate the potential of the approach.

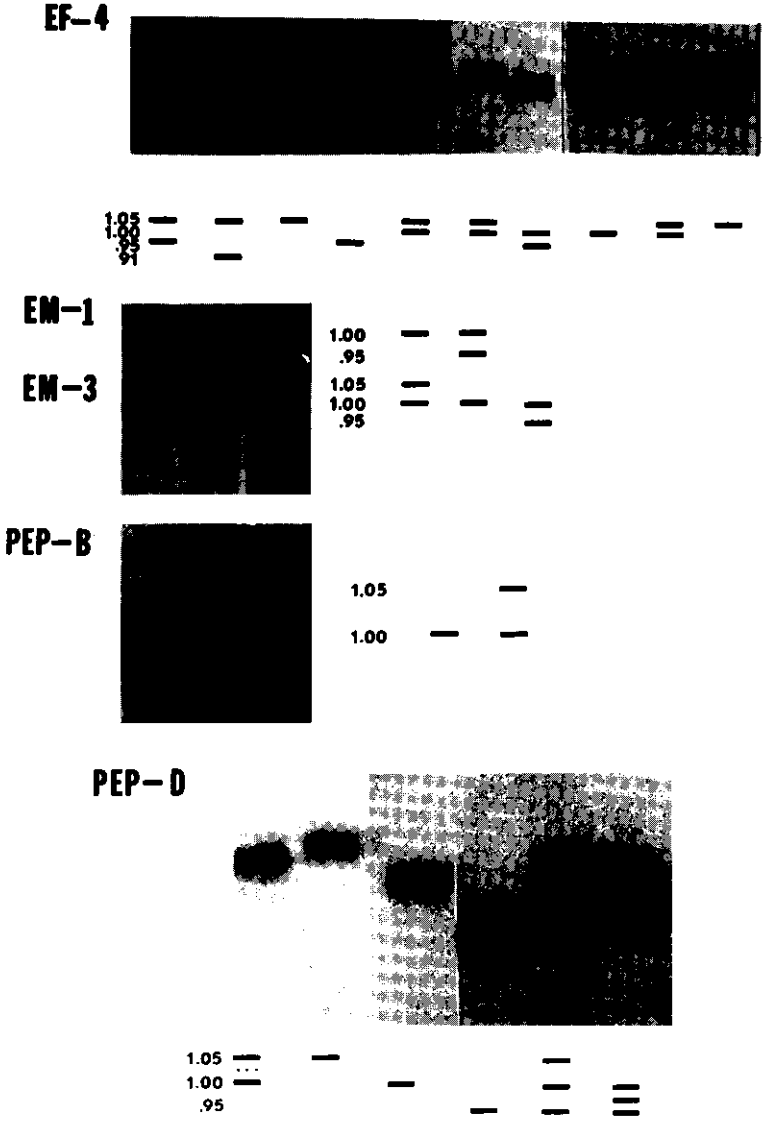

Figure 4: Electrophoretograms of Esterases; EF-4, EM-1 and EM-3 and Peptidases; PEP-B and PEP-D. Photo reproductions of observed phenotypes. Line drawings are presumed genotypes with allele designations.

Table 1. Allele frequencies by population

Locus	Allele	EK	BR	M	KW	DT	CS	MI	WC	B	VI	GB	BJ	PL
EF-4	1.05	.409	.456	.460	.535	.448	.462	.500	.510	.587	.385			.385
	1.00	.515	.467	.44	.437	.500	.512	.455	.459	.370	.487			.564
	.95	.076	.076	.100	.028	.052	.026	.05	.020	.043	.128			.026
	.91	.000	.000	.000	.000	.000	.000	.000	.010	.000	.000			.026
	N*	168	46	50	71	77	39	22	49	46	39			48
EM-1	1.00	.943			1.00	.975					.906	.971		
	.95	.029			.000	.025					.094	.029		
	N	70			40	40					16	17		
EM-3	1.05				.038	.050					.067	.059		
	1.00				.963	.925					.867	.941		
	.94				.000	.025					.067	.000		
	N				40	40					15	17		
PEP-B	1.05	.026			.024	.032				.115	.032		.045	
	1.00	.974			.976	.968				.885	.968		.955	
	N	58			42	47				48	31		33	
PEP-D	1.05				.053	.091					.000		.068	
	1.00				.468	.490					.595		.477	
	.91				.478	.409					.405		.455	
	N				47	55					42		33	

*N = Number of animals; Populations: Elliott Key, EK; Boca Raton, BR; Marathon, M; Key West, KW; Dry Tortugas, DT; Cay Sal Bank (Bahamas) CS; Mores Island (Bahamas) MI; Walker's Cay (Northern Bahamas) WC; Belize, B; Virgin Islands VI; Grand Bahama Island, GB; Biscayne Bay Juveniles, BJ; Elliott Key Post Larvae, PL.

Table 2. Allele frequencies for EF-4 in various post larval samples

Allele	BCL* 4/17/78	BCL 3/23/77	BCL 11/7/76	EKL* 3/14/78	EKL 3/21/78
1.05	.425	.460	.430	.490	.385
1.00	.550	.480	.472	.427	.564
.95	.025	.050	.044	.083	.026
.91	.000	.010	.044	.000	.026
N†	20	50	50	39	48

*Collections from Boca Chica (BCL) and Elliot Key (EKL)
†N = Number of animals.

When one observes significant differences in genotypic frequencies at a single locus between populations it is suggestive but not proof of genetic separation. However when a a number of loci are different one can conclude the populations are genetically isolated (Selander and Johnson, 1973). Lack of statistical differences on the other hand contributes little except when many loci show this result.

Differences seen in analyses thus far can be listed as follows: (1) At the EF-4 locus (Table 3), Belize is different from Elliott Key, Boca Raton, Dry Tortugas and the Virgin Islands (St. Thomas area). Walker's Cay (northern Bahamas) differs from Boca Raton. (2) At the EF-4 locus (Table 4) no difference from either Boca Chica or Elliott Key are observed between any post larval collection and Florida adult population. One larval collection (Boca Chica 3/23/77) was different from adult lobsters from Belize. (3) At the EM-1 locus (Table 5) Key West was different from Virgin Islands. (4) At the Pep-B locus, (Table 5) differences were observed between Belize and both Key West and Elliott Key. (5) At the Pep-D locus, (Table 5) differences were observed

Table 3. Chi-square contingency table comparing zygotic frequencies by population at EF-4 Locus

	EK	VI	DT	BR	B	CS	M	WC	MI
VI	2.096	-							
DT	3.947	.868	-						
BR	6.812	4.695	3.566	-					
B	18.441**	15.805**	12.402**	12.954**	-				
CS	5.538	6.952	5.170	7.121	5.657	-			
M	.792	9.432	4.778	4.369	8.681	2.432	-		
WC	.895	6.988	6.011	10.282**	5.755	.651	4.552	-	
MI	.520	4.231	3.052	1.718	4.346	1.750	2.045	2.597	-
KW	9.894	9.657	4.950	4.404	7.626	3.161	5.528	4.207	1.082

** $P < .05$

Table 4. Chi-square contingency table for EF-4 locus in post larvae and some selected adult populations

	EK	B	BR	WK	VI	BCL 11/76	BCL 3/77	BCL 4/78	EKL 3/14/7
EK	-								
B	18.441**	-							
BR	6.872	12.954**	-						
WK	0.895	5.775	10.282**	-					
VI	2.096	15.805**	4.695	6.988	-				
BCL 11/7/76	6.625	9.269	4.868	4.608	4.992	-			
BCL 3/23/77	2.740	14.319**	6.919	4.616	4.792	5.392	-		
BCL 4/17/78	2.614	7.579	5.093	2.575	3.730	2.248	2.933	-	
EKL 3/14/78	4.873	5.944	4.870	3.926	3.454	2.102	5.419	3.443	-
EKL 3/21/78	1.870	16.766**	2.505	8.196	4.171	5.236	3.127	2.819	6.189

**$P < .05$

between Biscayne Bay juvenile and the Virgin Islands.

Differences in rare allele frequencies were also noted that do not lend themselves to a direct test by the Chi square method. These were the 0.91 allele (EF-4 locus) in post larvae arriving in Florida but not observed in any Florida juvenile or adult population and the 1.05 allele (Pep-D) in three Florida populations but not in the Virgin Islands (Table 1). In the former case this allele was observed in larvae with a frequency of 0.017. The probability of analyzing 412 Florida adults and juveniles and not observing this allele by chance is infinitesimally small. Thus, at least this portion of incoming larvae did not originate in Florida. Other explanations are being explored but appear unlikely.

As for the 1.05 allele in Pep-D, a similar argument can be made. This allele occurred in Florida populations with a frequency of 0.075. The probability of not seeing this allele, assuming it was present, in 42 Virgin Islands animals by chance is also very small.

With these facts, it is possible to make some speculations concerning recruitment of larvae to Florida. First, it is unlikely that Belize is a significant contributor to Florida recruitment. Further if it is assumed that Belize is representative of other Caribbean stocks whose larvae might be carried through the Yucatan Channel then there is little or no contribution from these sources. On the other hand, water circulation directly off Belize may be part of a local gyre mixing little with the main Caribbean water flow passing through the Jamaica and Cayman Islands area. The latter may be more representative of flow from the Lesser Antilles, portions of the Venezuelan coast

Table 5. Chi-square contingency tables comparing zygotic frequencies by population

EM-1 LOCUS

	EK	GB	KW	DT
EK	-			
GB	.001	-		
KW	2.372	2.395	-	
DT	.025	.019	2.051	-
VI	2.960	1.281	7.925**	2.657

PEP-B LOCUS

	VI	DT	KW	B	EK
VI	-				
DT	1.467	-			
KW	.098	.690	-		
B	3.714	.110	5.974**	-	
EK	.062	.071	.008	7.214**	-
BBJ	.154	.205	.557	2.615	.524

PEP-D LOCUS

	KW	DT	BBJ
KW	-		
DT	8.353	-	
BBJ	9.183	1.826	-
VI	4.333	9.888	9.984**

** $P < .05$

and further east as well as the southern coasts of the Greater Antilles. It is essential to obtain animals from such locales as Jamaica, the Caymans, Trinidad, selected areas in the Lesser Antilles, and possibly the Venezuelan coast. Since there are a number of areas in the Caribbean likely to be under the influence of local gyres, they should be assessed as well.

Populations to the north of the Greater Antilles (e.g. Florida and the Bahamas) and the Virgin Islands show a different pattern of relationship. In examining which populations are different at some locus, e.g., Virgin Islands vs most Florida populations, and which show no difference at any loci, e.g., various Bahama populations (one exception, Table 3), it is tempting to speculate a westerly flow of larvae. Although few larvae may be directly transported from the Virgin Islands to Florida, intermediate populations might be greatly contributory to Florida recruitment. Thus larval flow from an area such as the north coast of Cuba to both Florida and the western Bahamas might lead

to similar genetic structure. Geographic locaiton of rare alles such as the 0.91 in the EF 4 locus and 1.05 in the Pep-D locus will go far in clarifying exact relationships.

In summary, although definitive larval recruitment patterns have not yet been fully established, we believe the feasability of the biochemical population genetic approch has. As more enzyme loci are examined in a larger number of populations, the emergence of clear pictures of genetic relationships will occur. We anticipate that these data will allow us to predict probable sources of larvae for not only Florida populations but others as well. In some cases it should be possible to calculate maxima and minima for relative larval contributions to specific populations. All of these data will clearly be useful in establishing the foundation for sound fishery resource management policy of *Panulirus argus.*

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