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Title: AN ANALYSIS OF STOCK SEPARATION IN THE PINK SHRIMP, PANDALUS BOREALIS

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This study investigated whether one continuous interbreeding population of Alaska pink shrimp (Pandalus borealis) occurred from the Bering Sea east to Yakutat Bay. Study areas included: the Eastern Bering Sea; Pavlof Bay, South Alaska Peninsula; Chignik Bay, North Alaska Peninsula; Kodiak Island; and Yakutat Bay, Eastern Gulf of Alaska. Three methods of stock identification were used: the analysis of genetic variation in the enzyme system phosphoglucomutase (PGM) with isoelectric focusing of polyacrylamide gels; the analysis of morphological variation; and the analysis of age and growth differences between study areas.

Bering Sea pink shrimp were distinct morphologically and genetically (based on one locus) from the other study areas. This suggested that Bering Sea shrimp were a separate population or stock. Strong morphological differences between Kodiak Island and Yakutat Bay shrimp suggested that these areas might also be separate breeding populations. Pavlof Bay and Chignik Bay on the Western Alaska Peninsula were not distinct from one another but were different from other study areas. This suggested that together they might make up another population. These findings did not invalidate the current management approach of treating each bay as a separate stock. The results did suggest that, at the least, Kodiak Island, Yakutat Bay, the Bering Sea and probably Western Alaska Peninsula shrimp should be treated as individual breeding units for purposes of management.

AN ANALYSIS OF STOCK SEPARATION IN THE PINK SHRIMP, *PANDALUS BOREALIS*

by

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AN ANALYSIS OF STOCK SEPARATION IN THE PINK SHRIMP, PANDALUS BOREALIS

INTRODUCTION

This study tested the hypothesis that one continuous interbreeding stock of pink shrimp occurred from the Bering Sea east to Yakutat Bay. Five study areas were selected based on recommendations by ADF&G (Kodiak, Alaska) personnel. They included (from east to west):

1. Yakutat Bay, Eastern Gulf of Alaska
2. Kiliuda Bay, Kodiak Island
3. Chignik Bay, North Alaska Peninsula
4. Pavlof Bay, South Alaska Peninsula
5. Eastern Bering Sea

Based on data availability, certain stock delineation criteria (Lackey and Hubert, 1978) were investigated in pink shrimp. The criteria and methods used were:

1. Analysis of genetic variation. Determined if allellic frequencies differed significantly between the five study areas by analyzing genetic variation for two enzyme systems reported to be polymorphic in pink shrimp.

2. Analysis of morphological variation. Determined if significant differences existed between study areas by analyzing morphological characters with univariate and multivariate techniques.

3. Description and comparison of identifiable population attributes. Determined if significant area differences existed in shrimp by analyzing area-specific growth curve constants calculated from area-specific age estimates.

In Alaska, commercial fishing and its associated support facilities are significant contributors to the state's economy. In recent years an increase in fishing vessels, and consequently effort, has caused many of the fish populations to be over-exploited. One such case involved the pink shrimp fishery near Kodiak Island during the 1970's. Populations have continued to decline in western Alaska waters since 1978 despite the fact that the fishery is managed with a

"closed season for biological protection of stocks during critical time periods....[and bay by bay quotas] determined by stock assessment programs" (Balsiger, 1981).

The pink shrimp is the most abundant shrimp species present in the North Pacific and Bering Sea. The greatest concentrations occur in bays and on offshore banks in southwestern Alaska near the Kodiak and Shumagin Island groups and west along the south side of the Alaska Peninsula to Unalaska Island (Alaska Department of Fish and Game [ADF&G], 1977).

Basic life history of the pink shrimp has been investigated throughout its range, including the Pacific (Butler, 1964, 1971, 1980; Ivanov, 1969) and Atlantic Ocean populations (Rasmussen, 1953; Allen, 1959; Haynes and Wigley, 1969). Squires (1968) related environmental features to growth in pink shrimp. Shrimp management techniques, methods of stock assessment, and quantitative year-class analysis have also been reviewed (Frady, 1981). Studies of population dynamics and their relationship to shrimp management strategies (Kutkuhn, 1966; Abramson and Tomlinson, 1972; Gotshall, 1972; Fox, 1972; Geibel and Heimann, 1976) support the argument that precise delineation of unit stocks is required to ensure realistic estimates from contemporary yield models.

Genetic studies of the pink shrimp include Johnson et al. (1974) that used starch gel electrophoresis to separate pink shrimp from four other species of northern Pacific pandalid shrimp. The phosphoglucomutase (PGM) enzyme system was polymorphic for all five species and it was suggested the polymorphism could prove useful in separating breeding groups. To determine if stocks of pink shrimp could be identified, A. Giorgi (unpublished results[1]) used starch gel electrophoresis to analyze muscle protein and 19 enzyme systems in shrimp samples from three bays on Kodiak Island. The PGM enzyme system was polymorphic but the gene frequencies were statistically

[1] A. Giorgi, "Genetic Applications in Shrimp Fisheries Management," report to Alaska Department of Fish and Game, Kodiak, Alaska, February 28, 1978.

inseparable. In addition, leucine aminopeptidase (LAP) was analyzed, but proved to be uninterpretable.

Although there is poor resolution of the protein bands in starch gel electrophoresis, this method is popular because large numbers of samples can be processed quickly (Johnson et al., 1972, 1974; Utter et al., 1974, 1976; Cushing, 1975). In recent years, polyacrylamide gels, somtimes known as gradient pore gels, have been used in other fields of research for high resolution because they separate macromolecules by charge and size. When subjected to the process of isoelectric focusing, these gels fractionate proteins with an equilibrium method based on the isoelectric point, resulting in even higher resolution capabilities. This is distinct in principle from electrophoresis that involves a dynamic separation according to electric charge at particular pH values. Isoelectric focusing applies an electric field to proteins in a pH gradient produced by carrier ampholytes. The process causes the migration of the macromolecules to the regions of their isoelectric pH values where they concentrate in narrow bands. The refined resolution of isoelectric focusing could therefore make it possible to identify polymorphism where starch gel techniques did not (Fawcett, 1968; Shaw, 1969; Leaback and Wrigley, 1976).

From the recent history of the pink shrimp fishery off the coast of Alaska, it was evident that a more precise delineation of shrimp stocks was needed. By better defining the stock units within the geographic range of the pink shrimp, more realistic estimates for yield models could be obtained, and thereby offer a basis for better management.

MATERIALS AND METHODS

Genetic Variation

Pink shrimp were collected and fresh-frozen from Yakutat Bay, Kodiak Island, and the Bering Sea. Collections were made randomly in these areas at several sampling stations during the 1981 ADF&G/National Marine Fisheries Service (NMFS) summer and fall cruise season by ADF&G personnel, the author, and NMFS personnel, respectively (see Appendix A for station samples used).

Initially two tissues and two enzyme systems were analyzed: digestive gland for the LAP system and tail muscle for the PGM system. Shrimp specimens were chosen to represent as many sizes (ages) as possible. Tissue homogenates were prepared at 4°C by diluting the sample in 0.2 M Tris-HCl, pH = 7.0 for LAP and in 0.3 M Tris-HCl, pH = 8.0 for PGM (approximately 1:3, weight to volume). Diluted samples were ground manually in a 10 ml glass homogenizer (modification of Siciliano and Shaw, 1976). Homogenates were cleared by centrifugation (5 min at 5,000 rpm, 4°C). The aqueous phase was decanted and combined with 0.1% bromphenol blue (dye marker) in 10% glycerol (4:1, volume to volume).

Polyacrylamide mini-slab gels (8- x 10- x 0.8-mm) were made by modifying the procedure of Righetti and Drysdale (1976). The gels used an acrylamide to bisacrylamide (N,N'-methylene-bis-acrylamide) ratio of 30:1.2. For LAP, the gel contained 5.1827% polyacrylamide, 12.4585% sucrose, 0.0004% riboflavin, 1.9934% Bio-Lyte 3/5[2], 1.9934% Bio-Lyte 4/6[3], and 0.9967% Bio-Lyte 5/7[4]. To facilitiate polymerization, 0.3322% TEMED (N, N, N', N'-tetramethylethylenediamine) was added and then the gel was placed 10 cm from a UV fluorescent light for 1 hr.

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[2] Narrow range 20% ampholyte solution (Bio-Rad Laboratories, Richmond, California).

[3] Narrow range 40% ampholyte solution (Rio-Rad Laboratories, Richmond, California).

[4] Ibid.

For PGM, the gel contained 5.1827% polyacrylamide, 12.4585% sucrose, 2.4917% Bio-Lyte 5/7, and 2.4917% Bio-Lyte 7/9[5]. In place of riboflavin, 0.0498% ammonium persulphate was used. A 15 min degassing of the ammonium persulphate solution, the addition of 0.3322% TEMED, and 2 min degassing of the gel mixture before adding TEMED, were used to aid polymerization.

Mini-slab gel isoelectric focusing was performed using a mini-slab apparatus purchased from Idea Scientific Company, Corvallis, Oregon. The mini-slab gel, containing wells for 15 samples, was sealed vertically in the apparatus with melted 2% agarose. The gel was electrophoresed using 150 V for 1 hr at 4°C to remove oxidation products (Vesterberg, 1973). For LAP, the anodic and cathodic electrode solutions were 1% acetic acid and 0.2% ethylenediamine. For PGM, they were 1% acetic acid and 1% ethylenediamine (PGM solutions from Sutton and Burgess, 1978).

Following electrophoresis, sample wells #6 through 11 (a total of six samples) were each loaded with 5 µl of dye marker/sample using a 25 µl syringe (the syringe was used in all loadings). Marker proteins, as described by Bours (1973), were placed in adjacent wells for gel to gel comparisons. Sample wells #4 and 12 each contained 10 µl of 0.05% carbonic anhydrase (bovine, Sigma Chemical Co., product no. C-7500) while wells #5 and 13 contained 10 µl of 0.05% myoglobin (equine, Sigma Chemical Co., product no. M-0630 Type I). To aid comparison between study areas, at least one shrimp specimen from Kodiak was included in each gel. The outermost wells were not used for analysis because runs testing for gel homogeneity showed severe drift and streaking in samples applied there.

Isoelectric focusing with fresh anodic and cathodic solutions was done using 100 V at 4°C. Run time for LAP gels was 4.5 to 5 hr; for PGM gels it was 6 hr. Times were determined by observing when bromphenol blue reached the gel bottom.

Focused gels were washed at room temperature in a shaker bath with 3% trichloroacetic acid for a minimum of 12 hr (but not more than 24

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[5] Ibid.

hr) to remove carrier ampholytes that may have interfered with staining reagents (modified from Bours, 1973).

The LAP portions of the gel were placed in a histochemical stain containing 25 ml Tris-maleate buffer (pH = 6.0), 25 ml distilled water, 25 mg Black K salt and 20 mg L-leucine-beta-naphthylamide-HCl (modified from Shaw and Prasad, 1970). The PGM portions of the gel were placed in 50 ml of histochemical stain containing 83.5 mg alpha-D-glucose-1-phosphate (disodium salt with approximately 1% alpha-D-glucose-1,6-diphosphate), 42 mg EDTA, 48 mg histidine hydrochloride, 50 mg $MgCl_2$, 19 mg NADP, 3.5 mg phenazine methosulphate, 4 mg Nitro Blue tetrazolium, 40 units glucose-6-phosphate dehydrogenase, and 0.3 M Tris buffer, pH = 8.0 (modified from Sutton and Burgess, 1978). LAP and PGM gels, in their appropriate stains, were incubated in the dark at 37°C until bands appeared (usually within 24 hr). Gels were fixed by rinsing in distilled water for at least 1 hr.

Because the LAP and PGM histochemical stains were developed for starch gel electrophoresis, purified LAP (porcine, Sigma Chemical Co., product no. L-5006 Type IV-S) and purified PGM (rabbit, Sigma Chemical Co., product no. P-3397) were obtained to test the stains' effectiveness on focused polyacrylamide gels. The possibility that the isoelectric focusing or homogenizing process was inactivating LAP was examined by adding histochemical stain directly to centrifuge tubes containing: purified LAP (eight trials; 5:1, volume to volume); purified LAP with LAP homogenizing solution (five trials; 5:1:3, volume to volume); shrimp homogenate (22 trials using eight different shrimp, 5:1, volume to volume; six trials using two shrimp, 10:3, volume to volume); and shrimp homogenate with purified LAP (two trials using two shrimp; 5:1:3, volume to volume). All tubes were incubated in the dark at 37°C and checked for color changes.

The portions of the gel containing marker proteins (myoglobin and carbonic anhydrase) were stained with the method of Davie (1982). Using 0.25% Coomassie blue G-250 in 45% methanol and 9% acetic acid, the gel was stained for approximately 1 hr in a shaker bath. Destaining was initiated by placing the gel for 24 hr in 25% methanol

and 12.5% acetic acid. Destaining was completed in 7.5% acetic acid and 5% methanol.

Each gel was dried for long term storage by realigning the enzyme and marker protein portions on a plate of plexiglass. A sheet of dialysis membrane (immersed in water) was stretched over the gel and dried under a hood for 24 hr. Bands were identified and allele frequencies noted for each sex by area. Band classification systems developed and used in electrophoresis (e.g., Allendorf and Utter, 1979) and based on isozymes moving a characteristic distance during a fixed time period, were not applicable to isoelectric focusing since the migration distance was not directly time-dependent. Therefore, bands were identified in relation to protein markers and classified beginning with the most anodal band.

A chi-square test of homogeneity was done to determine if allelle frequencies were significantly different between sexes when study areas were combined. If the test was significant, partitioning of chi-square was done to determine which sexes differed. In each area, with sexes combined, a chi-square test of goodness of fit determined whether the phenotypes deviated significantly from a Hardy-Weinberg distribution. Those areas showing Hardy-Weinberg equilibrium were tested for between area differences using a chi-square test of homogeneity. If the test was significant, partitioning of chi-square was used to investigate those differences (Daniel, 1978).

Morphological Variation

Previously collected length and weight data were obtained from the NMFS Kodiak Laboratory for the following areas: Yakutat Bay (1981); Eastern Bering Sea (summer 1978 and 1979): Kodiak Island region (spring 1973, fall 1974, winter 1974 and 1975); and the Shumagin Island region or South Alaska Peninsula district (1973, 1974 and 1976) Previously collected length-frequency (i.e., carapace length-frequency) data were obtained from ADF&G, Kodiak, Alaska, for the following areas; Kiliuda Bay, Kodiak Island region (summer and fall 1979, 1980 and 1981); Chignik Bay (summer and fall 1979, 1980 and 1981); and Pavlof Bay from the South Alaska Peninsula District (summer

and fall 1980, summer 1981). The ADF&G lengthfrequencies were an estimate of area age composition since all ADF&G survey tows from the area of interest were weighted and combined according to tow catch weight. In addition, the length-frequencies incorporated a sexed subsample (representative of area tows) into each area data set so that sex could be extrapolated for the more numerous, unsexed length-frequencies (Jackson, 1979 and 1980). Each ADF&G data set therefore contained sexed length-frequencies indicative of shrimp length-frequency per nautical mile, with the exception of Kiliuda Bay fall 1979, Chignik Bay summer 1979, and Pavlof Bay summer 1980 that were unsexed since no sexed subsamples were available.

Modes, means and medians of length-frequencies and weight-frequencies were determined with each data set for males, transitionals, non-ovigerous females and ovigerous females. After inspection of modes, means, medians and frequency diagrams, it was assumed the individuals came from a normally distributed population. To test the appropriateness of combining sexes within each data set, means of carapace length and then wet weight were compared statistically by sex with one-way analysis of variances. If the F test was significant, the standard errors of the differences between means were computed for pairs of sexes. The number of degrees of freedom assigned to the standard error was determined by a modification of the Satterthwaite approximation (Snedecor and Cochran, 1980). Data by sex were combined accordingly for all data sets to make results consistent and comparable.

For the males and females, a one-way analysis of variance was also used to analyze for differences between 1981 study areas. The 1981 data sets were chosen since they were the most numerous and because the analysis of genetic variation was done on shrimp samples from that year. Groups with fewer than 10 individuals were not included in the analysis. Comparison of means was done as previously described with Hotelling's T^2 statistic (Morrison, 1976) also being computed to compare the mean vector (containing mean carapace length, total length if available, and wet weight) from one study area, to the mean vector of variables from another area. The ADF&G length-frequency data sets

were excluded from this portion of the analysis since their content was inappropriate.

Length and weight data were also obtained from samples acquired in the 1981 NMFS and ADF&G cruise season for the Northeast Alaska Peninsula, Kodiak Island, Yakutat Bay and the Bering Sea. Using a Mettler balance, specimens were weighed to the nearest 0.05 g. Fresh specimens measured at sea (Kodiak Island and Northeast Alaska Peninsula) were weighed to the nearest 0.1 g. Weights at sea were not taken if the balance fluctuated more than 0.5 g. Dial vernier calipers were used to measure carapace length and total body length to the nearest 0.5 mm. Carapace length was defined to be from the posterior margin of the eye socket to the posterior middorsal margin of the carapace. Total body length was defined to be from the posterior margin of the eye socket to the posterior tip of the telson, excluding spines. The total body length measurement (anterior tip of rostrum to posterior tip of telson) used by Butler (1964) and Haynes and Wrigley (1969) was not suitable due to the high incidence of damaged rostrums.

For Kodiak Island the author obtained length-weight measurements from both fresh and frozen specimens (the latter were thawed and drained before measuring). For Yakutat Bay and the Bering Sea, only frozen specimens were available for length-weight measurements. To check for differences between fresh and frozen specimens, nine groups of usually 40 individuals with both fresh and frozen measurements recorded, were compared. Means of carapace length, total body length and wet weight were analyzed for differences. Sexes were combined for analysis due to small sample size. Initially, equality of variances was tested. If variances were equal ($\alpha = 0.05$), the comparison of means of two independent samples and it's pooled variance were used. A paired sample test was not appropriate because a given group (e.g., 40 individuals) was intermixed during the freezing process so that fresh and frozen measurements did not correspond. For unequal variances, a t-test with the Satterthwaite approximation for number of degrees of freedom was used (Snedecor and Cochran, 1980).

For the Yakutat Bay, Kodiak Island, Shumagin Island, and Bering Sea length-weight data sets, log wet weight to log carapace length and wet weight to carapace length regressions were computed for each sex grouping. Additional regressions computed for the fresh Kodiak data set included log wet weight to log total length; wet weight to total length; and carapace length to total length. The log transformations were used to assist in linearizing the length and weight variables (Ricker, 1975).

The log wet weight to log carapace length regressions within the same study area (but from different data sets) were compared with the following method to test for differences through time and/or between data sets. Regression lines were computed separately for each data set (the full model). Data sets within an area were combined and the regression lines computed (the reduced model). The reduced model was then tested against the full model to determine if there were significant differences (Neter and Wasserman, 1974). Steel and Torrie's (1960) modification for three or more data sets was used to analyze the Kodiak Island data.

The frozen specimens collected from Yakutat Bay, Kodiak Island, and the Bering Sea had ten additional morphological (metric) characters measured using vernier calipers. They included: maximum width of carapace; maximum width of first abdominal segment posterior to carapace; length of rostrum (from posterior edge of eye orbit to anterior tip of rostrum); length of telson (from base at dorsal margin to posterior tip, excluding spines); length of outer uropod (excluding basal joint); maximum width of outer uropod (excluding basal joint); anterior-dorsal length of antennal scale (to anterior tip of lamella or spine, whichever was the most distal, and excluding basal joint); maximum width of antennal scale (excluding basal joint); maximum length of merus of third pereiopod along extensor edge; and maximum length of carpus of third pereiopod along extensor edge. In addition, three nonmetric characters were noted: the presence or absence of sternal spines in female specimens (McCrary, 1971); the presence or absence of Bopyroides hippolytes, a parasitic branchial isopod (Butler, 1980); and the presence or absence of egg cases,

usually 1 mm in length (species unknown), on the antennal scale and rostrum surfaces. A measurement was not recorded if the body part appeared damaged or regenerated. Unless missing, appendages of the animal's right side were always measured in preference to the left. All metric characters were measured to the nearest 0.2 mm with the exception of maximum width of carapace and maximum width of first abdominal segment which were measured to the nearest 0.5 mm. All characters were chosen for their repeatability.

To determine if multivariate discriminant function analysis was appropriate using the Yakutat Bay, Kodiak Island and Bering Sea data sets of morphological characters (i.e., were the areas different), a one-way analysis of variance on each character was done within each sex grouping to compare study areas. In addition, for each sex Hotelling's T^2 statistic (Morrison, 1976) compared the mean vector of metric variables from one study area to the mean vector of metric variables from another area.

Stepwise discriminant function analysis (SDFA), with the selection criterion of minimizing Wilks' Lambda (a measure of separation), was done using the subprogram DISCRIMINANT in the Statistical Package for the Social Sciences (SPSS). SDFA was done for each sex and then all sexes together to determine which (and how many) metric variables were important in discriminating between areas. Total length was excluded from SDFA because Pimentel (1974) suggested avoiding the use of measurements in combination with some of its parts (e.g., rostrum length, carapace length, telson length) since the best set of descriptive variables are linearly independent. The discriminating variables' effectiveness or the ability to separate areas was determined by noting: the number of significant discriminant functions; the overall Wilks' Lambda statistic; the results of testing pairs of groups (areas) for differences after SDFA; and the percentage of individuals correctly classified into regions, using their values from the discriminating variables. Cases were plotted along the two discriminant functions with their group centroids to better visualize separation between groups (Nie et al., 1975).

For nonmetric variables, the proportion of sample with a nonmetric characteristic (i.e., presence of parasitic isopods or presence of antennal scale eggs) was determined for each of the study areas. The z statistic was used to test for significant differences between study area proportions (Dixon and Massey, 1969). In females, the mean and modal carapace length at which sternal spines were present (i.e., females spawning for the first time) was also noted for each area.

Variation in Age and Growth

The sexed length-frequency distributions (LFD's) obtained from ADF&G for Kiliuda Bay, Chignik Bay, and Pavlof Bay were plotted to assign age classes. Four methods of plotting were used: the standard Petersen method (Tesch, 1971); the Petersen method applied to each sex (male, transitional and female) separately; the deviation method where each LFD was subtracted from a mean LFD (computed for a particular time period from several years of data) (Skúladóttir, 1981); and the deviation method applied to each sex and plotted separately (i.e., a mean LFD was computed for each sex and subtracted accordingly). ADF&G personnel (Kodiak, Alaska) also assigned age classes to the data and provided aging information that was incorporated into the analysis to help ensure reasonable age estimates.

To estimate whether growth rates were comparable between year-classes, age in years was plotted against carapace length. For each time period, carapace lengths for designated age groups of each study area were analyzed for differences using the Friedman two-way analysis of variance by ranks, where blocks were age and treatments were area. When differences were significant, the multiple comparison procedure of the Friedman test was used (Daniel, 1978).

From the age-length data, the FORTRAN computer program BGC II (Abramson, 1971) was used to calculate Von Bertalanffy growth curves and constants for each study area (Gotshall, 1972). These results were compared to P. borealis growth curve constants reported by Anderson (1981) for Pavlof Bay and Fox (1972) for bays of Kodiak Island.

RESULTS

Genetic Variation

The LAP histochemical stain applied to focused gels containing shrimp samples did not show the necessary color change to dark purple indicative of enzyme activity (Beckman et al., 1964). The stain was effective on gels when samples contained purified porcine LAP. Experiments in which stain was applied directly to homogenate had negative results except when purified LAP was present. Therefore, it was concluded the P. borealis specimens had no LAP activity.

The PGM enzyme system in P. borealis showed polymorphism for three alleles. One and two-banded phenotypes were observed (Fig. 1). Allele frequencies were tabulated, assuming random combination of alleles and a monomeric structure (Utter et al., 1974). Tests for allellic differences between sexes were significant at $\alpha = 0.01$ (Table 1). An interesting trend noted for all areas combined was, that as the shrimp aged (changed from male to female), the frequency of the A band allele decreased while the B band allele increased. With sexes combined, only Uganik Bay (Kodiak Island) deviated significantly from Hardy-Weinberg expected values (possibly due to sample size). Consequently, the Uganik Bay data were not included in tests of area differences. Tests of homogeneity for all sexes combined showed allellic frequencies of the Bering Sea to be significantly different ($\alpha = 0.05$) from Outer Marmot Bay (Kodiak Island). Among females, Bering Sea allellic frequencies were different from Yakutat Bay and Outer Marmot Bay ($\alpha = 0.10$).

Morphological Variation

Modes, means, medians and frequency diagrams of carapace length and wet weight (when available), for each data set by sex, revealed no extreme departure from normality. One-way analysis of variances to test the appropriateness of combining sexes within data sets, showed few nonsignificant differences. Those means not significantly different usually resulted from small sample sizes that ultimately

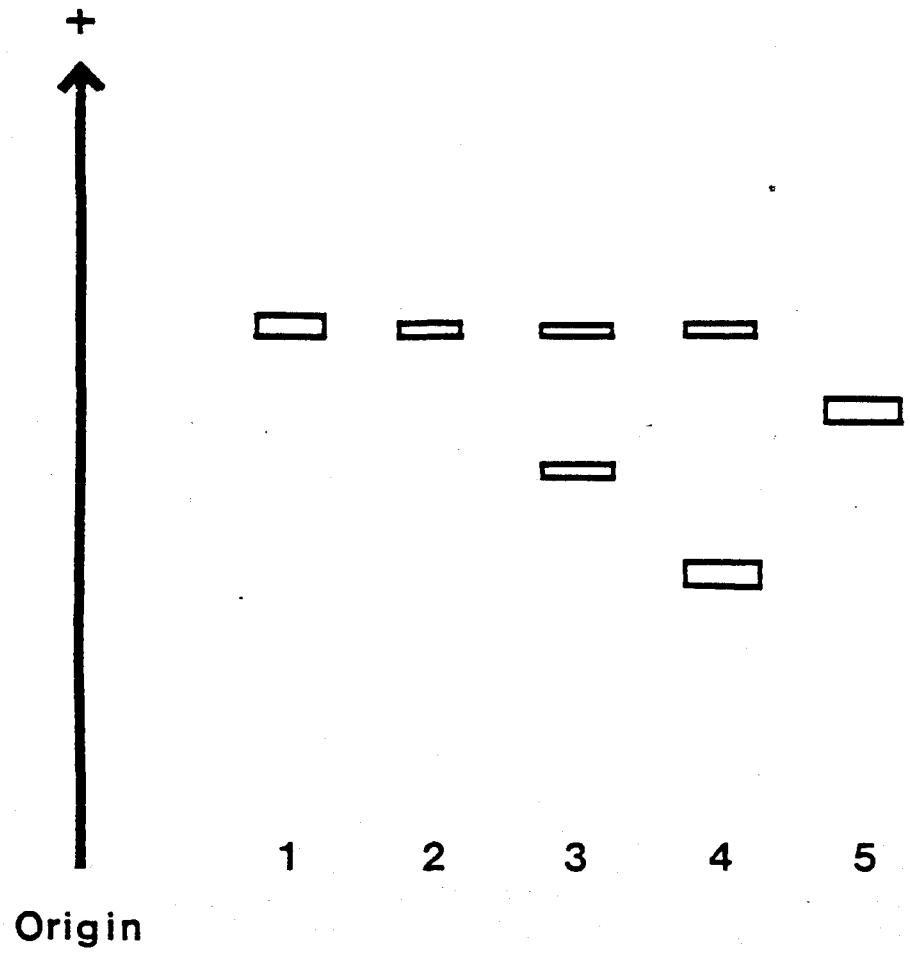

Figure 1. Results of polyacrylamide isoelectric focusing in pink shrimp (Pandalus borealis) from the northeastern Pacific Ocean (1981). Representation of the observed phosphoglucomutase (PGM) phenotypes in relation to the marker proteins carbonic anhydrase and myoglobin (not to scale). 1) Myoglobin, equine; 2) PGM band A; 3) PGM bands A and B; 4) PGM bands A and C; 5) Carbonic anhydrase, bovine.

Table 1. Differences in PGM allellic frequencies for the pink shrimp (Pandalus borealis) by sex and by 1981 study area (* significant at $\alpha = 0.05$; ** significant at $\alpha = 0.01$). Sexual stages included: males; the transitional phase between males and females; females; and the head roe phase among females in which eggs had not yet descended to the pleopods. Study areas of 1981 included the Bering Sea, Yakutat Bay and two bays of Kodiak Island (Outer Marmot and Uganik).

	n	Allellic frequencies A	B	C	d.f.	X^2
All Areas Combined						
1) Male	94	0.915	0.074	0.011		
2) Transitional	26	0.923	0.077	--		
3) Female	84	0.631	0.357	0.012		
4) Female with head roe	68	0.500	0.485	0.015		
5) All females	152	0.572	0.415	0.013		
Test of homogeneity in 1,2,3, and 4					6	43.77**
Test of homogeneity in 1,2, and 5					4	40.52**
All Sexes Combined						
1) Bering Sea	51	0.804	0.196	--	1[1]	3.03
2) Yakutat Bay	36	0.722	0.278	--	3[1]	5.32
3) Outer Marmot Bay (Kodiak Island)	36	0.667	0.292	0.041	3[1]	7.50
4) Uganik Bay (Kodiak Island)	13	0.577	0.423	--	1[1]	6.98**
5) Outer Marmot Bay and Uganik Bay	49	0.643	0.326	0.031	3[1]	15.12**
Test of homogeneity in 1,2, and 3					4	10.28*
Test of homogeneity in 2 and 3					2	3.18
Test of homogeneity in 1 and 2					1	1.59
Test of homogeneity in 1 and 3					2	6.95*

Table 1. Continued

	n	Allellic frequencies A	B	C	d.f.	X^2
Sexes and Areas Separate						
Males						
1) Bering Sea	36	0.944	0.056	--		
2) Yakutat Bay	20	1.000	--	--		
3) Outer Marmot Bay (Kodiak Island)	32	0.844	0.125	0.031		
Test of homogeneity in 1, 2, and 3					4	5.11
Transitionals						
1) Bering Sea	18	0.944	0.056	--		
2) Yakutat Bay	4	1.000	--	--		
3) Outer Marmot Bay (Kodiak Island)	4	0.750	0.250	--		
Test of homogeneity in 1, 2, and 3					2	2.12
Females						
1) Bering Sea	22	0.818	0.182	--		
2) Yakutat Bay	48	0.583	0.417	--		
3) Outer Marmot Bay (Kodiak Island)	12	0.500	0.417	0.083		
Test of homogeneity in 1, 2, and 3					4	9.90*
Test of homogeneity in 2 and 3					2	4.12
Test of homogeneity in 1 and 2					1	3.69
Test of homogeneity in 1 and 3					2	5.45
Females with Head Roe						
1) Bering Sea	26	0.500	0.500	--		
2) Outer Marmot Bay (Kodiak Island)	24	0.500	0.458	0.042		
Test of homogeneity in 1 and 2					2	0.20

Table 1. Continued

	n	Allellic frequencies A	B	C	d.f.	X^2
All Females						
1) Bering Sea	48	0.646	0.354	--		
2) Yakutat Bay	48	0.583	0.417	--		
3) Outer Marmot Bay (Kodiak Island)	36	0.500	0.444	0.056		
Test of homogeneity in 1, 2, and 3					4	6.49

[1] Degrees of freedom in chi-square goodness of fit test for Hardy-Weinberg distribution.

reduced the degrees of freedom. Therefore, four sex groupings (when sufficient data were available) were used in subsequent analyses.

None of the nine groups used to check for differences between fresh and frozen specimens showed a significant difference in their mean carapace length, total length or wet weight (Appendix B). It was therefore assumed that data from fresh and frozen specimens could be analyzed together.

The comparison of log carapace length to log wet weight regressions within study areas for examining variability and differences through time, showed highly significant differences (α = 0.01) for almost all sex groupings (Table 2). Females in Yakutat Bay and the Bering Sea were not significantly different.

Because there was considerable variability within study areas and through time (see also Fig. 2, Kodiak Island and Fig. 3, Chignik Bay), it was concluded comparisons of study areas should be made only between survey data sets of the same year. Males of the 1981 data sets showed no pattern (e.g., east to west) when comparing corresponding mean carapace lengths, total lengths and wet weights (Table 3). Females from the data sets were more different from one another but showed some similarities within the Chignik data sets and the Kodiak data sets (Table 4). The females of Yakutat also showed much in common with females of the Chignik data sets.

The multivariate T^2 tests were computed using 1981 mean carapace length, total length and wet weight (Table 5). All data sets showed significant differences among females, while among males, the only data sets not significantly different from one another were Kodiak and the Northeast Alaska Peninsula.

The similarity betwen Kodiak and Northeast Alaska Peninsula carapace length/weight data sets (at least among males), and the fact they were non-randomly sampled (i.e., they were selected to represent as many length classes as possible) made it inappropriate to conclude that differences existed with such tests. Consequently, the fresh specimen data for the two regions were combined before length-weight regressions were computed for the Kodiak Island area (Table 6). Individual regression equations were computed for males, females and

Table 2. Tests for differences in log carapace length (x) to log wet weight (y) regressions for the pink shrimp (Pandalus borealis) within the Bering Sea, Yakutat Bay, and Kodiak Island data sets, 1973-1981 (** significant at $\alpha = 0.01$). Source of data set (in parentheses) follows year of collection. Sexual stages included males, a transitional phase between males and females, females, and ovigerous or gravid females.

Area	n1	n2	n3	n4	n5	F
Bering Sea						
1) 1978/79 (NMFS) 2) 1981 (Author)						
Male	170	239				13.08**
Female	206	252				2.43
Yakutat Bay						
1) 1981 (NMFS) 2) 1981 (Author)						
Male	53	265				95.39**
Transitional	83	21				34.71**
Female	6	346				1.97
Kodiak Island						
1) Spring 1973 (NMFS) 2) Fall 1974 (NMFS) 3) Winter 1974 (NMFS) 4) Winter 1975 (NMFS) 5) 1981-Fresh (Author)						
Male	64	267	21	55	501	60.67**
1) Spring 1973 (NMFS) 2) Winter 1975 (NMFS) 3) 1981-Fresh (Author)						
Transitional	3	12	5			32.74**

Table 2. Continued

Area	n_1	n_2	n_3	n_4	n_5	F
1) Spring 1973 (NMFS)						
2) Fall 1974 (NMFS)						
3) Winter 1975 (NMFS)						
4) 1981-Fresh (Author)						
Female	161	7	13	1218		374.82**
1) Fall 1974 (NMFS)						
2) Winter 1974 (NMFS)						
3) Winter 1975 (NMFS)						
4) 1981-Fresh (Author)						
Ovigerous Female	46	64	58	23		7.40**

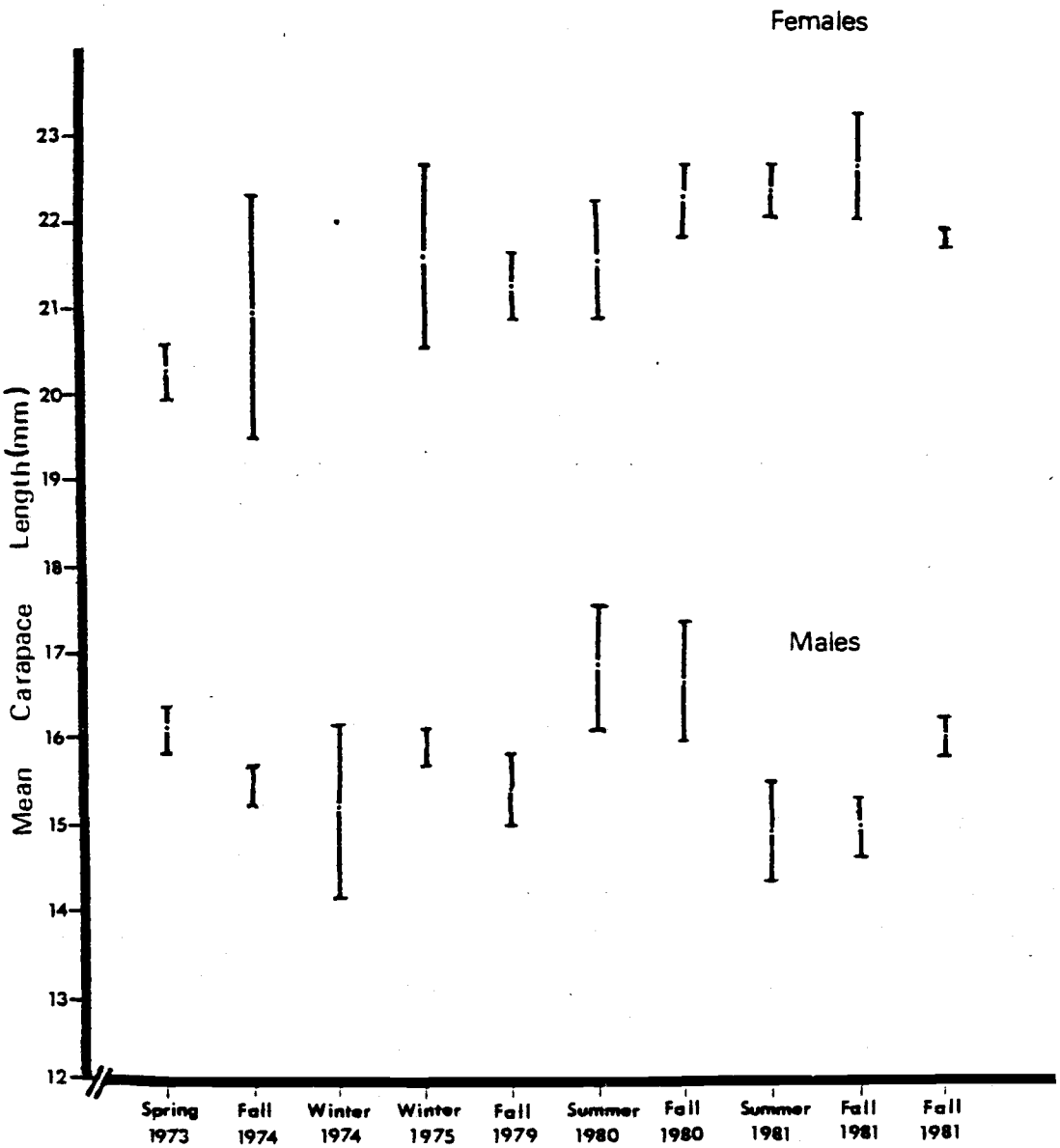

Figure 2. Differences in mean carapace length of pink shrimp (Pandalus borealis) from the Kodiak Island area (± 2 SE). Data were obtained from NMFS (1973-1975) and ADF&G (1979-1980). Summer 1981 and fall 1981 at left refer to the ADF&G data; fall 1981 at right refers to data collected by author.

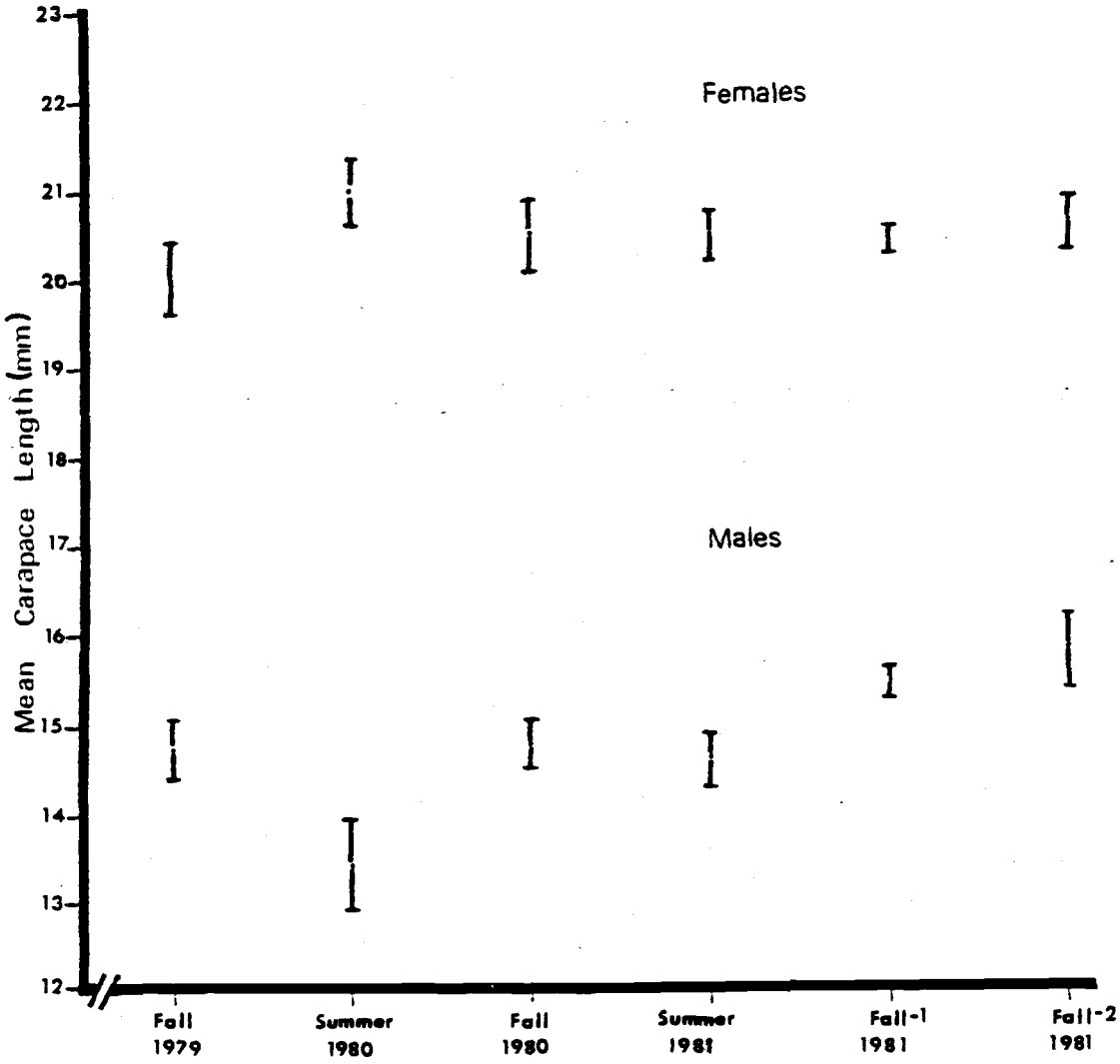

Figure 3. Differences in mean carapace length of pink shrimp (Pandalus borealis) from Chignik Bay (± 2 SE). Data were obtained from ADF&G (1979-1981).

Table 3. Comparison of mean carapace length (C), total length (T) and wet weight (W) in pink shrimp (Pandalus borealis) males for 1981 data sets ('–' refers to significant difference at $\alpha = 0.05$; '+' refers to nonsignificant difference at $\alpha = 0.05$). Data sets are arranged from most eastern (Yakutat) to most western (Bering Sea).

		Yakutat (NMFS)	Yakutat (author)	Kodiak (fresh)	Kodiak (summer)	Kodiak (fall)	Kodiak (frozen)	N.E. Ak. Penin.	Chignik (summer)	Chignik (fall-1)	Chignik (fall-2)	Pavlof (summer)	Bering Sea
Yakutat (NMFS)	C	+	–	–	–	–	–	+	–	–	+	–	+
	T	+											
	W	+	+	–			+	+					–
Yakutat (author)	C		+	–	+	+	+	+	–	+	+	–	–
	T		+	–			–	+					–
	W		+	–			–	+					–
Kodiak (fresh)	C			+	–	–	+	+	–	+	+	–	+
	T			+			+	+					–
	W			+			+	+					–
Kodiak (summer)	C				+	+	–	+	+	+	–	+	–
	T				+								
	W				+								
Kodiak (fall)	C					+	–	+	+	+	–	+	–
	T					+							
	W					+							
Kodiak (frozen)	C						+	+	–	+	+	–	+
	T						+	+					–
	W						+	+					–

Table 3. Continued

		Yakutat (NMFS)	Yakutat (author)	Kodiak (fresh)	Kodiak (summer)	Kodiak (fall)	Kodiak (frozen)	N.E. Ak. Penin.	Chignik (summer)	Chignik (fall-1)	Chignik (fall-2)	Pavlof (summer)	Bering Sea
N.E. Ak. Penin. (author)	C							+	+	+	+	+	+
	T							+					+
	W							+					+
Chignik (summer)	C								+	+	+	+	-
	T								+				
	W								+				
Chignik (fall-1)	C									+	+	-	+
	T									+			
	W									+			
Chignik (fall-2)	C										+	-	+
	T										+		
	W										+		
Pavlof (summer)	C											+	-
	T											+	
	W											+	
Bering Sea	C												+
	T												+
	W												+

Table 4. Comparison of mean carapace length (C), total length (T) and wet weight (W) in pink shrimp (Pandalus borealis) females for 1981 data sets ('–' refers to significant difference at $\alpha = 0.05$; '+' refers to nonsignificant difference at $\alpha = 0.05$). Data sets are arranged from most eastern (Yakutat) to most western (Bering Sea).

		Yakutat (author)	Kodiak (fresh)	Kodiak (summer)	Kodiak (fall)	Kodiak (frozen)	N.E. Ak. Penin.	Chignik (summer)	Chignik (fall-1)	Chignik (fall-2)	Pavlof (summer)	Bering Sea
Yakutat (author)	C	+	–	–	–	–	–	+	+	+	+	–
	T	+	–			–	–					–
	W	+	–			–	–					–
Kodiak (fresh)	C		+	–	–	+	–	–	–	–	–	–
	T		+			–	–					–
	W		+			–	–					–
Kodiak (summer)	C			+	+	–	–	–	–	–	–	+
	T			+								
	W			+								
Kodiak (fall)	C				+	–	–	–	–	–	–	+
	T				+							
	W				+							
Kodiak (frozen)	C					+	+	–	–	–	–	–
	T					+	–					–
	W					+	–					–
N.E. Ak. Penin.	C						+	–	–	–	–	–
	T						+					–
	W						+					–

Table 4. Continued

		Yakutat (author)	Kodiak (fresh)	Kodiak (summer)	Kodiak (fall)	Kodiak (frozen)	N.E. Ak. Penin.	Chignik (summer)	Chignik (fall-1)	Chignik (fall-2)	Pavlof (summer)	Bering Sea
Chignik (summer)	C							+	+	+	+	-
	T							+				
	W							+				
Chignik (fall-1)	C								+	+	+	-
	T								+			
	W								+			
Chignik (fall-2)	C									+	+	-
	T									+		
	W									+		
Pavlof (summer)	C										+	-
	T										+	
	W										+	
Bering Sea	C											+
	T											+
	W											+

Table 5. Value and significance of Hotelling's T^2 statistic testing for mean vector differences between 1981 data sets of male (M) and female (F) pink shrimp (Pandalus borealis). Mean vector of each study area included a mean value for wet weight (g) total length (mm) and carapace length (mm). Total length was not available and therefore not included in mean vector differences involving Yakutat (NMFS).

	Yakutat (NMFS)		Kodiak (frozen)		Kodiak (fresh)		N.E. Ak. Penin.		Bering Sea (author)	
	M	F	M	F	M	F	M	F	M	F
Yakutat (author)										
T^2	160.8	small	141.2	731.6	67.4	457.6	29.7	112.4	713.2	1558.6
F	80.15	sample	46.83	243.11	22.4	152.31	9.84	37.30	236.77	517.79
P	<0.0001	size	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Yakutat (NMFS)										
T^2			257.2	small	85.1	small	128.2	small	307.0	small
F			127.97	sample	42.49	sample	63.25	sample	152.97	sample
P			<0.0001	size	<0.0001	size	<0.0001	size	<0.0001	size
Kodiak (frozen)										
T^2					20.1	150.6	7.6	227.8	134.2	223.1
F					6.69	50.12	2.49	75.59	44.51	74.10
P					0.0002	<0.0001	0.0623	<0.0001	<0.0001	<0.0001
Kodiak (fresh)										
T^2							3.0	56.0	375.7	738.1
F							0.99	18.64	124.87	245.66
P							0.3976	<0.0001	<0.0001	<0.0001
N.E. Ak. Penin.										
T^2									84.9	811.4
F									28.08	269.17
P									<0.0001	<0.0001

Table 6. Length-weight and length-length regression equations for the Fall 1981 Kodiak and Northeast Alaska Peninsula pink shrimp (Pandalus borealis).

x	y	Regression Equation	r
Males:			
(n = 506)			
Log total length	Log wet weight	y = 3.0168 x - 4.9838	0.9587
Log carapace length	Log wet weight	y = 2.7647 x - 2.8917	0.9552
Carapace length	Total length	y = 3.3722 x + 8.6422	0.9492
Females:			
(n = 1218)			
Log total length	Log wet weight	y = 2.9282 x - 4.7947	0.9678
Log carapace length	Log wet weight	y = 2.9705 x - 3.1430	0.9456
Carapace length	Total length	y = 3.6261 x + 4.4997	0.9100
Ovigerous Females:			
(n = 23)			
Log total length	Log wet weight	y = 2.5677 x - 4.0637	0.9147
Log carapace length	Log wet weight	y = 2.9085 x - 3.0716	0.9120
Carapace length	Total length	y = 3.6185 x + 1.5702	0.8742

ovigerous females. Transitionals (where n = 5) were pooled with males since a comparison of means of two independent samples revealed no significant differences ($\alpha = 0.05$). In addition, log carapace length to log wet weight regressions were computed from Yakutat Bay, Bering Sea, and Shumagin Island length-weight data sets (Appendix C).

The Yakutat Bay, Kodiak Island, and Bering Sea length-weight data sets that also contained data for 13 additional metric and nonmetric characters, were initially examined to determine if the areas differed. An analysis of variance for each metric character within each sex grouping showed significant differences in all male characters ($\alpha = 0.01$) except for rostrum length and two pereiopod measurements (Appendix D). For transitionals, between area differences were not statistically significant (Appendix E), while in females all variables showed significant differences between areas (Appendix F). No ovigerous females occurred in the Yakutat Bay data set, therefore, no analysis was done for that sex grouping.

Hotelling's T^2 statistic was also used to test for between area differences in the metric/nonmetric data sets (Appendix G). By including 13 metric characters in the mean vector, however, very small sample sizes resulted since few uninjured specimens had been available for all 13 measurements. Where reasonable sample sizes did occur (e.g., no less than five individuals), the T^2 statistic was always significant. It was concluded that the male and female data sets differed between areas and therefore were appropriate for discriminant function analysis.

As with the T^2 statistic, SDFA used only those individuals having a complete set of measurements for variables in the analysis. Therefore, an initial SDFA run with 12 metric variables (excluding total length) was used on males, females and all sexes to determine which variable was least important in discriminating groups (determined by lowest F value). This variable was eliminated in the subsequent run and resulted in an increased number of eligible individuals. The two-step procedure was repeated until the number of cases reached a reasonable size (at least 10% of the original data set). The number of discriminating variables was always kept at a

maximum since this improved separation between groups (i.e., decreased Wilks' Lambda). For males, 98 cases (10.6%) were used in SDFA with five discriminating variables. For females, 469 cases (44.4%) were used with eight discriminating variables. For all sexes, 664 cases (30.4%) were used with 10 discriminating variables. Figures 4, 5, and 6 show plots along the two discriminant functions obtained for males, females, and all sexes respectively.

The contribution of the various morphological characters in discriminating between areas showed dramatic differences between sex groups (Table 7). For the SDFA of males, only one discriminant function (Table 8) was statistically significant. Therefore among males, only two areas, Yakutat Bay and Kodiak Island, were completely distinguishable from one another (see Fig. 4 and F values of Table 9). For that function, merus length, abdominal segment width and uropod width were the most important discriminating variables. For females, the most important discriminating variables were carapace length and wet weight for the first discriminant function, while telson length and uropod length were the most important contributors for the second function. Both functions were statistically significant (Table 8) as exhibited by the fact that after completion of SDFA all pairs of regions showed highly significant differences (Table 9). The two significant discriminant functions computed for sexes combined (Table 8) showed carapace width, uropod width, carapace length and merus length to be meaningful contributors for the first function while telson length was the most important discriminating variable in the second function (Table 7).

When each sex grouping had individuals classified according to their values from discriminating variables, good results (i.e., relatively high percentages correctly classified) were obtained (Table 10). However, with only one significant discriminant function in males, the percentage correctly classified would have been greatly reduced if the Bering Sea sample size had been larger.

For females and sexes combined, the discriminant functions showed good separation abilities for three regions. In addition to the classification results, this was evidenced by two significant

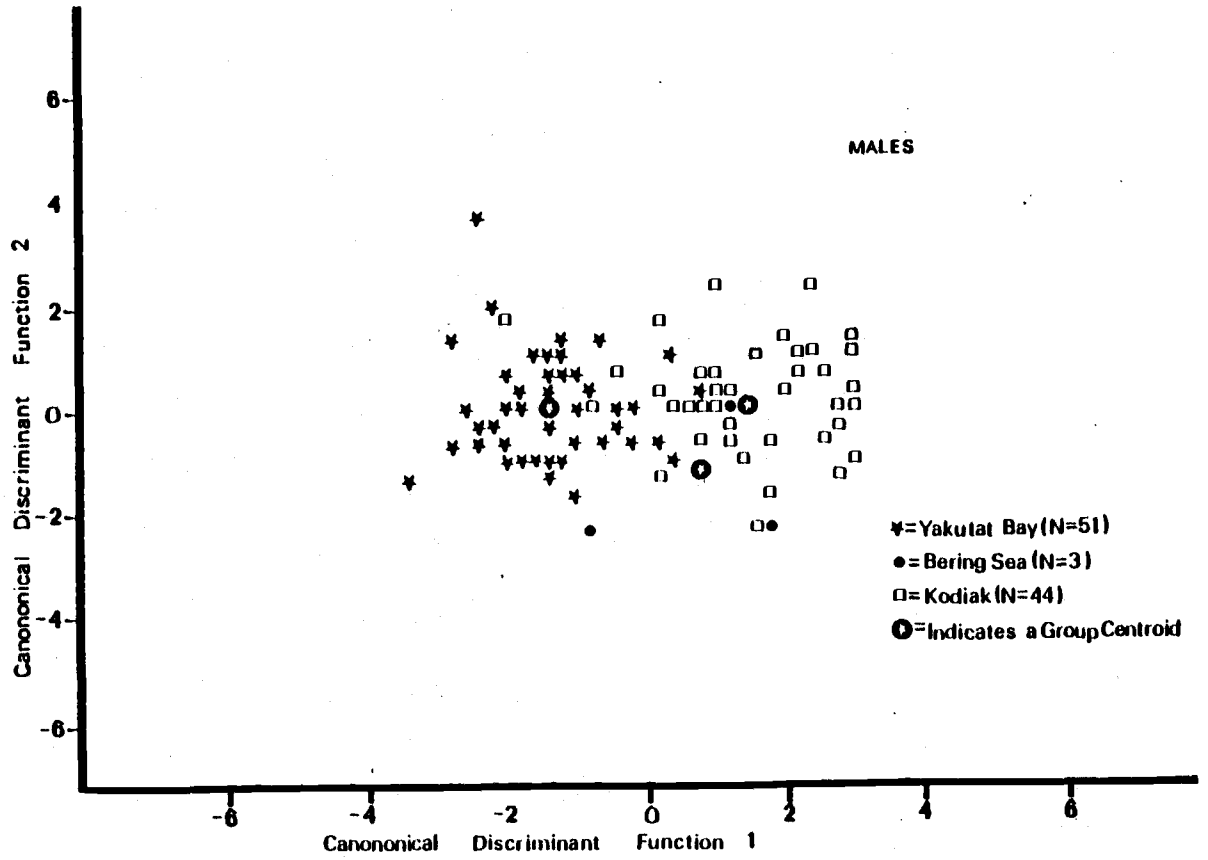

Figure 4. Results from discriminant function analysis of pink shrimp (Pandalus borealis) males collected in 1981. Scatterplot shows morphological differences in pink shrimp (i.e., by separating them into groups based on their values in the discriminating variables) for Yakutat Bay and Kodiak Island.

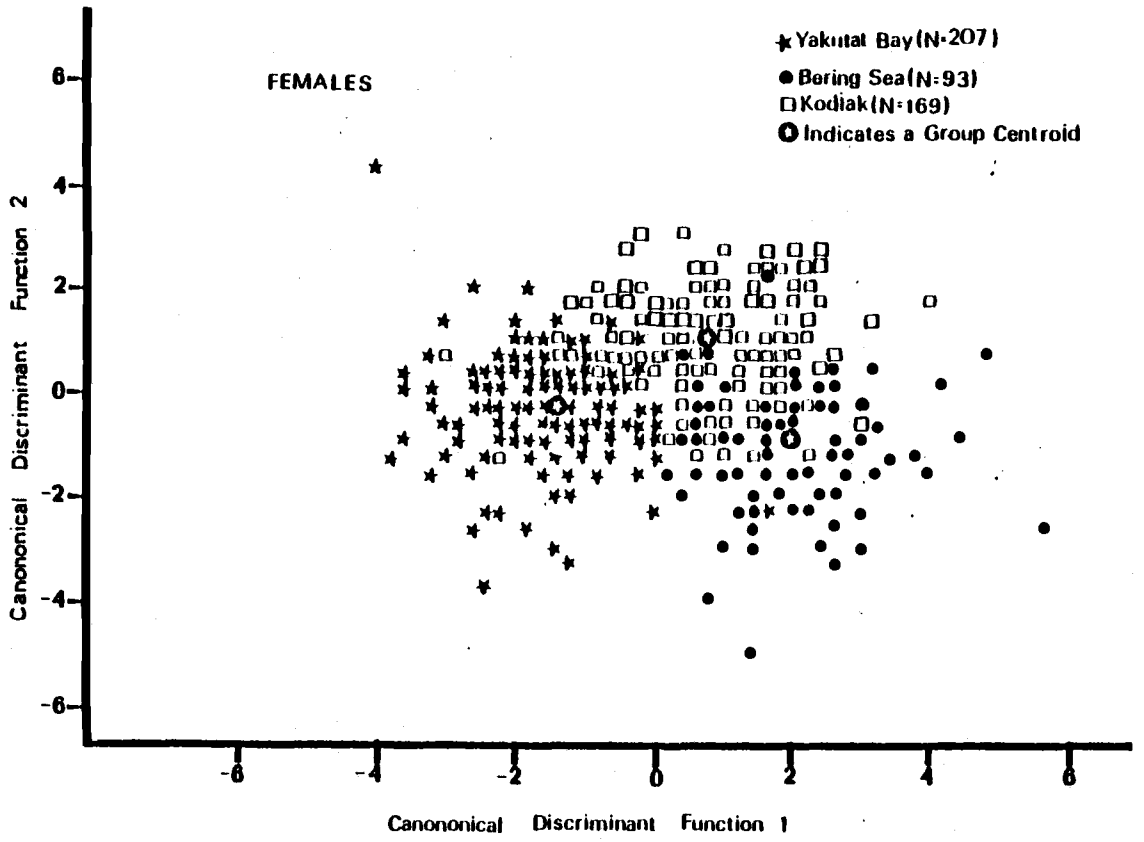

Figure 5. Results from discriminant function analysis of pink shrimp (Pandalus borealis) females collected in 1981. Scatterplot shows morphological differences in pink shrimp (i.e., by separating them into groups based on their values in the discriminating variables) for Yakutat Bay, the Bering Sea and Kodiak Island.

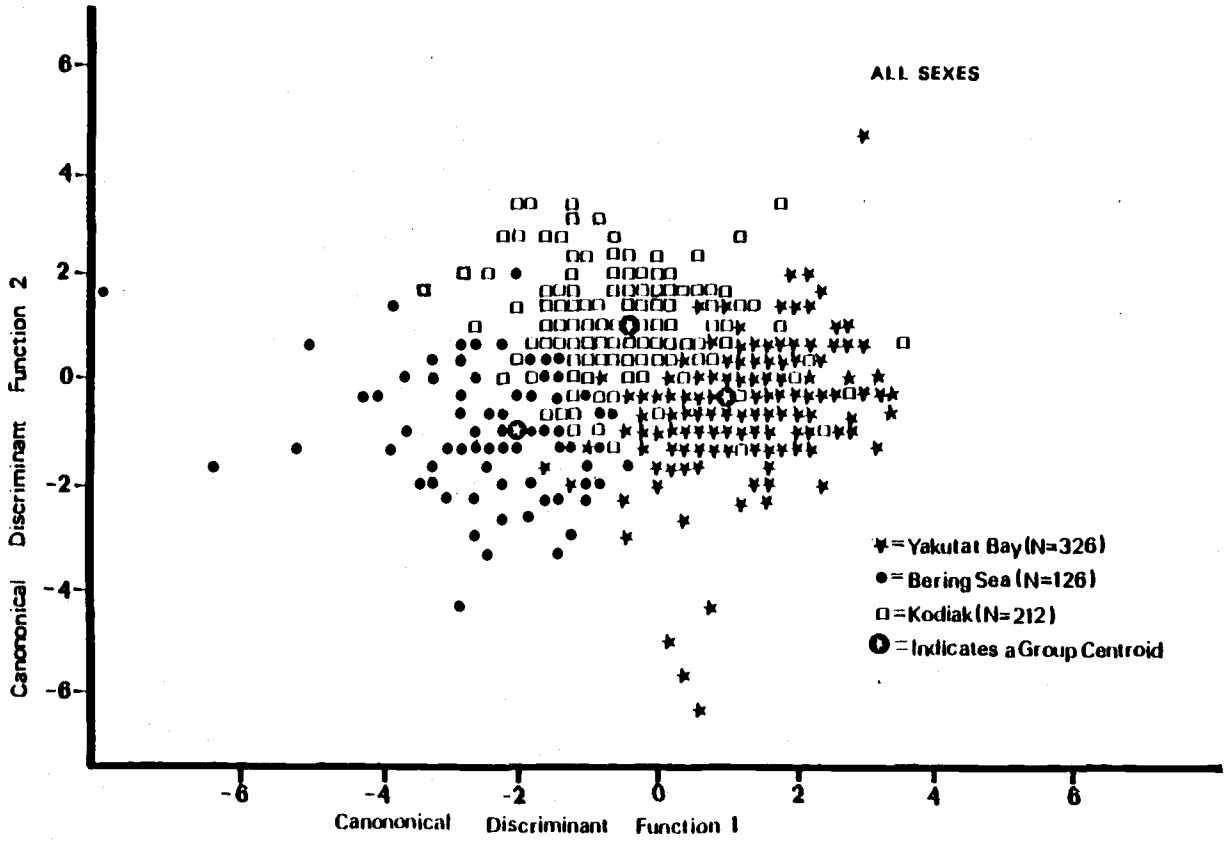

Figure 6. Results from discriminant function analysis of pink shrimp (Pandalus borealis) combined sexes collected in 1981. Scatterplot shows morphological differences in pink shrimp (i.e., by separating them into groups based on their values in the discriminating variables) for Yakutat Bay, the Bering Sea and Kodiak Island.

Table 7. Contribution of various morphological characters in discriminating between Yakutat Bay, Kodiak Island and the Bering Sea as determined by SDFA on pink shrimp (Pandalus borealis) males, females, and all sexes combined (1981).

Characters (in the order added by DISCRIMINANT)	Wilks' Lambda	P	Standardized Canonical Discriminant Functions	
			Funct. 1	Funct. 2
MALES:				
First abdominal segment width	0.7962	< 0.0001	1.1419	0.7318
Merus length pereiopod 3	0.4349	< 0.0001	-1.7315	1.9038
Uropod width	0.3496	< 0.0001	1.0340	0.3675
Rostrum length	0.3262	< 0.0001	-0.3900	-0.4285
Uropod length	0.3147	< 0.0001	0.0671	-2.2376
FEMALES:				
Wet weight	0.6369	< 0.0001	1.2153	0.6794
Carapace length	0.4639	< 0.0001	-2.2415	0.6252
Telson length	0.3273	< 0.0001	0.4826	-1.4029
First abdominal segment width	0.2728	< 0.0001	0.4238	0.4343
Uropod width	0.2499	< 0.0001	0.9925	0.3140
Carapace width	0.2323	< 0.0001	-0.2809	0.8412
Uropod length	0.2192	< 0.0001	-0.7791	-1.3942
Antennal scale length	0.2083	< 0.0001	0.7676	0.0467
ALL SEXES:				
Uropod width	0.8353	< 0.0001	-2.2836	0.8744
Carapace length	0.6601	< 0.0001	1.8911	0.6818
Carapace width	0.5236	< 0.0001	2.9265	2.4182
Telson length	0.3583	< 0.0001	-0.1528	-4.2177
Merus length pereiopod 3	0.3169	< 0.0001	1.5719	0.0800
Wet weight	0.2899	< 0.0001	-1.0636	1.4823

Table 7. Continued

Characters (in the order added by DISCRIMINANT)	Wilks' Lambda	P	Standardized Canonical Discriminant Functions	
			Funct. 1	Funct. 2
Uropod length	0.2745	< 0.0001	-0.6306	-1.5734
Antennal scale length	0.2690	< 0.0001	-0.9307	-0.6025
Antennal scale width	0.2656	< 0.0001	-0.5287	0.1284
First abdominal segment width	0.2628	< 0.0001	-0.1780	1.4178

Table 8. Significance of discriminant functions computed for pink shrimp (Pandalus borealis) males, females, and all sexes of Yakutat Bay, Kodiak Island, and the Bering Sea, 1981 (** significant at $\alpha = 0.01$).

Discriminant function	Canonical correlation	Percentage of variance	Remove specified discriminant function	Wilks' Lambda after removing	X^2
MALES:			None removed	0.3147	107.53**
1	0.8418	96.66	1	0.9362	6.13
2	0.2526	3.34			
FEMALES:			None removed	0.2083	725.55**
1	0.8080	73.85	1	0.6002	236.11**
2	0.6323	26.15			
ALL SEXES:			None removed	0.2628	877.37**
1	0.7664	71.40	1	0.6369	296.22**
2	0.6026	28.60			

Table 9. Testing of differences in SDFA discriminating variables for pink shrimp (Pandalus borealis), between pairs of 1981 study areas using the F statistic (** significant at α = 0.01).

	Area 2	
Area 1	Yakutat	Bering Sea
MALES:		
Bering Sea	3.57**	
Kodiak	35.60**	1.49
FEMALES:		
Bering Sea	97.23**	
Kodiak	73.08**	45.44**
ALL SEXES:		
Bering Sea	88.83**	
Kodiak	55.36**	48.45**

Table 10. Results of classifying individual pink shrimp (Pandalus borealis) into study areas, using their values from the SDFA discriminating variables.

Actual Group	Number of cases	Predicted Group Membership			Total percentage correctly classified
		Yakutat	Bering Sea	Kodiak	
MALES:					
Yakutat Bay	51	46 (90.2%)	3 (5.9%)	2 (3.9%)	
Bering Sea	3		2 (66.7%)	1 (33.3%)	
Kodiak	45	3 (6.7%)	7 (15.6%)	35 (77.8%)	
					83.84
FEMALES:					
Yakutat Bay	207	192 (92.8%)	2 (1.0%)	13 (6.3%)	
Bering Sea	93	1 (1.1%)	78 (83.9%)	14 (15.1%)	
Kodiak	169	15 (8.9%)	18 (10.7%)	136 (80.5%)	
					86.57
ALL SEXES:					
Yakutat Bay	326	288 (88.3%)	9 (2.8%)	29 (8.9%)	
Bering Sea	126	5 (4.0%)	113 (89.7%)	8 (6.3%)	
Kodiak	212	21 (9.9%)	18 (8.5%)	173 (81.6%)	
					86.45

discriminant functions (Table 8), relatively low final Wilks' Lambda values (Table 7), significant differences between all pairs of regions after SDFA (Table 9), and by their scatterplots that contained three visually distinct groups (see Figs. 5 and 6).

Analysis of the three nonmetric characters (Table 11) revealed low rates of egg infestation in Yakutat Bay and the Bering Sea. A significantly higher rate occurred in the Kodiak Island area. Although the Bering Sea had a low occurrence of parasitic isopods, this was significantly higher than Yakutat Bay and Kodiak Island where no occurrences were recorded. In addition, first-time spawning females (those with sternal spines) were slightly larger in the Kodiak Island area.

Variation in Age and Growth

Age estimates for Kiliuda Bay, Chignik Bay and Pavlof Bay (Appendix H) were plotted against carapace length for each year-class to determine if growth rates were comparable. Figures 7, 8 and 9 showed that within an area year-classes appeared to grow at a similar rate.

The testing of differences in carapace lengths for designated age groups (between study areas) was done for summer survey data and then fall survey data (Table 12). A Friedman two-way analysis of variance of summer data showed no significant differences between Kiliuda Bay, Chignik Bay and Pavlof Bay. However, the fall data had significant differences ($\alpha = 0.05$). Investigation with multiple comparisons showed Kiliuda Bay and Pavlof Bay to be significantly different ($\alpha = 0.05$). Kiliuda Bay shrimp were larger for a given age (i.e., growth was faster). Note that Kiliuda Bay and Chignik Bay also had a relatively high difference in ranks ($\alpha = 0.10$). The same size difference occurred between Kiliuda Bay and Chignik Bay shrimp. By comparing the age-length estimates for Kiliuda Bay, Chignik Bay and Pavlof Bay (Appendix H), it was evident that the Kiliuda Bay shrimp were larger (i.e., grew faster) than the shrimp of Chignik Bay and Pavlof Bay.

The BGC II computer program was used to calculate Von Bertalanffy growth curve constants for each study area (Table 13) from

Table 11. Analysis of pink shrimp (Pandalus borealis) nonmetric characters in Yakutat Bay, Kodiak Island and the Bering Sea for 1981 (* significant at $\alpha = 0.05$; ** significant at $\alpha = 0.01$).

	n	Proportion of data set with parasitic isopod	Proportion of data set with antennal scale eggs	z statistic for isopod	z statistic for eggs	Mode of carapace length (mm); females with sternal spines	Mean of carapace length (mm); females with sternal spines
Yakutat Bay 1981 (author)	836	0.0	0.0502			20.00	19.20
Kodiak Island 1981 (author)	482	0.0	0.3091			20.00	20.59
Bering Sea 1981 (author)	865	0.0104	0.0347			17.00	19.30
Yakutat Bay vs Kodiak Island				0.0	12.86**		
Kodiak Island vs Bering Sea				2.25*	14.22**		
Yakutat Bay vs Bering Sea				2.96**	1.59		

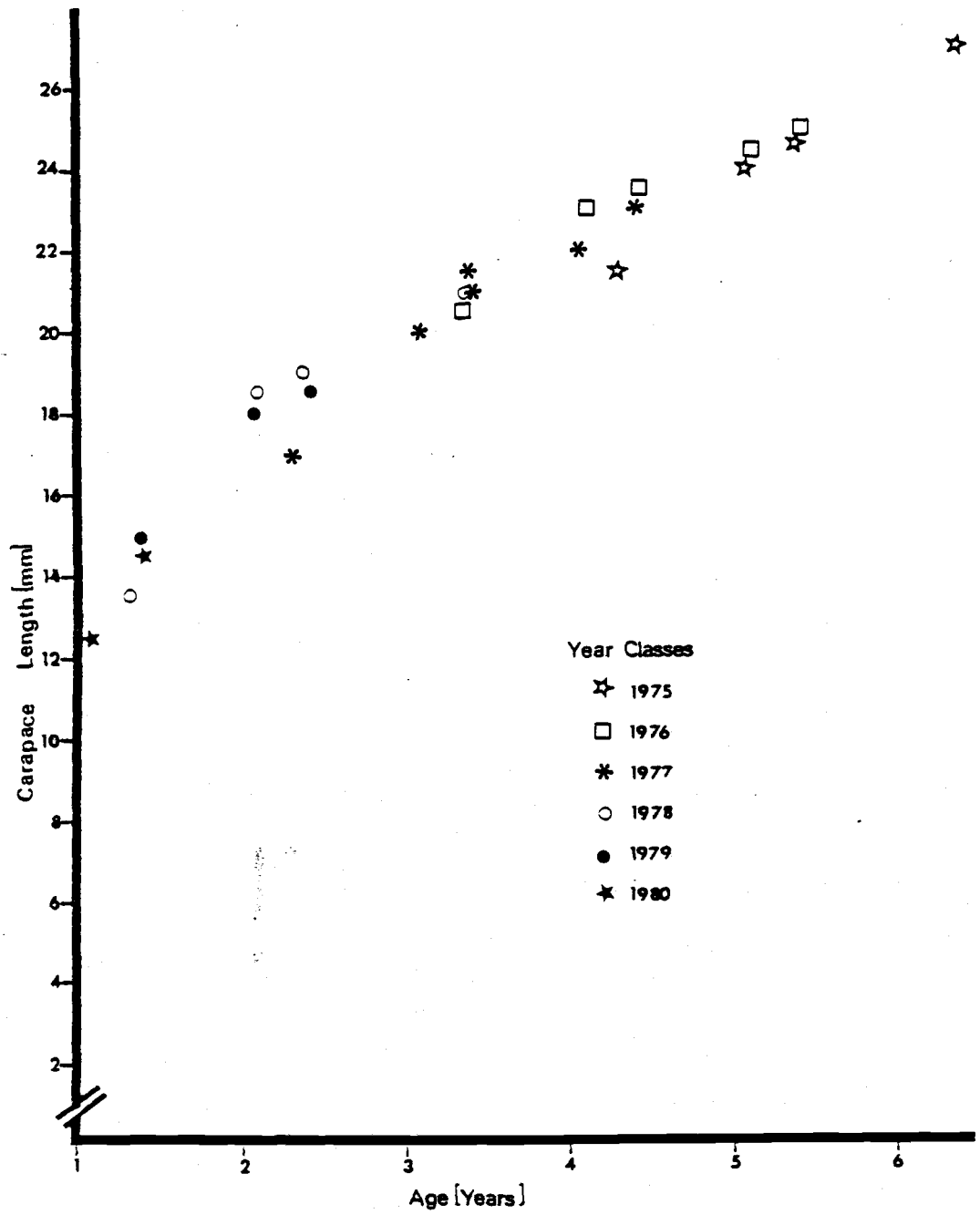

Figure 7. Apparent growth in Kiliuda Bay (Kodiak Island) pink shrimp (Pandalus borealis) of the 1975 to 1980 year-classes; based on the Von Bertalanffy growth equation.

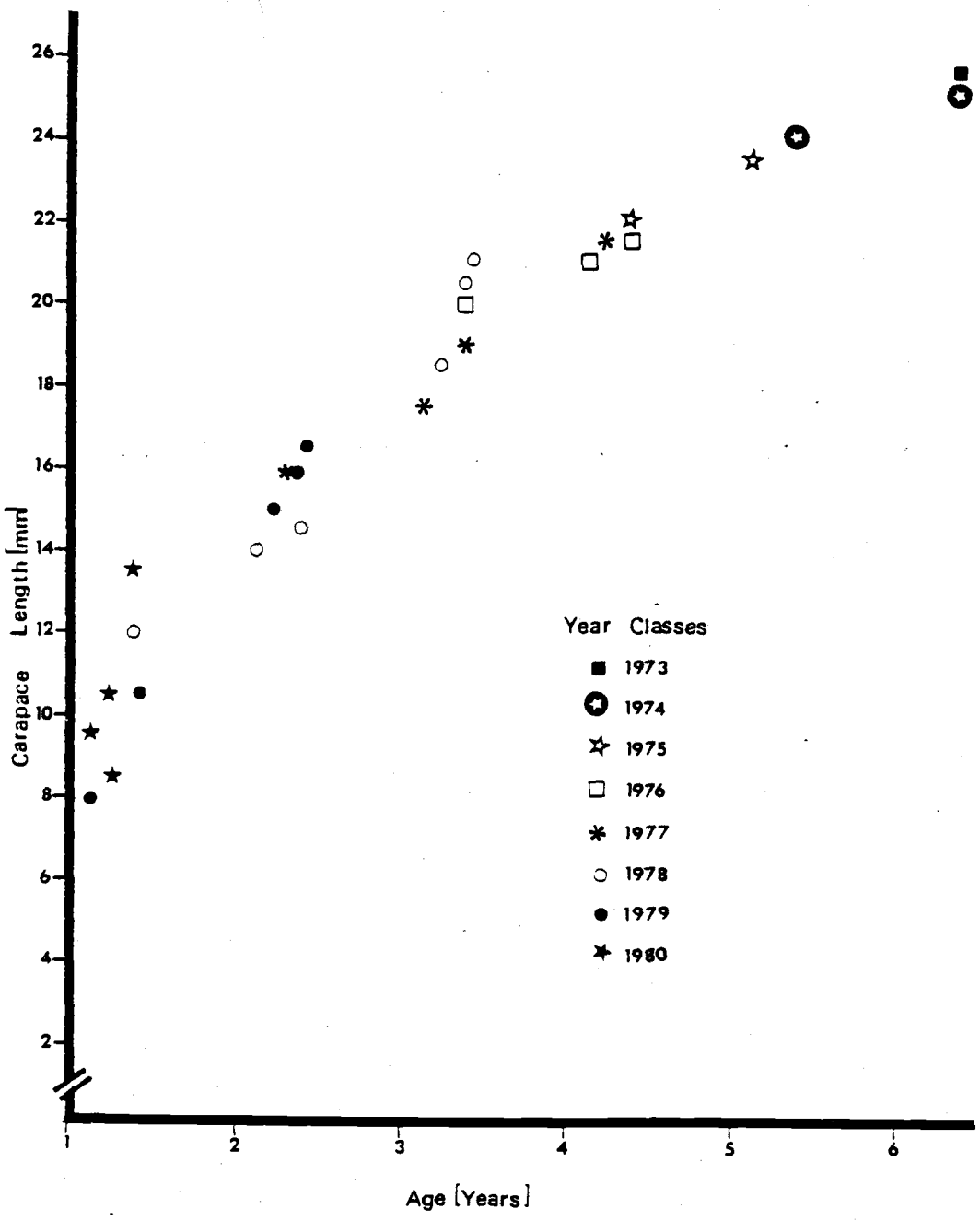

Figure 8. Apparent growth in Chignik Bay (Western Alaska Peninsula) pink shrimp (Pandalus borealis) of the 1973 to 1980 year-classes; based on the Von Bertalanffy growth equation.

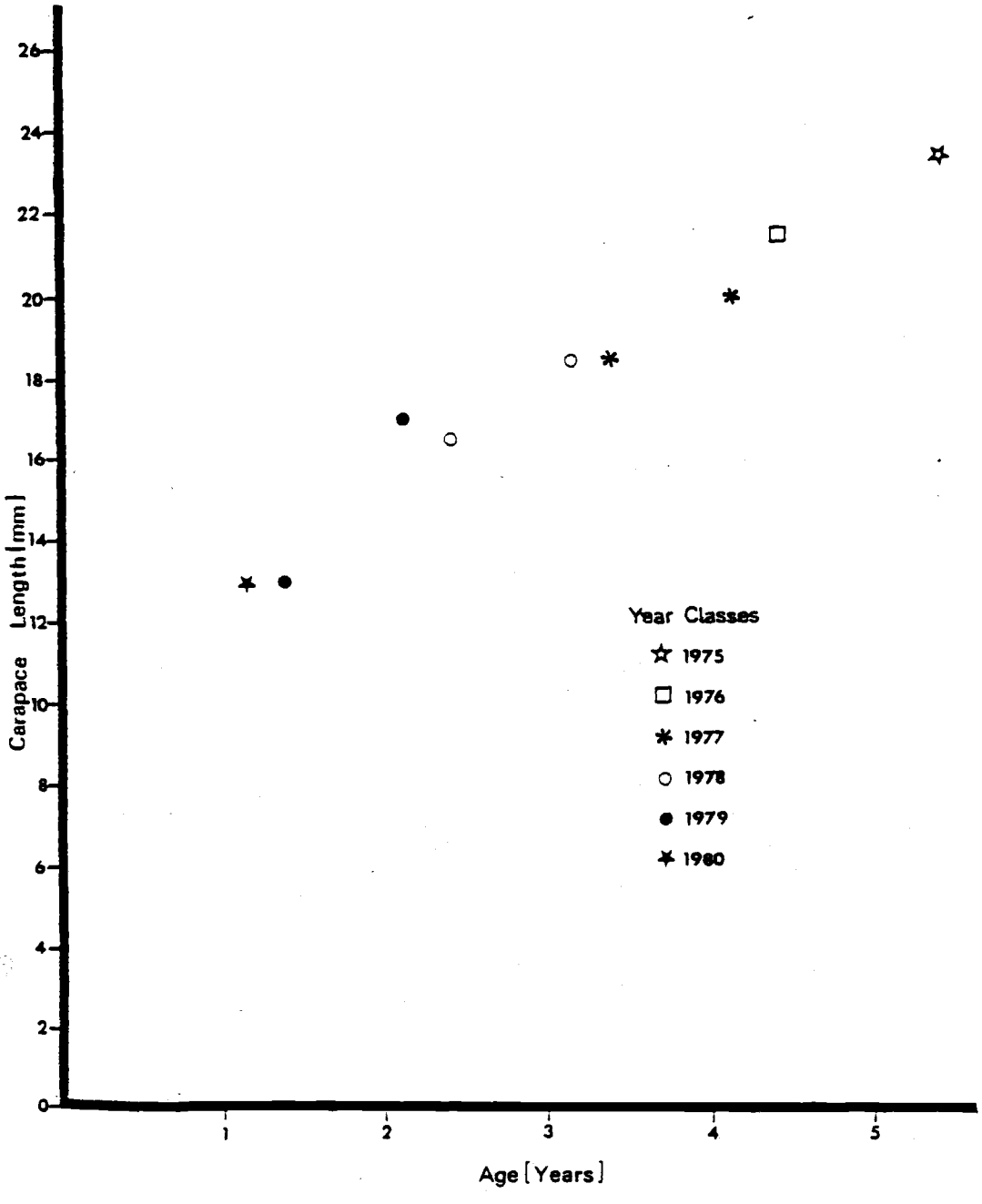

Figure 9. Apparent growth in Pavlof Bay (Western Alaska Peninsula) pink shrimp (Pandalus borealis) of the 1975 to 1980 year-classes; based on the Von Bertalanffy growth equation.

Table 12. Friedman two-way analysis of variance (by ranks) of 1979-1981 summer and fall survey data for pink shrimp (Pandalus borealis). The method tested for differences in carapace lengths of age designations from Kiliuda Bay, Chignik Bay and Pavlof Bay. For the test blocks were age and treatments were area (* significant at $\alpha = 0.05$).

	Sums of ranks	X^2	Differences in ranks		
			Kil/Chig	Chig/Pav	Kil/Pav
Summer Survey Data					
Kiliuda Bay	11				
Chignik Bay	5				
Pavlof Bay	8				
		4.50	--	--	--
Fall Survey Data					
Kiliuda Bay	15				
Chignik Bay	8				
Pavlof Bay	7				
		7.60*	7	1	8*

Table 13. Pink shrimp (Pandalus borealis) Von Bertalanffy growth curve constants for Kiliuda Bay, Pavlof Bay, and Chignik Bay (1979-1981) where l_∞ is maximum expected carapace length, "K is a constant that determines the rate at which l_∞ is approached, and t_0 is a hypothetical age when the animal was zero length" (Fox, 1972).

Area	l_∞ (Carapace length in mm)	K	t_0 (years)
Kiliuda Bay[1]			
Summer data	26.31	0.43752	-0.4439
Fall and Summer data	30.99	0.24770	-1.2131
Kiliuda Bay[2]	22.99	0.03461	-0.3469[4]
Chignik Bay[1]	28.73	0.32584	-0.0392
Pavlof Bay[1]	37.35	0.13051	-2.0783
Pavlof Bay[3]	29.00	0.18000	-0.1083[5]

[1] Calculated by BGC II FORTRAN computer program (Abramson, 1971) using age-length data.

[2] Reported by Fox (1972).

[3] Reported by Anderson (1981).

[4] Age originally reported in months.

[5] Assume age originally reported in months.

age-carapace lengths of Appendix H. Program limitations are discussed in the following section.

DISCUSSION

Study results showed that substantial differences existed in the pink shrimp population from Southeast Alaska to the Eastern Bering Sea. The three areas of investigation--genetic, morphological and growth--revealed varying degrees of heterogeneity based on data from five chosen study areas.

Genetic Variation

For pink shrimp specimens, only the PGM enzyme system was interpretable. Results showed that western (Bering Sea) individuals, particularly females, were significantly different from central (Kodiak Island) and eastern (Yakutat Bay) shrimp (Table 1). No Alaska Peninsula specimens were collected for analysis. The three PGM alleles identified in this study agreed with the starch-gel electrophoretic findings of Johnson et al. (1974) and Giorgi[1] for pink shrimp. Unfortunately, the technique of isoelectric focusing did not identify additional alleles (i.e., produce a finer level of resolution) as was hoped. Due to the Uganik Bay shrimp not meeting the assumptions of Hardy-Weinberg equilibrium, this study did not compare bay areas within Kodiak Island. However, because there were no significant differences in PGM allellic frequencies from central and eastern area shrimp, it was assumed no significant differences would exist within central area shrimp. This would correspond to the electrophoretic findings of Giorgi[1] who compared pink shrimp from Kiliuda, Alitak and Ugak Bays on Kodiak Island and found no significant differences.

In contrast, no LAP enzyme activity was found for any shrimp specimens analyzed. Control tests with purified LAP ensured that the homogenizing and focusing processes were not inactivating the enzyme or histochemical stain. Absence of LAP was unexpected since a previous pink shrimp study by Giorgi[1] stated that "LAP also shows variation, but considerably more time needs to be invested in refining the staining technique in order for it to be genetically interpretable." Giorgi's conclusion probably resulted by mistaking

arbitrary orange bands, produced when LAP stain contacts any protein present, for bands of LAP. Actual zones of LAP activity are indicated by a color change to dark purple (Beckman et al., 1964). Further corroborating evidence comes from the fact that no other study is known to have reported the presence of LAP in pandalid shrimp. In addition, DeVillez (1965) reported no LAP in the digestive juice of a related species, the crayfish (Orconectes virilis).

In this study, allele frequencies of PGM appeared to be related to shrimp life history stage (as well as geographic location; western shrimp were genetically different from other areas). This had not been reported previously in the literature. It would be of interest biologically and useful in terms of stock delineation (since multiple enzyme studies allow for more accurate interpretation) to investigate whether other enzyme systems in the pink shrimp show similar trends.

Morphological Variation

The morphologic measurements obtained were chosen to include as many measurable body parts as possible. No formal tests of the precision of these measurements were made. However, it was assumed that all measurements were made with the same degree of precision. For example, those measurements thought to show more variation during the measuring process (e.g., carapace width, abdominal segment width) were measured to the nearest 0.5 mm. The remainder that involved usually smaller hard body parts, were measured to the nearest 0.2 mm.

To ultimately assess morphological differences between the five study areas, initial analyses discussed in detail in the Materials and Methods section were used to minimize variation within and between data sets. In general, analyses showed females to be a good indicator of area differences (as in the assessment of genetic differences between areas) while males, smaller and presumably less different between areas, were not. Saila and Flowers (1969) who used SDFA to analyze morphological variation in the lobster (Homarus americanus), found a definite difference between inshore and offshore specimens that was also more distinct in females than in males. This sexual

difference was supported by a lobster tagging study that showed strong homing abilities in displaced females (an indication of discrete groups).

Examples of sexual disparity in this study were:

1. The comparison between 1981 study areas using mean differences (Tables 3 and 4). Males showed no discernible pattern in mean differences while females showed differences related to geographic location.

2. The analysis of variance of three metric characters for males (Appendix D) showed no significant difference in eastern, central and western shrimp. Females, however, showed significant area differences for all metric characters (Appendix F).

3. Males had only one statistically significant discriminant function in SDFA. As a result, only central and eastern shrimp were distinguishable from one another (Fig. 4). Females, in contrast, yielded two significant discriminant functions with good separation for three regions (Fig. 5). In fact, females showed slightly better criteria to correctly classify individuals (Table 10) than when sexes were combined. Females within a given study area are probably more homogeneous than the combined sex group. Therefore, discriminating between them became a much easier task. This was apparent in the low number of discriminating variables important to each group's first discriminant function. For all sexes, four variables had almost equal contribution to the first discriminant function while the female's discrimimant function had only two variables of importance.

Saila and Flowers (1969) found that in SDFA size could be "an overpowering factor in detecting variables which were significant in separating populations on a morphometric basis. To minimize this effect specimens in samples to be compared were matched lengthwise." Matching of lengths was not done in this study. However, due to females of P. borealis being the largest size group, transitionals

being the next largest etc., it was assumed that size variation was taken into account, in a general sense, by individually analyzing sex groupings.

Variation in Age and Growth

The Petersen graphical method was most useful in identifying ages up to 3+. The deviation method proved particularly useful for age groups older than 3+.

However, as a result of the unique shrimp life history (i.e., individuals beginning as males and then transforming to females), complications occur when modes of length-frequency distributions are used for assigning ages. Sexed length-frequency distributions give a clearer picture of age structure than unsexed frequencies, however, accurate aging of older age classes (>3+) requires a long-term monthly series. This is due to a

> "splitting [e.g. in the Kodiak Island area] of the 2+ [age] group at approximately 30 months of age with one faction entering transition while the other does not. These... factions assume differential growth rates, resulting in portions of a given age group in successive size modes" (P.B. Jackson, Alaska Department of Fish and Game, Kodiak, Alaska. Letter to author, August 19, 1982).

For example, in Southeast, Alaska one could find three females of 20 mm carapace length having three substantially different weights, presumably due to being three different ages from the area of greatest overlap in the length-frequency distribution (J.A. McCrary, Alaska Department of Fish and Game, Kodiak, Alaska. Letter to author. September 29, 1982). An additional complication is that the proportion of a given year-class entering transition is not consistent from year to year (Rasmussen, 1953).

The sampling strategy must also be considered when aging length-frequency distributions. "Diel variation and more generally vertical distribution [will] influence the representation of each age group in length frequency distributions; availability of each age

group may vary greatly depending on time of day and trawl type." Sampling locations could also affect the age groups represented (Northwest Alantic Fisheries Organization [NAFO], 1981).

Differential gear selectivity among age classes must also be considered in relation to the younger (male) age groups (NAFO, 1981). It is thought that the 0+ age group or the early postlarval stage (<8.0 mm in carapace length), is not available to trawl gear. Among the 1+ group, the distribution is sometimes skewed due to gear selection for larger animals in the age group (the data in this study did not show appreciable skewness). A result is the actual mean size is often smaller for the 1+ age group than indicated by the length-frequency distribution (J.A. McCrary, Alaska Department of Fish and Game, Kodiak, Alaska. Letter to author, September 29, 1982). Therefore, the age estimates obtained in this study are at best approximate, since only three consecutive years of data were available with at most three, but usually two sampling periods per year.

The observation that growth was slower in Western Alaska Peninsula shrimp than Kiliuda Bay shrimp, follows the growth trend reported by Ivanov (1969). Ivanov showed that growth of pink shrimp in the Bering Sea was slower than Western Gulf of Alaska (Kodiak Island area) shrimp. Maturation was also approximately one year later for Bering Sea shrimp. Ivanov attributed the differences to cooler Bering Sea water temperatures in which he reported an average of 1.5-2.0° C compared to 4-4.5° C for the Western Gulf of Alaska. The Western Alaska Peninsula shrimp of this study were located between the Bering Sea and Kodiak Island area (west to east) and showed intermediate growth rates when compared to Ivanov's study areas.

The BGC II FORTRAN program used to calculate Von Bertalanffy growth curve and constants, had the limitation of being able to use only equally spaced age groups. Therefore, the ages were averaged for a given area and year, while all carapace lengths were included. In the case of Kiliuda Bay, enough observations were available to analyze the summer data set separately. The discrepancy between the combined and summer growth curve estimates is substantial. Misidentification of age groups could account for the discrepancy and/or the low

l_∞ values. However, the early summer growth curve estimates is substantial. However, the early summer shrimp, particularly transforming females, grow considerably during and after this period (Butler, 1980). This might explain the low l_∞ value obtained for summer data and the nonsignificant area differences in mean carapace length (Table 12) from summer data sets. The combined fall and summer estimates would appear to be a more reasonable description of P. borealis growth. A comparison of only fall estimates (not computed in this study due to few observations) would have perhaps been the best descriptor of area growth since molting stops during mating and spawning (from fall until spring of following year).

For Kiliuda Bay, the BGC II estimate of growth curve constant l_∞ showed a reasonable value when considering the known maximum lengths of P. borealis for the area. These BGC II estimates appeared more reasonable than those reported by Fox (1972) (Table 13). However, for Pavlof Bay, the estimates of Anderson (1981) appear to be better approximations. The poor BGC II estimates for Pavlof Bay undoubtedly resulted from the small number of age-length estimates used due to lack of available data sets.

CONCLUSIONS AND SIGNIFICANCE OF STUDY

This study was the first attempt to delineate stocks of pink shrimp in the northeastern Pacific Ocean by analyzing genetic and morphological variability in combination with age and growth. The stock delineation methods used and their findings follow:

1. Analysis of genetic variation. It was concluded that Bering Sea shrimp were genetically distinct from Kodiak Island and Yakutat Bay shrimp for the PGM locus.

2. Analysis of morphological variation. Of the sex groupings, females proved to be the best indicator of area differences. The morphometric data sets showed Bering Sea, Kodiak Island, and Yakutat Bay shrimp to be morphologically distinct from one another. Northeast Alaska Peninsula shrimp were not significantly different from Kodiak Island shrimp.

The low occurrence of Bopyroides hippolytes, a parasitic branchial isopod in Bering Sea shrimp, was significantly higher than in Yakutat and Kodiak Island where no occurrences were recorded. The occurrence of egg cases, usually 1 mm in length (species unknown), on the antennal scale and rostrum surfaces of Kodiak Island pink shrimp was significantly higher than for Yakutat Bay and Bering Sea shrimp.

For Pavlof Bay and Chignik Bay on the Western Alaska Peninsula, only length-frequency data were available. Females of Chignik Bay and Pavlof Bay were not significantly different in carapace length. Female shrimp of both bays were significantly different in carapace length from the Bering Sea, Kodiak Island, and Yakutat Bay.

3. Analysis of age and growth. The size of Kiliuda Bay shrimp for a given age was significantly different (larger) when compared to corresponding sizes/ages in Chignik Bay and Pavlof Bay. Therefore, Kiliuda Bay shrimp appeared to grow faster than Pavlof Bay and Chignik Bay shrimp.

The stock delineation results showed the Bering Sea to be morphologically and genetically distinct (based on one locus) from the

other study areas. This was strong evidence to suggest that Bering Sea shrimp were a separate population or stock. Strong morphological differences existed between Kodiak Island and Yakutat Bay shrimp to suggest that these areas might also be separate breeding populations. The Northeast Alaska Peninsula shrimp did not show evidence of being distinct from Kodiak Island area shrimp. Pavlof Bay and Chignik Bay on the Western Alaska Peninsula were not distinct from one another but were different from other study areas. This suggested that together the two bays might make up another population. Note, however, that the lack of data for these bays would indicate further study is needed.

These findings did not invalidate the current management approach by ADF&G of treating each bay as a separate stock. These results did suggest that, at the least, Kodiak Island, Yakutat Bay, the Bering Sea and probably Western Alaska Peninsula shrimp should be treated as individual breeding units for purposes of management.

Other findings and accomplishments of this study included:

1. The absence of the LAP enzyme in P. borealis.

2. In PGM, the tendency for the relative frequency of the allele identified as A, to decrease and the relative frequency of the allele identified as B, to increase as the shrimp ages and progresses from the male to female sexual stage.

3. The first known application of the technique of isoelectric focusing to the field of fisheries research. The technique, however, provided results similar to previous (and less expensive) starch gel electrophoretic studies.

4. The development of a length-weight model for the Kodiak Island area that will be of use to management's stock assessment program.

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APPENDICES

Appendix A. NMFS/ADF&G 1981 survey sampling stations with number of pink shrimp (Pandalus borealis) used by sex in polyacrylamide isoelectric focusing.

	Number of shrimp analyzed				
	Male	Trans.	Female	Female with Head Roe	Total
Bering Sea (1981)					
Sta. D-3, Haul #11	1	1	2		
Sta. E-18, Haul #52	2	3	3		
Sta. D-18, Haul #53	6	2	4		
Sta. K-24, Haul #96	1			2	
Sta. J-23, Haul #102	1	2	1		
Sta. J-24, Haul #103	5	1	1	1	
Sta. O-32, Haul #153				8	
Sta. Q-28, Haul #213	2			2	
Subtotal	18	9	11	13	51
Kodiak (1981)					
Uganik Bay (data sheet #33)	3		1	9	
Outer Marmot (data sheet #36)	8		4	9	
Outer Marmot (data sheet #39)	8	2	2	3	
Subtotal	19	2	7	21	49

Appendix A. Continued

	Number of shrimp analyzed				
	Male	Trans.	Female	Female with Head Roe	Total
Yakutat (1981)					
Composite of Tows #1-9	2	1	5		
Composite of Tows #10-17 (part I)	3		6		
#10-17 (part II)	1		9		
Composite of Tows #18-24	4	1	4		
Subtotal	10	2	24	0	36
TOTAL	47	13	42	34	136

Appendix B. Testing of difference in mean wet weight, carapace length, and total length for fresh (measured when alive) and frozen (thawed before measured) pink shrimp (Pandalus borealis). Specimens collected in the Kodiak Island area during Fall 1981.

	Wet Weight			Carapace Length			Total Length		
Group	F	d.f.	t	F	d.f.	t	F	d.f	t
1	1.02	76	0.46	1.00	77	1.19	1.11	76	-0.40
2	1.02	80	-0.58	1.13	80	0.39	1.02	80	-0.11
3	1.23	75	-0.78	1.02	78	0.18	1.12	76	-0.36
4	1.02	34	-0.19	1.10	34	0.14	1.10	34	-0.07
5	1.12	42	-0.37	1.06	42	0.84	1.10	42	-0.52
6	1.02	76	-0.74	1.04	78	0.38	1.09	76	-0.65
7	1.01	78	-0.02	1.06	78	-0.08	1.00	72	-0.81
8	1.14	78	-0.27	1.02	80	0.30	1.46	74	0.11
9	1.00	76	0.46	1.12	77	1.19	1.08	76	-0.40

Appendix C. Log carapace length (x) to log wet weight (y) regressions of pink shrimp (Pandalus borealis) for Yakutat Bay, Bering Sea and Shumagin Island length-weight data sets (1973-1981). Source of data set (in parentheses) follows year of collection.

Area	n	Regression Equation	r
Yakutat Bay			
1981 (NMFS)			
1981 (Author)			
Male	318	y = 2.5736 x - 2.7011	0.9285
Transitional	104	y = 3.1599 x - 3.4914	0.8716
Female	352	y = 2.7254 x - 2.8707	0.9203
Ovigerous female	105	y = 3.1170 x - 3.4045	0.8886
Bering Sea			
1978/79 (NMFS)			
Male	170	y = 3.2483 x - 3.4736	0.9022
Female	206	y = 2.9704 x - 3.1095	0.8906
1980 (Author)			
Male	239	y = 2.7093 x - 2.7732	0.9421
Transitional	109	y = 2.6415 x - 2.6705	0.9640
Female	252	y = 2.7054 x - 2.7431	0.9525
Shumigan Island			
1973 (NMFS)			
Male	332	y = 2.7609 - 2.9442	0.9924
Female	63	y = 2.8712 - 3.0762	0.9439
Ovigerous female	191	y = 2.8845 - 3.0634	0.9429
1974 (NMFS)			
Male	350	y = 2.7411 - 2.9744	0.9595
1976 (NMFS)			
Male	291	y = 2.7612 - 2.9326	0.9903
Ovigerous female	185	y = 2.4395 - 2.5116	0.8609

Appendix D. One-way analysis of variance to test for difference in means of male pink shrimp (Pandalus borealis) morphological characters from Yakutat Bay, Kodiak Island, and Bering Sea 1981 data sets (** significant at $\alpha = 0.01$).

Character	Mean			n	F
	Yakutat Bay	Kodiak	Bering Sea		
Wet weight (g)	2.44	3.01	3.38	657	46.34**
Carapace length (mm)	15.38	15.86	16.01	920	10.48**
Total length (mm)	59.72	63.24	67.35	694	70.33**
Carapace width (mm)	7.34	7.94	7.76	708	19.24**
First abdominal segment width (mm)	6.67	7.36	7.66	797	93.73**
Rostrum length (mm)	25.48	25.91	25.94	136	0.53
Telson length (mm)	11.67	11.94	13.12	341	29.36**
Uropod length (mm)	10.65	10.83	11.73	665	46.05**
Uropod width (mm)	2.53	2.86	3.07	687	112.64**
Antennal scale length (mm)	13.33	13.79	14.71	748	73.45**
Antennal scale width (mm)	2.56	2.81	3.01	873	100.23**
Merus length on pereiopod 3 (mm)	15.53	15.26	15.37	644	1.42
Carpus length on pereiopod 3 (mm)	4.55	4.57	4.52	594	0.43

Appendix E. One-way analysis of variance to test for difference in means of transitional (sexual stage between male and female) pink shrimp (Pandalus borealis) morphological characters from Yakutat Bay, Kodiak Island, and Bering Sea 1981 data sets (** significant at $\alpha = 0.01$).

Character	Mean			n	F
	Yakutat Bay	Kodiak	Bering Sea		
Wet weight (g)	3.90	4.59	4.76	134	1.56
Carapace length (mm)	18.59	17.50	17.78	185	1.16
Total length (mm)	71.24	74.67	75.13	131	1.10
Carapace width (mm)	8.64	8.38	8.64	147	0.06
First abdominal segment width (mm)	7.96	8.50	8.37	163	1.01
Rostrum length (mm)	29.16	31.20	32.05	10	0.54
Telson length (mm)	13.30	13.70	14.38	67	1.57
Uropod length (mm)	12.46	13.40	12.83	128	0.54
Uropod width (mm)	3.15	3.53	3.46	132	2.40
Antennal scale length (mm)	15.53	15.80	15.98	142	0.65
Antennal scale width (mm)	3.28	3.40	3.34	179	0.15
Merus length on pereiopod 3 (mm)	17.66	17.33	16.82	130	1.71
Carpus length on pereiopod 3 (mm)	5.15	5.50	4.97	117	1.32

Appendix F. One-way analysis of variance to test for difference in means of female pink shrimp (Pandalus borealis) morphological characters from Yakutat Bay, Kodiak Island, and Bering Sea 1981 data sets (** significant at α = 0.01).

Character	Yakutat Bay	Kodiak	Bering Sea	n	F
Wet weight (g)	5.13	7.36	8.47	898	234.72**
Carapace length (mm)	20.35	21.69	22.43	1057	94.42**
Total length (mm)	76.65	85.51	91.50	923	270.99**
Carapace width (mm)	9.64	11.14	10.98	919	149.35**
First abdominal segment width (mm)	8.67	10.28	10.45	975	256.90**
Rostrum length (mm)	32.40	34.96	37.61	171	20.29**
Telson length (mm)	14.93	16.00	17.67	560	129.08**
Uropod length (mm)	13.59	14.54	16.08	909	48.89**
Uropod width (mm)	3.55	4.15	4.49	914	267.84**
Antennal scale length (mm)	16.58	18.05	19.45	936	269.71**
Antennal scale width (mm)	3.60	4.11	4.41	1023	222.08**
Merus length on pereiopod 3 (mm)	19.59	20.11	20.48	834	16.43**
Carpus length on pereiopod 3 (mm)	5.73	6.08	6.07	791	33.14**

Appendix G. Value and significance of Hotelling's T^2 statistic testing for mean vector differences between Yakutat Bay, Bering Sea, and Kodiak Island pink shrimp (Pandalus borealis) in 1981. Mean vector of each study area included a mean value for wet weight (g), carapace length (mm), total length (mm), carapace width (mm), first abdominal segment width (mm), rostrum length (mm), telson length (mm), uropod length (mm), uropod width (mm), antennal scale length (mm), antennal scale width (mm), merus length of third pereiopod (mm), and carpus length of third pereiopod (mm).

	Male				Female			
Comparison	n	T^2	F	p	n	T^2	F	p
Yakutat Bay vs Bering Sea	32 1	71.00	3.35	0.0085	33 5	213.48	10.95	<0.0001
Yakutat Bay vs Kodiak	32 26	135.55	8.19	<0.0001	33 50	122.37	8.02	<0.0001
Bering Sea vs Kodiak	1 26	38.03	1.52	0.2299	5 50	156.53	9.31	<0.0001

Appendix H. Age estimates (in years) of the pink shrimp (Pandalus borealis) for Kiliuda Bay, Chignik Bay and Pavlof Bay from modes of ADF&G length-frequency files (1979-1981).

	Carapace length (in mm) for estimated year-classes							
Age[1]	1973	1974	1975	1976	1977	1978	1979	1980
Kiliuda Bay								
1.12								12.5
1.33						13.5		
1.40							15.0	
1.43								14.5
2.09						18.5		
2.12							18.0	
2.33					17.0			
2.40						19.0		
2.43							18.5	
3.09					20.0			
3.33				20.5				
3.40					21.0			
3.40					21.5			
3.43						21.0		
4.09				23.0				
4.12					22.0			
4.33			21.5					
4.40				23.5				
4.43					23.0			
5.09			24.0					
5.12				24.5				
5.40			24.5					
5.43				25.0				
6.43			27.0					

Appendix H. Continued

	Carapace length (in mm) for estimated year-classes							
Age[1]	1973	1974	1975	1976	1977	1978	1979	1980
Chignik Bay								
1.15							8.0	9.5
1.28								8.5
1.28								10.5
1.41						12.0		
1.42								13.5
1.43							10.5	
2.15						14.0		
2.28							15.0	
2.41					16.0			
2.42							16.0	
2.43						14.5		
2.45							16.5	
3.15					17.5			
3.28						18.5		
3.41				20.0				
3.42						20.5		
3.43					19.0			
3.45						21.0		
4.15				21.0				
4.28					21.5			
4.41			22.0					
4.43				21.5				
5.15			23.5					
5.41		24.0						
6.41	25.5							
6.43		25.0						

Appendix H. Continued

Age[1]	Carapace length (in mm) for estimated year-classes							
	1973	1974	1975	1976	1977	1978	1979	1980
Pavlof Bay								
1.14								13.0
1.40							13.0	
2.14							17.0	
2.40						16.5		
3.14						18.5		
3.40					18.5			
4.14					20.0			
4.40				21.5				
5.40			23.5					

[1] Assumed an April 1 hatching date (J.A. McCrary, Alaska Department of Fish and Game, Kodiak, Alaska. Letter to author, September 29, 1982).