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

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ABSTRACT

An analysis of genetic and morphological variability in combination with age and growth in northeastern Pacific Ocean pink shrimp (*Pandalus borealis*) is reported. Bering Sea shrimp were genetically distinct from Kodiak Island and Yakutat Bay shrimp at the PGM locus, and female shrimp from each of these locations were morphologically distinguishable. No significant morphological differences were found between Northeast Alaska Peninsula and Kodiak Island shrimp. Significant size and growth differences were found in some Kodiak Island and Alaska Peninsula samples. The results suggest that Kodiak Island, Yakutat Bay, Bering Sea, and probably western Alaska Peninsula should be treated as separate stocks for management purposes.

INTRODUCTION

In Alaska, commercial fishing and its associated support activities are major contributors to the state's economy. In recent years an increase in the number of fishing vessels, and consequent fishing effort, has caused many of the fish populations to be overexploited. One such case involved the pink shrimp (*Pandalus borealis*) fishery near Kodiak Island during the 1970s. Shrimp 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" (Balsinger 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).

The basic life history of the pink shrimp has been investigated throughout its range, including Pacific (Butler 1964, 1971, 1980; Ivanov 1969) and Atlantic Ocean populations (Rasmussen 1953; Allen 1959; Haynes and Wigley 1969). Squires (1968) studied apparent environmental influences on 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.

The unit stock is one of the most fundamental concepts in fisheries science. Larkin (1972) considered a population unit or stock to be a self-perpetuating or interbreeding population of organisms sharing a common environment and gene pool. Lackey and Hubert (1978) define a unit stock to be a group of organisms that can be treated as a single unit for management purposes.

Rounsefell and Everhart (1953) note that "in managing a particular fishery it is essential to know whether the catch comes from one population or perhaps several." When an entire fishery depends on one fish stock this stock will be affected by exploitation throughout its geographic distribution. However, if the fish stocks are discrete, concentrated fishing may decimate populations in some areas while having minimal affects on adjacent populations. Population recovery may be slow in the affected areas if members of adjacent stocks do not tend to invade and repopulate the area. Therefore, sensible fisheries management must consider the extent to which animals being exploited comprise a self-sustaining unit (Rounsefell and Everhart 1953; Larkin 1972; Lackey and Hubert 1978).

Many population dynamics models, developed to estimate the maximum sustained yield from a fishery, have evolved from the unit stock concept. To realistically apply these models a unit stock with definable characteristics must be identified and described. Examples of such characteristics include growth, natural mortality,

and recruitment. This does not imply that for successful fisheries management all biological or genetic units must be identified and treated separately. Instead, the population unit considered for management purposes must be comprised of animals "which are similar enough in their vital parameters not to obscure the data needed for efficient management" (Lackey and Hubert 1978; Tyler and Gallucci 1980).

A wide range of morphological characters are used to delineate fish populations (Barlow 1961; Cushing 1968, 1975). The comparison of body measurements and meristic or "nonmetric" features has been used extensively in geographic variation studies. However, Gould and Johnston (1972) note that "geographic variation is not likely to be due to adaptation of a few characters to a single environmental variable, but is doubtless a multidimensional process involving the adaptation of many characters to a variety of interdependent environmental factors whose gradients and ranges probably overlap in rather complex fashion." Consequently, with the aid of computers, several multivariate investigations have appeared in the literature in recent years. Organisms studied include whelks (Phillips et al. 1973), crayfish (Chambers et al. 1979), amphipods (Crocker and Gable 1977), lobster (Saila and Flowers 1969), insects (Atchley 1971; Zimmerman and Ludwig 1975; Scheiring 1977), turtles (Iverson 1977), snakes (Benton 1980), birds (Johnston and Selander 1971), and mammals (Baker et al. 1978; Smith 1979; Hartman 1980).

Because morphological characters may vary due with environment, documenting genetic variation in combination with morphologic differences offers stronger evidence for true stock delination. A distinct cluster of individuals with gene flow among all members tends to have different gene and allele (alternate forms of genes) frequencies in comparison to other clusters in different environments. Therefore, relative gene or allele frequencies are used to detect geographic variation or shifts from area to area (Cushing 1968, Ehrlich and Raven 1969; Gould and Johnston 1972; Avise 1974; Bryant 1974; Baker et al. 1978; Tyler and Gallucci 1980).

Biochemical techniques, such as starch gel electrophoresis with histochemical staining, have been widely used in fisheries research to determine allele frequencies. Genetic studies of the pink shrimp include Johnson et al. (1974), who used starch gel electrophoresis to separate pink shrimp from four other species of northern Pacific pandalid shrimp. The phosphoglucosmutase (PGM) enzyme system was polymorphic in all five species and it was suggested that the polymorphism could prove useful in separating breeding groups. To determine if stocks of pink shrimp could be identified, A. Giorgi (unpublished results¹) used starch gel electrophoresis to analyze and 19 enzyme systems in shrimp muscle protein samples from three bays on Kodiak Island. The PGM enzyme system was polymorphic but the gene frequencies were statistically inseparable. In addition, leucine aminopeptidase (LAP) was analyzed, but proved to be uninterpretable.

¹ A. Giorgi, "Genetic applications in shrimp fisheries management," report to Alaska Department of Fish and Game, Kodiak, Alaska, February 28, 1978.

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, sometimes 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 which involves a dynamic separation by electric charge at particular pH values. In isoelectric focusing an electric field is applied to proteins in a pH gradient produced by carrier ampholytes. The process causes the migration of the macromolecules to regions of their isoelectric pH values where they concentrate in narrow bands. The refined resolution of isoelectric focusing could make it possible to identify polymorphism where starch gel techniques prove inadequate (Fawcett 1968; Shaw 1969; Leback and Wrigley 1976).

Lackey and Hubert (1978) note that in addition to the analysis of genetic variation, morphological variation, and the defining of stocks with characteristic attributes (e.g., growth rate), other methods can be used to delineate stocks. They include age (year-class) composition, which may be estimated by length or weight frequencies (a single stock will be fairly uniform from area to area); comparing incidence of disease or parasites; comparing catch and effort records (similar statistics for two adjacent areas is evidence for one continuous stock) comparing geographic distribution; and comparing life histories.

From the recent history of the pink salmon 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 their geographic range, more realistic estimates for yield models could be obtained, offering a basis for improved management.

This study tested the hypothesis that one homogeneous 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 were (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, selected stock delineation criteria of Lackey and Hubert (1978) were investigated. The criteria and methods used were:

1. Analysis of genetic variation, to determine if allele frequencies differed significantly between the five study areas by examining

genetic variation in two enzyme systems reported to be polymorphic in pink shrimp.

2. Analysis of morphological variation, to determine if significant differences existed between study areas by studying morphological characters using both univariate and multivariate methods.
3. Description and comparison of identifiable population attributes, to determine if significant area differences existed in shrimp by estimating area-specific growth curves constants from area-specific age estimates.

MATERIALS AND METHODS

Genetic Variation

Pink shrimp were collected from Yakutat Bay, Kodiak Island, and the Bering Sea, and frozen. 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 (see Appendix A for a list of station samples used).

Initially two tissues and two enzyme systems were analyzed: the digestive gland for the LAP system and the tail muscle for the PGM system. Tissue homogenates were prepared by diluting the sample at 4°C 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 at 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). An acrylamide to bisacrylamide (N,N'-methylene-bis-acrylamide) ratio of 30:1.2 was used. For LAP, the gel contained 5.1827% polyacrylamide, 12.4585% sucrose, 0.0004% riboflavin, 1.9934% Bio-Lyte 3/5², 1.9934% Bio-lyte 4/6³, and 0.9967% Bio-Lyte 5/7⁴. To facilitate polymerization, 0.3322% TEMED (N, N, N', N'-tetramethylethylenediamine) was added and then the gel was placed in 10 cm from a UV fluorescent light for 1 hr.

For PGM, the gel contained 5.1827% polyacrylamide, 12.4585% sucrose, 2.4917% Bio-Lyte 5/7⁴, and 2.4917% Bio-Lyte 7/9⁵. 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.

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

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

⁴ Ibid.

⁵ Ibid.

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 (six samples) were each loaded with 5 μ l of dye marker using a 25 μ l 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 μ l of 0.05% carbonic anhydrase (bovine, Sigma Chemical Co., product no. C-7500) while wells #5 and 13 contained 10 μ l 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 because 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 hours; for PGM gels it was 6 hours. A run was considered complete when the 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 hours (but not more than 24 hours) to remove carrier ampholytes that may have interfered with staining reagents (modified from Bours, 1973).

The LAP portions of the gel were placed in 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 MgCl₂, 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 hours). Gels were fixed by rinsing in distilled water for at least an hour.

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. To investigate the possibility that the isoelectric focusing or homogenizing process had inactivated LAP, histochemical stain was added 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 using 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 hour in a shaker bath. Destaining was initiated by placing the gel for 24 hours 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 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 hours. 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 allele frequencies were significantly different between sexes when study areas were combined. If the test was significant, the chi-square was partitioned to determine which sexes differed. In each area, with sexes combined, a chi-square goodness of fit procedure was used to determine 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, the chi-square was partitioned 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 length-frequencies 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 included a sexed subsample (representative of area tows) with 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 for which 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. Inspection of modes, means, medians, and frequency distributions suggested distributions were close to normal. 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 a one-way analysis of variance. If the F-test was significant, the standard errors of the differences between means were computed for pairs of sexes. The number of degree 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 in all data sets to make results consistent and comparable.

For the males and females, a one-way analysis of variance was also used to test 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 statistics (Morrison 1976) also being computed to compare the mean vector (containing mean carapace length, total length, and wet weight) from one study area to the mean vector from another area. The ADF&G length-frequency data sets were excluded from this portion of the analysis since the required data was unavailable.

Length and weight data were also obtained from samples acquired in the 1981 NMFS and ADF&G cruises to the Northeast Alaska Peninsula, Kodiak Island, Yakutat Bay, and the Bering Sea. Using a Mettler balance, specimens were weighted 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 weight to the nearest 0.5 mm. This study defined carapace length to be the distance from the posterior margin of the eye sockeye to the posterior mid-dorsal margin of the carapace. Total body length was defined to be the distance 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 unsuitable because of the high incidence of damaged rostrums.

The author obtained length-weight measurements from both fresh and frozen specimens from Kodiak Island. Frozen specimens were thawed and drained before measuring. Only frozen specimens were available from Yakutat Bay and the Bering Sea for length-weight measurements. To check for differences between fresh and frozen specimens, nine groups of about 40 individuals with both fresh and frozen measurements recorded were compared. Means of carapace length, total body length, and wet weight were calculated. Sexes were combined because of small sample sizes. First, equality of variances was tested. If variances were not significantly different ($\alpha = 0.05$), the comparison of means of two independent samples and its pooled variance were used. When variances were significantly different, 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, the logarithm of wet weight was regressed on the logarithm of carapace

length and wet weight was regressed on carapace length for each sex grouping. Additional regressions for the fresh Kodiak data set included the logarithm of wet weight on the logarithm of total length; wet weight on total length; and carapace length on total length. The logarithmic transformations were used to assist in linearizing the length to weight relationship (Ricker 1975).

The logarithmic wet weight - carapace length regressions within the same study area (but from different data sets) were compared with the following method. 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.

Ten additional morphological (metric) characters were measured on the frozen specimens collected from Yakutat Bay, Kodiak Island, and the Bering Sea using vernier calipers. They were: 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 pereopod along extensor edge; and maximum length of carpus of third pereopod along extensor edge. In addition, three nonmetric characters were noted: the presence or absence of sternal spines in females (McCrary 1971); the presence or absence of *Bopyroides hippolytes*, a parasitic branchial isopod (Butler 1980); and the presence or absence of egg cases, usually about 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. Metric characters were measured to the nearest 0.2 mm with the exception of maximum width of the carapace and maximum width of the first abdominal segment which were measured to the nearest 0.5 mm. All characters chosen can be reliably measured or observed.

To determine the feasibility of multivariate discriminant function analysis for Yakutat Bay, Kodiak Island, and Bering Sea morphological characters, a one-way analysis of variance was done for each character within each sex grouping. In addition, for each sex Hotelling's T^2 statistic (Morrison 1976) was used to evaluate the significance the mean vector of differences in metric variables from each pair of study areas.

Stepwise discriminant function analysis (SDFA), with Wilks' Lambda as the selection criterion (a measure of separation), was performed using the program DISCRIMINANT in the Statistical Package for the Social Sciences (SPSS). SDFA was done for each sex and all sexes together to determine which metric variables were important to discriminating between areas. Total length was excluded from SDFA; Pimentel (1974) suggests avoiding the use of total measurements in combination with some of their parts (e.g., rostrum length, carapace length, telson length) to avoid problems from linear dependence. The discriminating variables'

effectiveness or ability to separate areas was evaluated by noting the number of significant discriminant functions i.e., the number of distinguishable areas; the overall Wilks' Lambda statistic; the results of testing pairs of groups (areas) for differences after SDFA; and the percentage of individuals correctly classified by region, using observed values of the discriminating variables. Cases were plotted against the two most significant 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 files obtained from ADF&G for Kiliuda Bay, Chignik Bay, and Pavlof Bay were organized into length-frequency distributions (LFDs) 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, in which each LFD was subtracted from a mean LFD computer for a particular time period from several years of data (Skuladóttir 1981); and the deviation method applied to each sex and plotted separately (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 assure reasonable age estimates.

To compare growth rates of different 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 examined for differences using the Friedman two-way analysis of variance by ranks, in which blocks were ages and treatments were areas. When differences were significant, a multiple comparison procedure for 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. gorealis* growth curve constants reported by Anderson (1981) for Pavlof Bay, and by Fox (1972) for Kodiak Island bays.

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 the stain was applied

directly to homogenate gave negative results except when purified LAP was present. It was concluded that the *P. borealis* specimens had no LAP activity.

The PGM enzyme system in *P. borealis* showed polymorphism at three alleles. One and two-banded phenotypes were observed (Figure 1). Allele frequencies were tabulated, assuming random combination of alleles and a monomeric structure (Utter et al. 1974). Tests for allelic 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 those from Uganik Bay (Kodiak Island) deviated significantly from Hardy-Weinberg expected values. Uganik Bay data were excluded in tests of area differences. Tests of homogeneity showed allele frequencies from the Bering Sea samples were significantly ($\alpha = 0.05$) from those of Yakutat Bay and Outer Marmot Bay (Kodiak Island). Allele frequencies of Yakutat Bay and Marmot Bay samples were not significantly different.

Morphological Variation

Modes, means, medians, and frequency distributions of carapace length and wet weight (when available), for each data set by sex, revealed no extreme departure from normality. One-way analysis of variance to test the appropriateness of combining sexes within data sets showed few nonsignificant differences. Those means not significantly different usually came from data sets with small sample sizes. Therefore, four sex groupings were used in subsequent analyses when sufficient data were available.

None of the nine groups used to check for differences between fresh and frozen specimens showed a significant difference in mean carapace length, total length or weight (Appendix B). It was therefore assumed that it was unnecessary to analyze data from fresh and frozen specimens separately.

The comparison of data set regression lines within study areas to examine variability and differences through time showed highly significant differences ($\alpha = 0.01$) for almost all sex groupings (Table 2). The exceptions were regressions for females in Yakutat Bay and the Bering Sea.

Because there was considerable variability within study areas and through time (see also Figure 2, Kodiak Island and Figure 3, Chignik Bay), it was concluded that comparisons of study areas should be made only between survey data sets of the same year. Males of the 1981 data sets showed no geographic pattern in carapace length, total length, and wet weight (Table 3). Females from the data sets were more different but showed some similarities within the Chignik and the Kodiak data sets (Table 4). The females from Yakutat also showed much in common with females of the Chignik data sets.

The multivariate T^2 tests computed for the 1981 comparisons were much less tolerant (Table 5). All data sets showed significant differences for females. For males, the only data sets not significantly different were Kodiak and the Northeast Alaska Peninsula.

The similarity between Kodiak and Northeast Alaska Peninsula length-weight data sets, at least for males, and the fact they were selectively sampled selected to

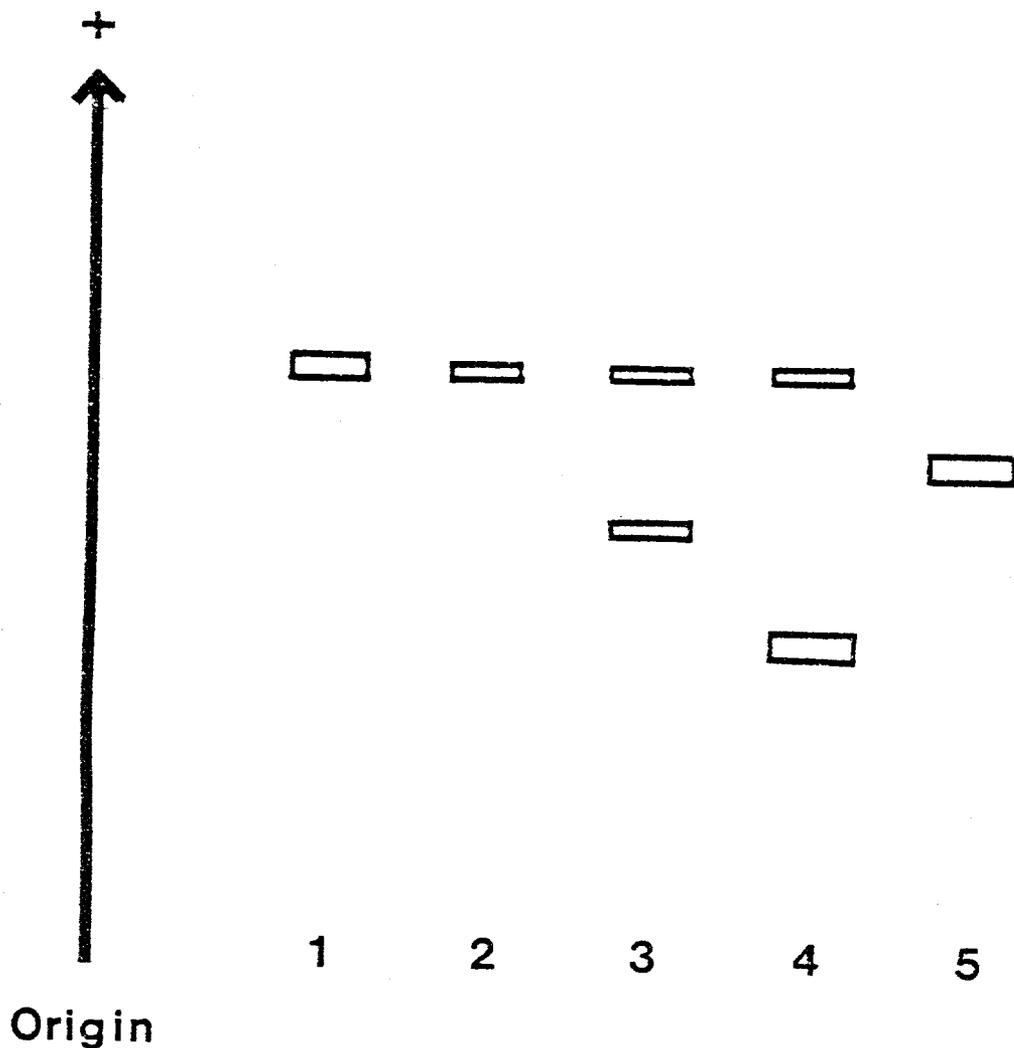


Figure 1. Results of polyacrylamide isoelectric focusing in pink shrimp (*Pandalus borealis*) from the northeastern Pacific Ocean (1981). Representation of the observed phosphoglucomutase (PGM) phenotypes in relation to the marker proteins carbonic anhydrase and myoglobin (not to scale). (1) Myoglobin, 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 allele 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 for females in which eggs had not yet descended to the pleopods. Study areas in 1981 included the Bering Sea, Yakutat Bay, and two bays of Kodiak Island (Outer Marmot and Uganik).

	n	Relative allele frequencies			d.f.	χ^2
		A	B	C		
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

-Continued-

Table 1. Differences in PGM allele 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 for females in which eggs had not yet descended to the pleopods. Study areas in 1981 included the Bering Sea, Yakutat Bay, and two bays of Kodiak Island (Outer Marmot and Uganik) - continued.

	n	Relative allele frequencies			d.f.	X ²
		A	B	C		
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*
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	1.00	--	--		
3) Outer Marmot Bay (Kodiak Island)	4	0.750	0.250	--		
Test of homogeneity in 1, 2, and 3					2	2.12

-Continued-

Table 1. Differences in PGM allele 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 for females in which eggs had not yet descended to the pleopods. Study areas in 1981 included the Bering Sea, Yakutat Bay, and two bays of Kodiak Island (Outer Marmot and Uganik) - continued.

	n	Relative allele frequencies			d.f.	χ^2
		A	B	C		
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*
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
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 the chi-square goodness-of-fit test for Hardy-Weinberg distribution.

Table 2. Tests for differences in log (carapace length) (independent variable) to log (wet weight) (dependent variable) 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	n_1	n_2	n_3	n_4	n_5	F
Bering Sea						
1978/79 (NMFS)						
1981 (Author)						
Male	170	239				13.08**
Female	206	252				2.43
Yakutat Bay						
1981 (NMFS)						
1981 (Author)						
Male	53	265				95.39**
Transitional	83	21				34.71**
Female	6	346				1.97
Kodiak Island						
Spring 1973 (NMFS)						
Fall 1974 (NMFS)						
Winter 1974 (NMFS)						
Winter 1975 (NMFS)						
1981-Fresh (Author)						
Male	64	267	21	55	501	60.67**

-Continued-

Table 2. Tests for differences in log (carapace length) (independent variable) to log (wet weight) (dependent variable) 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 (continued).

Area	n ₁	n ₂	n ₃	n ₄	n ₅	F
Spring 1973 (NMFS) Winter 1975 (NMFS) 1981-Fresh (Author)						
Transitional	3	12	5			32.74**
Spring 1973 (NMFS) Fall 1974 (NMFS) Winter 1975 (NMFS) 1981-Fresh (Author)						
Female	161	7	13	1218		374.82**
Fall 1974 (NMFS) Winter 1974 (NMFS) Winter 1975 (NMFS) 1981-Fresh (Author)						
Ovigerous Female	46	64	58	23		7.40**

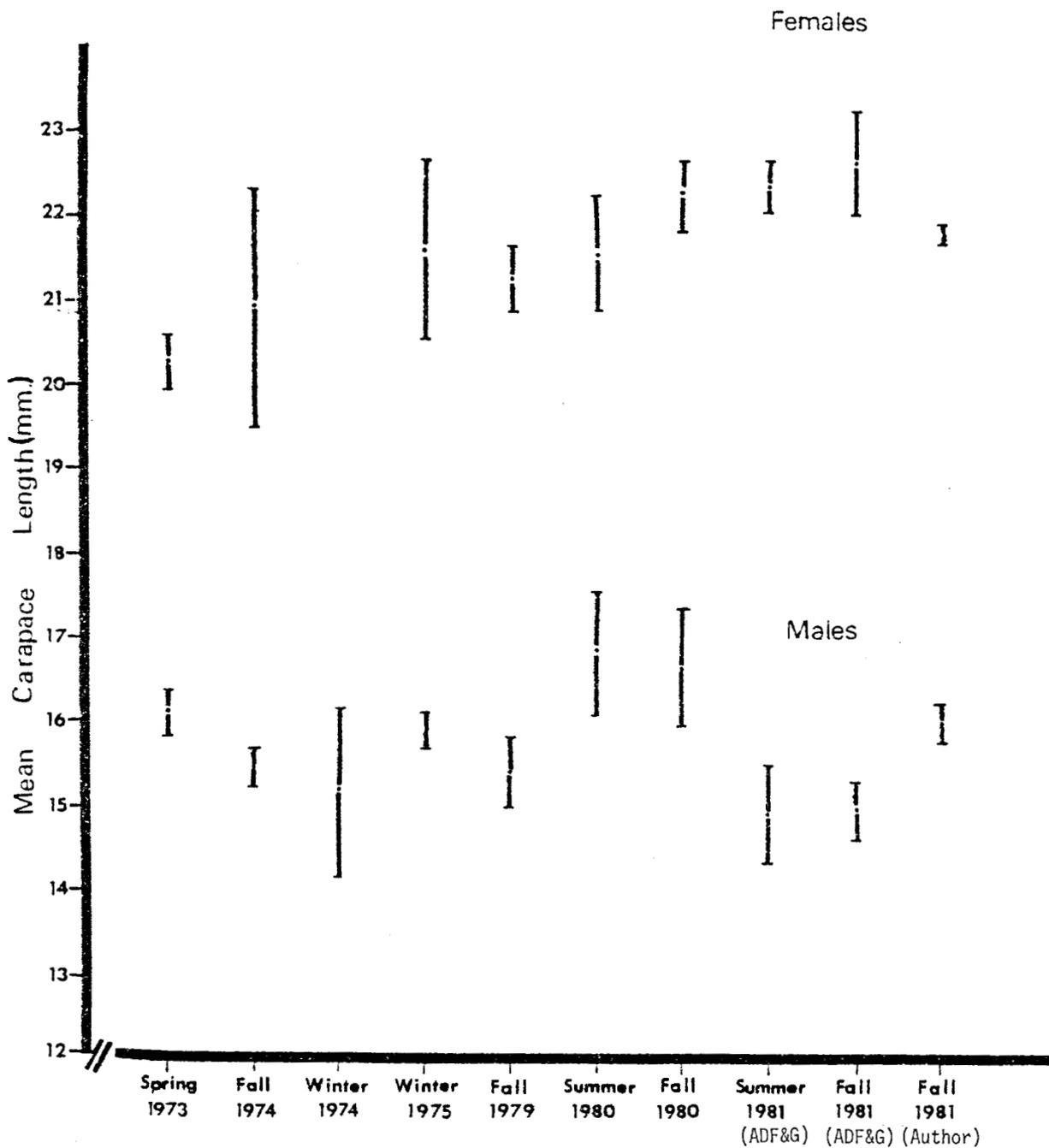


Figure 2. Mean carapace length of pink shrimp (*Pandalus borealis*) from the Kodiak Island area by season and year (± 2 SE). Data were obtained from NMFS (1973-1975) and ADF&G (1979-1980).

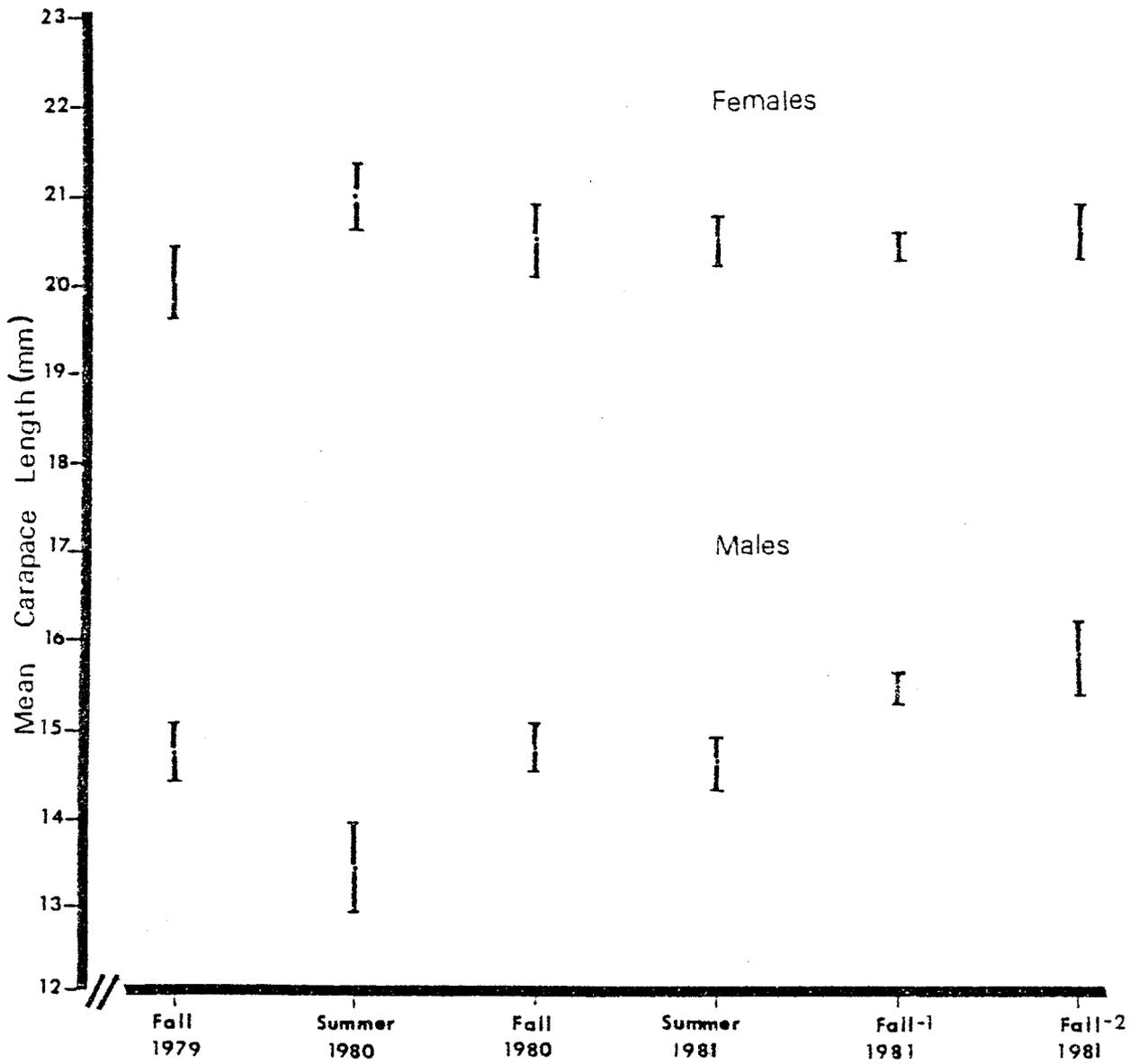


Figure 3. Mean carapace length of pink shrimp (*Pandalus borealis*) from Chignik Bay by season and year (± 2 SE). Data were obtained from ADF&G (1979-1981).

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 ('-' indicates significant difference at $\alpha = 0.05$; '+' indicates 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	C	+	-	-	-	-	-	+	-	-	+	-	+
(NMFS)	T	+											
	W	+	+	-			+	+					-
Yakutat	C		+	-	+	+	+	+	-	+	+	-	-
(author)	T		+	-			-	+					-
	W		+	-			-	+					-
Kodiak	C			+	-	-	+	+	-	+	+	-	+
(fresh)	T			+			+	+					-
	W			+			+	+					-
Kodiak	C				+	+	-	+	+	+	-	+	-
(summer)	T				+								
	W				+								
Kodiak	C					+	-	+	+	+	-	+	-
(fall)	T					+							
	W					+							
Kodiak	C						+	+	-	+	+	-	+
(frozen)	T						+	+					-
	W						+	+					-

-Continued-

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 ('-' indicates significant difference at $\alpha = 0.05$; '+' indicates nonsignificant difference at $\alpha = 0.05$). Data sets are arranged from most eastern (Yakutat) to most western (Bering Sea) - 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. C							+	+	+	+	+	+
Penin. T							+					+
(author) W							+					+
Chignik C								+	+	+	+	-
(summer) T								+				
W								+				
Chignik C									+	+	-	+
(fall-1) T									+			
W									+			
Chignik C										+	-	+
(fall-2) T										+		
W										+		
Pavlof C											+	-
(summer) T											+	
W											+	
Bering C												+
Sea 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 ('-' indicates significant difference at $\alpha = 0.05$; '+' indicates 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. Comparison of mean carapace length (C), total length (T), and wet weight (W) in pink shrimp (*Pandalus borealis*) females for 1981 data sets ('-' indicates significant difference at $\alpha = 0.05$; '+' indicates nonsignificant difference at $\alpha = 0.05$). Data sets are arranged from most eastern (Yakutat) to most western (Bering Sea) - 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 C							+	+	+	+	-
(summer) T							+				
W							+				
Chignik C								+	+	+	-
(fall-1) T								+			
W								+			
Chignik C									+	+	-
(fall-2) T									+		
W									+		
Pavlof C										+	-
(summer) T										+	
W										+	
Bering C											+
Sea T											+
W											+

Table 5. Value and significance of Hotelling's T^2 statistic between 1981 data sets of male (M) and female (F) pink shrimp (*Pandalus borealis*). Vector components were wet weight (g) and carapace length (mm).

	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

represent as many length classes as possible) made it inappropriate to conclude that differences existed. 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 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 which also contained data for 13 additional metric and nonmetric characters, were initially examined to determine area differences. 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 pereopod measurements (Appendix D). For transitionals, no between-area differences were 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 (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 with a complete set of measurements. An initial SDFA with 12 metric variables (excluding total length) was employed with 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. This two-step procedure was repeated until the number of cases increased to 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. 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 shows plots against 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 Figure 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

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

Independent Variable (x)	Dependent Variable (y)	Regression Equation	Correlation (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

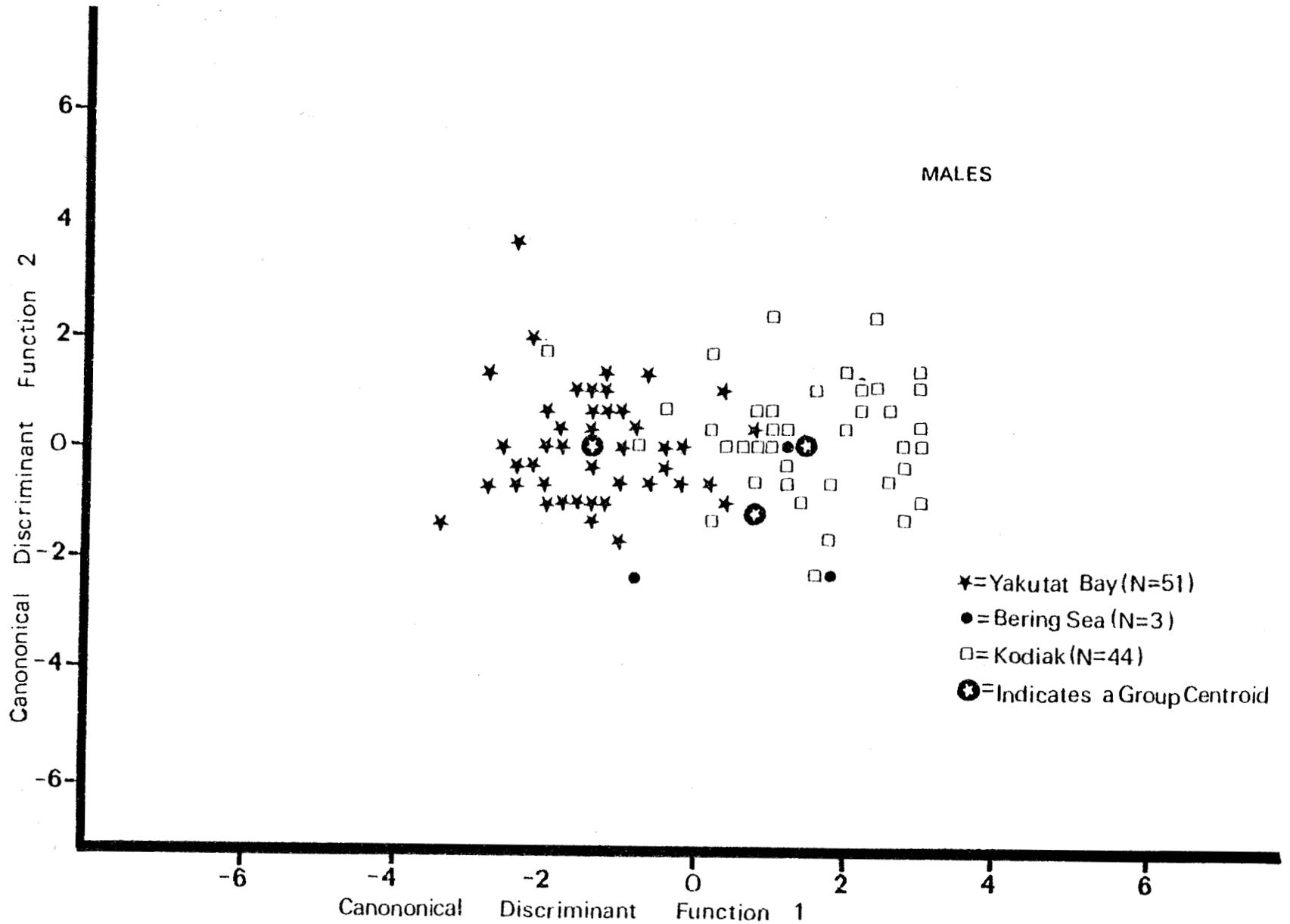


Figure 4. Results from discriminant function analysis of male pink shrimp (*Pandalus borealis*) collected in fall 1981. The scatterplot shows morphological differences in pink shrimp for Yakutat Bay and Kodiak Island.

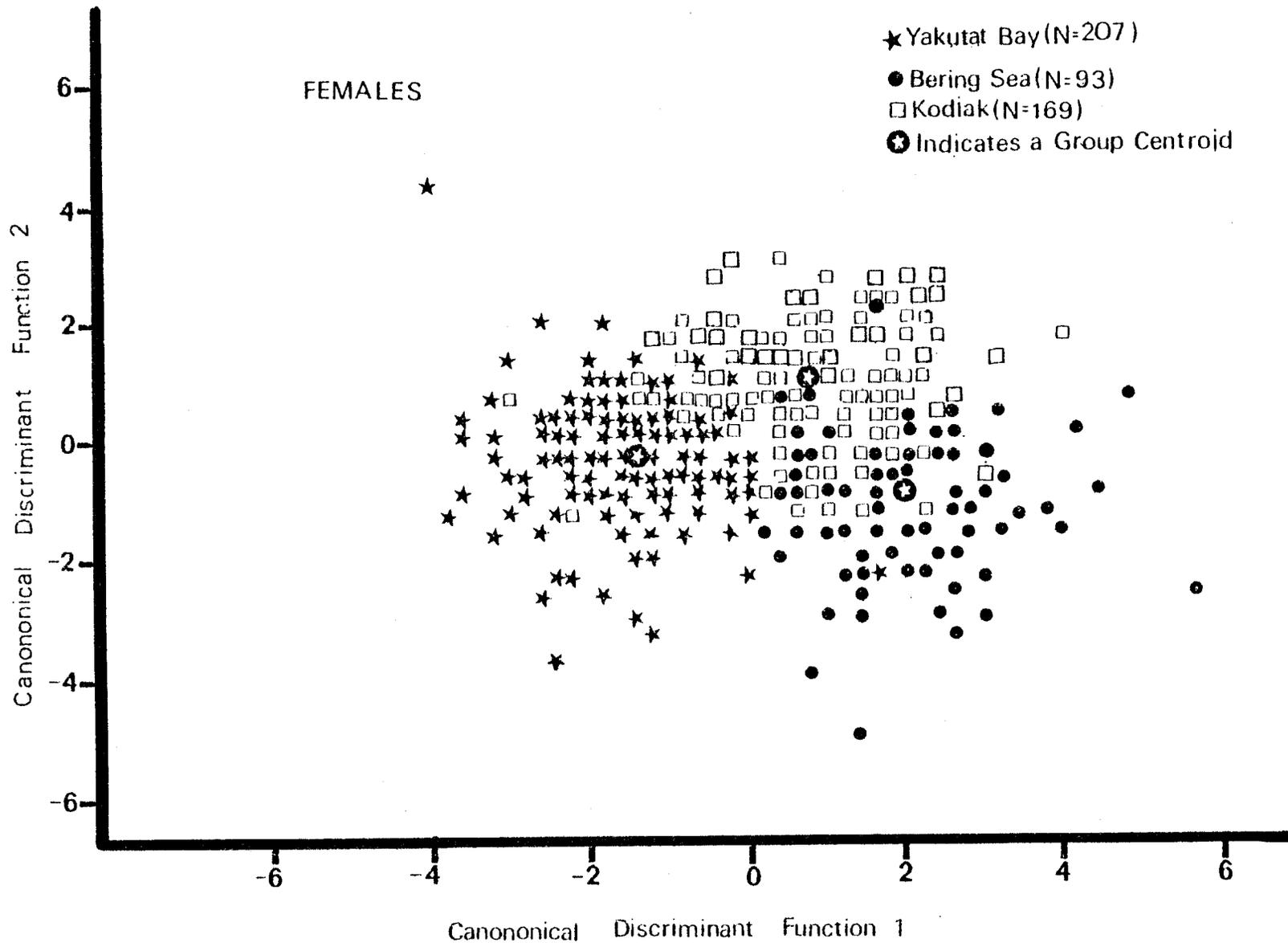


Figure 5. Results from discriminant function analysis of female pink shrimp (*Pandalus borealis*) collected in fall 1981. The scatterplot shows morphological differences in pink shrimp for Yakutat Bay, the Bering Sea, and Kodiak Island.

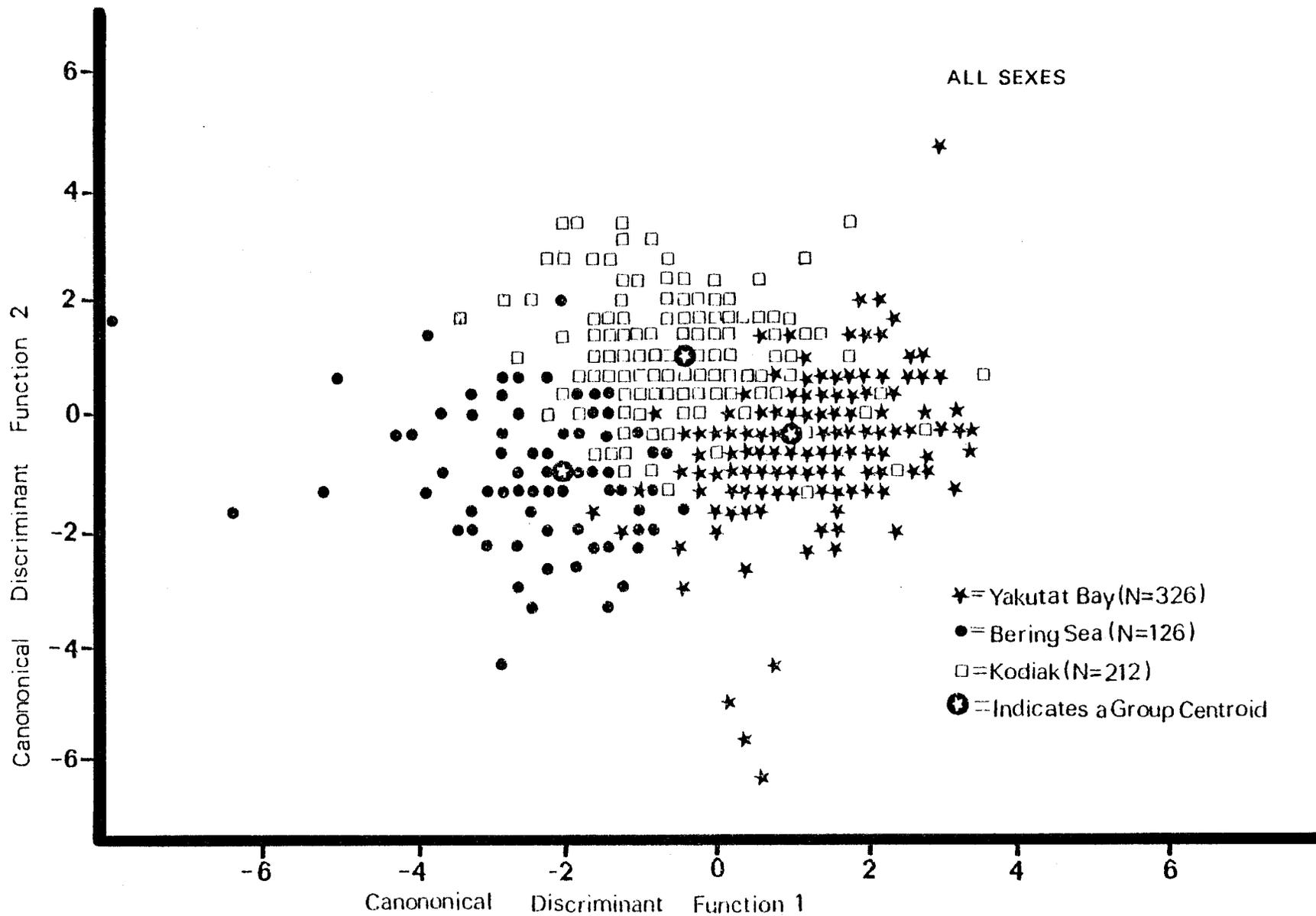


Figure 6. Results from discriminant function analysis of all sex groupings of pink shrimp (*Pandalus borealis*) collected in fall 1981. The scatterplot shows morphological differences in pink shrimp for Yakutat Bay, the Bering Sea, and Kodiak Island.

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 pereopod 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

-Continued-

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) - continued.

Characters (in the order added by DISCRIMINANT)	Wilks' Lambda	P	Standardized Canonical Discriminant Functions	
			Funct. 1	Funct. 2
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 pereopod 3	0.3169	< 0.0001	1.5719	0.0800
Wet weight	0.2899	< 0.0001	-1.0636	1.4823
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	χ^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 $\alpha = 0.01$).

Area 1	Area 2	
	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**

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, relatively high percentages of individuals were correctly classified (Table 10). However, with only one significant discriminant function in males, the percentage correctly classified would probably have been greatly reduced if the Bering Sea sample size had been larger.

For females and sexes combined, the discriminant functions showed good separation for three regions. In addition to the classification results, this was demonstrated by two significant 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 scatterplots that contained three visually distinct groups (see Figures 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 samples from the Bering Sea had a low occurrence of parasitic isopods, it was significantly higher than in Yakutat Bay and Kodiak Island bays 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 show that year-classes grew at a similar rate.

The testing of differences in carapace lengths for designated age groups between study areas was done separately for summer survey data and 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 exhibited significant differences ($\alpha = 0.05$). Further 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 large difference in ranks (significant at $\alpha = 0.10$). 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 age-carapace lengths of Appendix H. Program limitations are discussed in the following section.

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

Actual Group	Number of cases	Predicted Group Membership			Percentage of total 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%)	185 (8.5%)	173 (81.6%)	
					86.45

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		

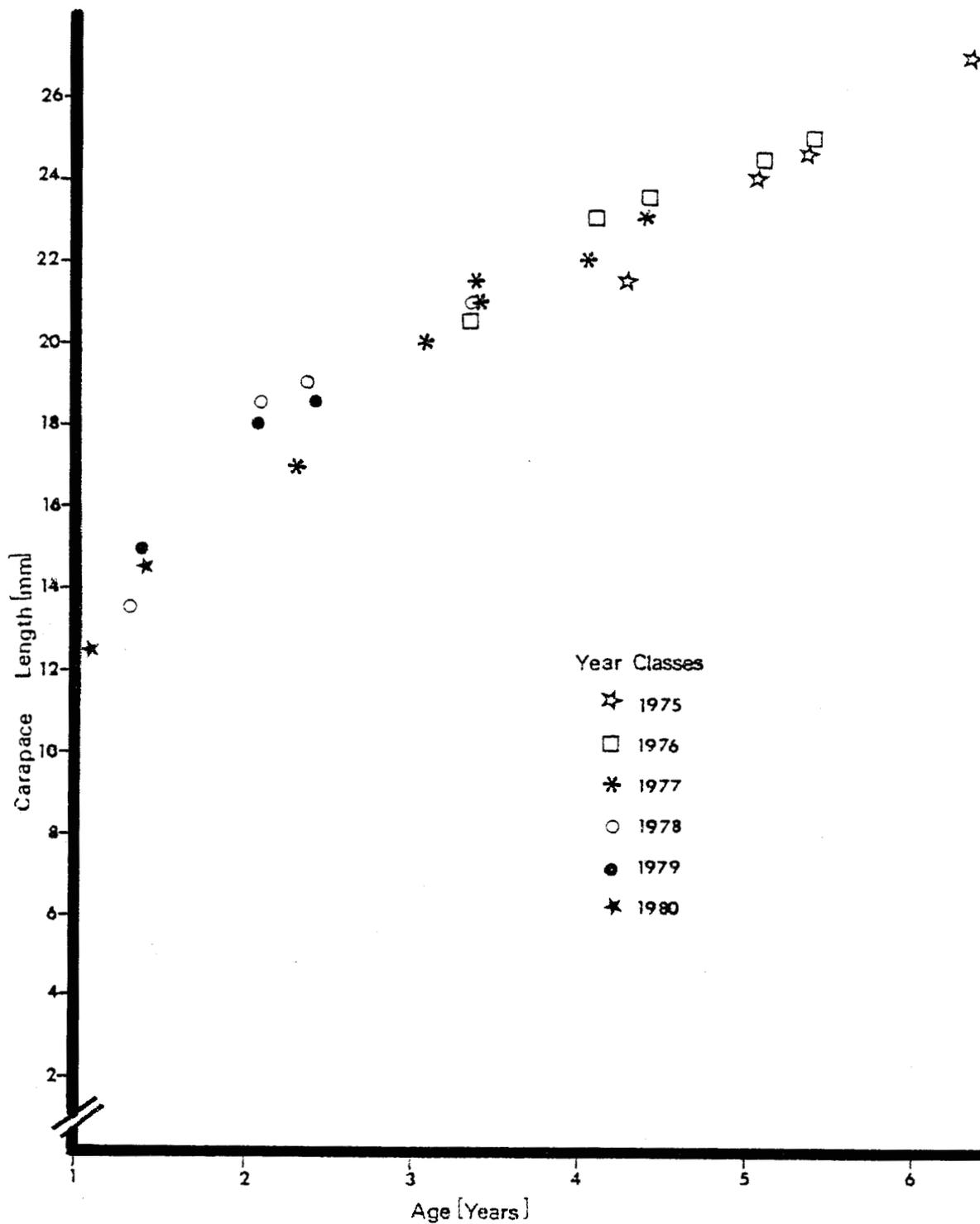


Figure 7. Apparent growth in Kiliuda Bay (Kodiak Island) pink shrimp (*Pandalus borealis*) of the 1975 to 1980 year-classes, based on the Von Bertalanffy growth equation.

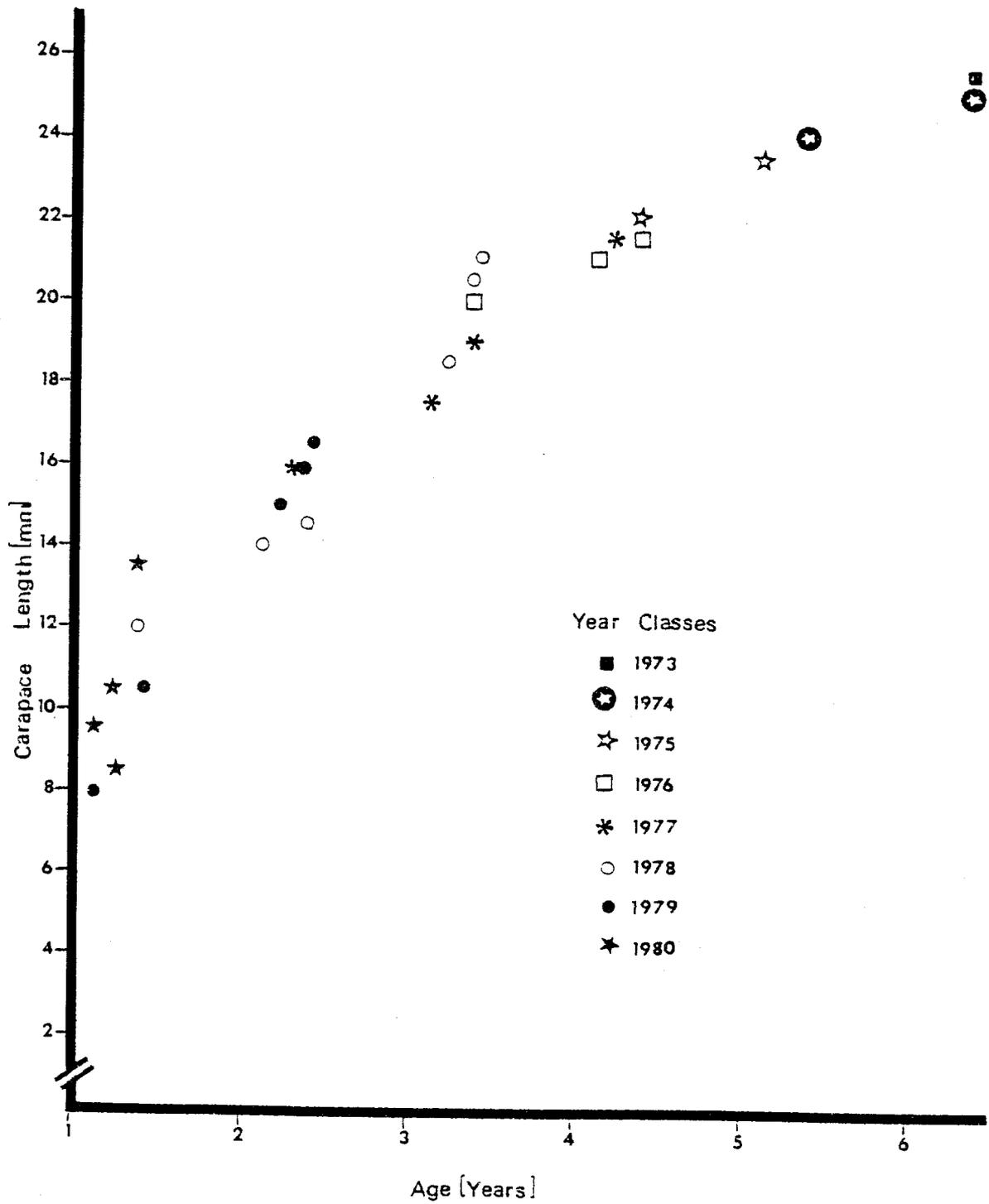


Figure 8. Apparent growth in Chignik Bay (Western Alaska Peninsula) pink shrimp (*Pandalus borealis*) of the 1973 to 1980 year-classes, based on the Von Bertalanffy growth equation.

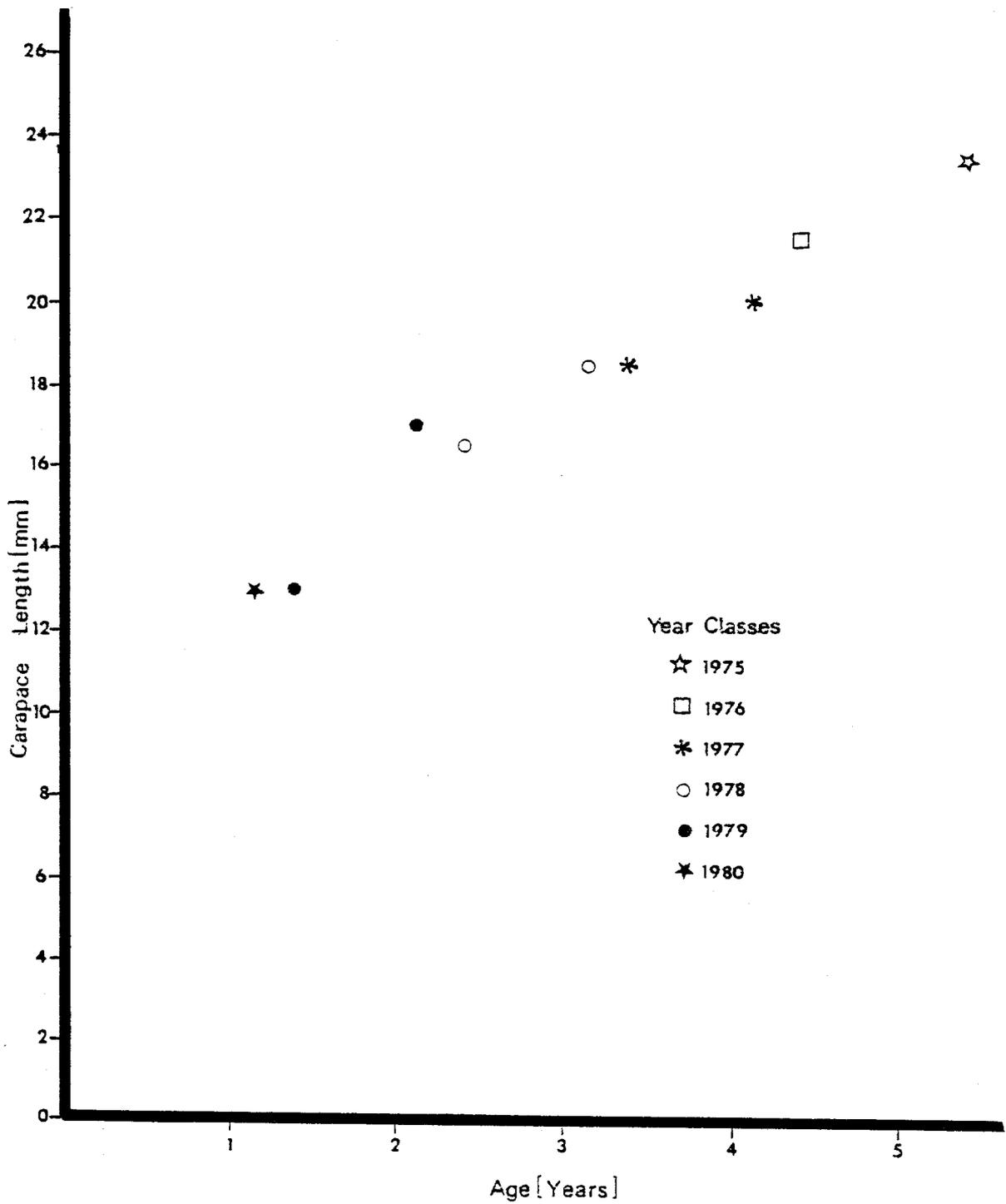


Figure 9. Apparent growth in Pavlof Bay (Western Alaska Peninsula) pink shrimp (*Pandalus borealis*) of the 1975 to 1980 year-classes, based on the Von Bertalanffy growth equation.

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 tests for differences in age designations (by carapace lengths) from Kiliuda Bay, Chignik Bay, and Pavlof Bay. Blocks are ages and treatments are areas (* significant at $\alpha = 0.05$).

	Sums of ranks	χ^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), 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 the 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 Age was assumed to have been reported in months.

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 demonstrated 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. Results from the three PGM alleles identified in this study agreed with the starch-gel electrophoretic findings of Johnson et al. (1974) and Giorgi¹ for pink shrimp. Unfortunately, isoelectric focusing did not identify additional alleles as had been hoped. Because Uganik Bay shrimp did not meet the assumptions of Hardy-Weinberg equilibrium, this study did not compare individual Kodiak bay areas. However, because there were no significant differences in PGM allele frequencies in central and eastern area shrimp, it was assumed there were no significant differences within central area shrimp. This corresponds to the electrophoretic findings of Giorgi¹ who compared pink shrimp from Kiliuda, Alitak, and Ugak Bays on Kodiak Island and found no significant differences.

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 Giorgi¹ states 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 probably mistook the 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). 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 has not been reported previously in the literature. It would be of biological interest and useful in terms of stock delimitation (since multiple enzyme studies allow 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. 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, which involved smaller body parts, were measured to the nearest 0.2 mm.

To accurately assess morphological differences between the five study areas, initial analyses discussed in detail in the Materials and Methods section were used to minimize extraneous 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 which was also more distinct in females than in males. This sexual difference was supported by a lobster tagging study showing strong homing abilities in displaced females. Examples of sexual disparity found in this study are listed below.

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 proximity.
2. The analysis of variance of metric characters. For males (Appendix D), three characters showed no significant difference in eastern, central, and western shrimp. Females, however, showed significant differences for all metric characters (Appendix F).
3. The SDFA which yielded only one statistically significant discriminant function for males. As a result, only central and eastern male shrimp were distinguishable (Figure 4). The SDFA for females, in contrast, yielded two significant discriminant functions with good separation for three regions (Figure 5). In fact, females could be better classified (Table 10) than combined sexes. This is probably because females within a given study area were more homogeneous than the group of all sexes. Therefore, discriminating between them became a much easier task. This was apparent in the number of discriminating variables important to each group's first discriminant function. For sexes combined, four variables had almost equal contribution to the first discriminant function while the female discriminant function had only two variables of importance.

Saila and Flowers (1969) found that in SDFA physical 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, because sex is so strongly related to size in *P. borealis*, it was assumed that size variation had been 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, because of the unique life history of the shrimp, with individuals beginning as males and subsequently transforming to females, complications occurred when modes of length-frequency distributions were used to assigning ages.

Sexed length-frequency distributions give a clearer picture of age structure than unsexed frequencies, but a long-term monthly series is required for accurate aging of age classes older than 3+. This is ascribed to a "splitting of the 2+ [age] group at approximately 30 months of age [Kodiak Island area] 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 Southeastern Alaska one could find three females of 20 mm carapace length having three substantially different weights, presumably because they were of 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 varies 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 Atlantic 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 post-larval stage (<8.0 mm in carapace length), is not available to trawl gear. Among the 1+ group, it is assumed the distribution is skewed by gear selection toward larger animals in the age group. A result is that the actual mean size is often smaller for this 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, agrees with the growth cline reported by Ivanov (1969). He showed that growth of pink shrimp in the Bering Sea was slower than in Western Gulf of Alaska (Kodiak Island area) shrimp. Maturation was approximately one year later for Bering Sea shrimp. Ivanov attributed the differences to cooler Bering Sea water temperatures, for 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 those from Ivanov's study areas.

The BGC II FORTRAN program used to calculate Von Bertalanffy growth curve and constants would accept only equally spaced age groups. Consequently 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. However, the early summer shrimp, particularly transforming females, do exhibit substantial growth 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 appear to be a more reasonable description of *P. borealis* growth.

For Kiliuda Bay, the BGC II estimate of the growth curve constant l_{∞} was a reasonable value considering the known maximum length 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 closer to the truth. The poor BGC II estimates for Pavlof Bay probably resulted from the small number of age-length estimates available.

CONCLUSIONS AND SIGNIFICANCE OF STUDY

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

Analysis of Genetic Variation

It was concluded that Bering Sea shrimp were genetically distinct from Kodiak Island and Yakutat Bay shrimp at the PGM locus.

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. 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 although low, 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 in Yakutat Bay and Bering Sea shrimp.

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

Analysis of Age and Growth

The size of Kiliuda Bay shrimp at a given age was significantly larger when compared to samples of corresponding ages from Chignik Bay and Pavlof Bay. Kiliuda Bay shrimp appeared to grow faster than Pavlof Bay and Chignik Bay shrimp.

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

areas. This strong evidence suggests that Bering Sea shrimp are a separate population or stock. Marked morphological differences between Kodiak Island and Yakutat Bay shrimp suggest that these areas might also have separate breeding populations. The Northeast Alaska Peninsula shrimp did not appear to differ from Kodiak Island area shrimp. Shrimp from Pavlof Bay and Chignik Bay on the Western Alaska Peninsula were not mutually distinct but were different from other study area samples. This suggests that together they might make up another population. Note, however, that the paucity of data from these two bays make this conclusion tenuous.

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

Other findings and accomplishments of this study include:

1. The absence of the LAP enzyme in *P. borealis*,
2. At the PGM locus, the tendency for the frequency of the allele identified as A to decrease and the frequency of the allele identified as B to increase as the shrimp age and progress 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, and
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				Total
	Male	Trans.	Female	Female with Head Roe	
<u>Bering Sea (1981)</u>					
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
<u>Kodiak (1981)</u>					
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

-Continued-

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

	Number of shrimp analyzed				Total
	Male	Trans.	Female	Female with Head Roe	
<u>Yakutat (1981)</u>					
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.

Group	Wet Weight			Carapace Length			Total Length		
	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) (independent variable x) to log (wet weight) (dependent variable 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

-Continued-

Appendix C. Log (carapace length) (independent variable x) to log (wet weight) (dependent variable 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 (continued).

Area	n	Regression Equation	r
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	13.97	14.71	748	73.45**
Antennal scale width (mm)	2.56	2.81	3.01	873	100.23**
Merus length on pereopod 3 (mm)	15.53	15.26	15.37	644	1.42
Carpus length on pereopod 3 (mm)	4.55	4.57	4.52	594	0.43

-Continued-

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 pereopod 3 (mm)	17.66	17.33	16.82	130	1.71
Carpus length on pereopod 3 (mm)	5.15	5.50	4.97	117	1.32

-Continued-

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 $\alpha = 0.01$).

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 pereopod 3 (mm)	19.59	20.11	20.48	834	16.43**
Carpus length on pereopod 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. Vector components were 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).

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

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).

Age ¹	Carapace length (in mm) for estimated year-classes							
	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				

-Continued-

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) - continued.

Age ¹	Carapace length (in mm) for estimated year-classes							
	1973	1974	1975	1976	1977	1978	1979	1980
4.43					23.0			
5.09			24.0					
5.12				24.5				
5.40			24.5					
5.43				25.0				
6.43			27.0					
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			

-Continued-

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) - continued.

Age ¹	Carapace length (in mm) for estimated year-classes							
	1973	1974	1975	1976	1977	1978	1979	1980
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						
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			

-Continued-

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) - continued.

Age ¹	Carapace length (in mm) for estimated year-classes							
	1973	1974	1975	1976	1977	1978	1979	1980
4.14					20.0			
4.40				21.5				
5.40			23.5					

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

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