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Genetic Structure of Red King Crab Populations in Alaska Facilitates Enforcement of Fishing Regulations

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ABSTRACT

Horizontal starch-gel electrophoresis of proteins has proven to be a powerful tool for the management of many marine species. This technique provides data on the genetic relationships of reproductively isolated populations, thereby helping scientists to optimally manage these self-recruiting stocks. Additionally, when large genetic differences are found between populations, collections from unknown origin may be genetically screened and unambiguously classified.

We examined collections of red king crab from thirteen localities in Southeast Alaska, the Aleutian Islands, and the eastern Bering Sea for genetic variation at 42 protein coding loci. Two highly polymorphic loci, *Pgdh* (Phosphogluconate dehydrogenase) and *Alp* (Alkaline phosphatase), were useful for discriminating population differences between major geographic areas. The eastern Bering Sea collections from Bristol Bay and Norton Sound were very different from all other collections. Further, Southeast Alaska collections appear to form a population unit discrete from the Kenai, Alaska Peninsula, and Aleutian collections. Additional polymorphic loci appear to be useful in further differentiating populations, and we are continuing our study.

In January, 1989, we analyzed 89 red king crab samples of unknown origin. These samples were from a boatload of crabs allegedly caught near Adak Island in the Aleutian Islands. Enforcement personnel from Alaska Department of Public Safety and biologists from Alaska Department of Fish and Game believed that the crabs were actually caught in Bristol Bay during an area closure. Our data clearly showed that the crabs could not have come from Adak Island and that they probably originated from the Norton Sound/Bristol Bay population. Based on these findings the vessel owner and the skipper agreed to pay the state $565,000 in penalties for fishing violations.

We believe that these genetic data should be of considerable use in the harvest management of Alaskan red king crab. Additionally, the knowledge by fishermen that unknown samples may be identified to population of origin may deter illegal fishing and improve the quality of catch statistics used to manage crab fisheries.

INTRODUCTION

The red king crab, *Paralithodes camtschatica* (Tilesius), is a large anomuran decapod of the family Lithodidae which is distributed from the Chukchi Sea south along the western side of the North Pacific Ocean to the Sea of Japan (Sato, 1958) and along the eastern side to British Columbia (Butler and Hart, 1962). Since the mid-1950s major Alaskan fisheries for this species have occurred primarily in Bristol Bay, around Kodiak Island, around the Aleutian Islands, and along the southern coast of the Alaska Peninsula (Blau, 1985). Red king crab stocks have experienced an extreme decline in abundance in the last decade. To conserve this dwindling resource, commercial fisheries for red king crab were open only in limited areas during recent years.

The poor condition of red king crab stocks prompted attempts to evaluate causes of the declines (Blau, 1986; Otto, 1986) and to reexamine present methods of stock assessment and management (Otto, 1986). The delineation of genetic stock structure is an important concern in crustacean management (e.g., Davidson et al., 1985) and may provide critical insight into optimal harvest strategies for non-interbreeding populations. In 1987 we began biochemical genetic investigations of Alaska red king crab to determine (1) the amount of variation within populations, (2) the amount of divergence between populations, and (3) optimal sampling strategies to maximize allozyme activity and resolution (Seeb et al., 1990).

We previously surveyed three populations and found overall genetic variability to be low. However, two highly polymorphic loci distinguished geographically isolated collections of crabs (Seeb et al., 1990). As a result, we additionally examined 13 crab collections throughout Alaska to further ascertain the amount of genetic population subdivision and to evaluate how these genetic data could aid in defining self-recruiting management units.

In this study we demonstrated the enforcement potential of these data as illustrated by the analysis of confiscated crabs of unknown origin allegedly caught near Adak Island in the Aleutian Island chain. Enforcement personnel from Alaska Department of Public Safety and biologists from Alaska Department of Fish and Game believed that the crabs were actually caught in Bristol Bay during an area closure. Our data showed that the confiscated crabs did not belong to the same genetic stock as our known Adak Island samples, and they most likely originated from an eastern Bering Sea population.

MATERIALS AND METHODS

Red king crab were collected by personnel of the Alaska Department of Fish and Game from 13 sites ranging from Southeast Alaska to the eastern Bering Sea (Figure 1). Sampling included two separate locations from the Adak Island vicinity. Sample sizes ranged from 50-100 individuals from all populations with the exception of Excursion Inlet (N=26) and a very small sampling from Bristol Bay (N=6). Tissues (muscle, gill, hepatopancreas, and heart) were dissected from each individual, labeled, placed in a capped tube, and frozen as soon as possible at -15°C. Within a few weeks, all tissues were transported to the laboratory on dry ice and stored at -80°C until analysis.

Red king crab of unknown origin, allegedly caught near Adak Island in the Aleutian Islands, were confiscated by the Alaska Department of Public Safety. Tissues from these confiscated individuals were dissected and handled as above.

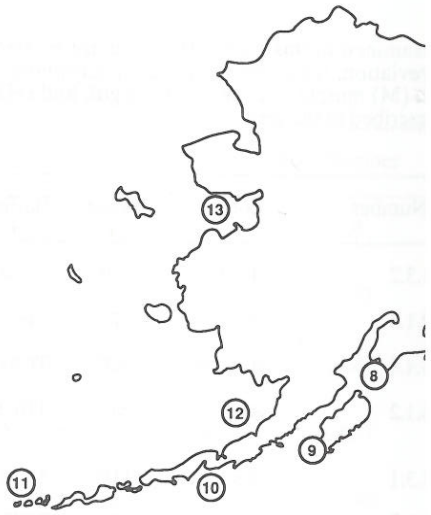

Figure 1. Sampling localities of red king crab.

Procedures for horizontal starch gel electroph
Hopkinson (1976), Allendorf et al. (1977),
(1990). A total of 42 loci were resolved using
(1) N-(3-aminopropyl)-morpholine, citrate (
1972); (2) Tris, borate, citrate, lithium hydrox
1970); (3) Tris, citrate (TC, pH 7.0; Shaw and
pH 8.0; Selander et al., 1971); (5) Tris, borate,
1963); (6) Tris-citrate (0.005 M), MgCl (0.02 M
pH 7.5 and a borate (0.03 M) tray buffer adjust

Allele frequency estimates were calculated f
unknowns, and used to generate a distance ma
chord distances (Cavalli-Sforza and Edwards,
in turn used to construct a phenogram (UPG
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hypothesis of panmixia between the two Adal
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table, where M is the number of populations
calculated as (M-1)(N-1).

Second, a discriminant analysis was perfor
describe the linear function that maximized s
Sea (represented by the Norton Sound populat
size was too small to accurately characterize th
Island populations and to identify the loci
separation. At each polymorphic locus, the n
was equivalent to N-1 where N is the numbe
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doses of particular alleles. Seven polymorphic
(*Ah*, *Alp*, *Gpi*, *Mdh1*, *Pgdh*, *Ldh3*, *Peplt2*), produ

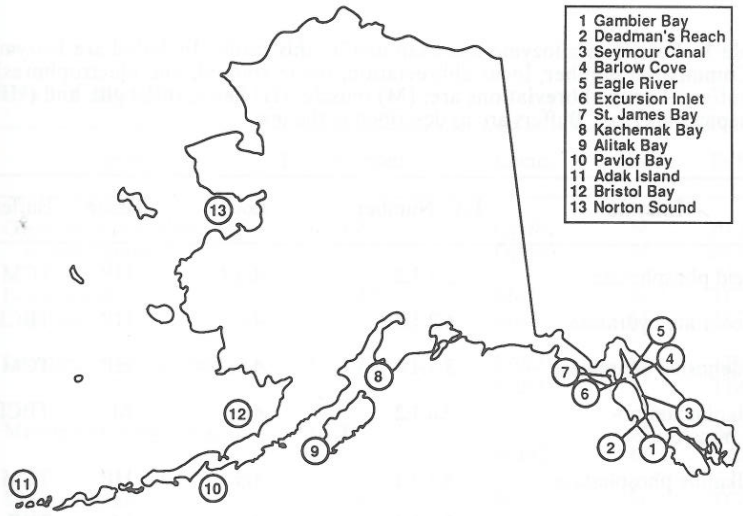

Figure 1. Sampling localities of red king crab.

Procedures for horizontal starch gel electrophoresis followed those of Harris and Hopkinson (1976), Allendorf et al. (1977), May et al. (1979), and Seeb et al. (1990). A total of 42 loci were resolved using the following buffers (see Table 1): (1) N-(3-aminopropyl)-morpholine, citrate (**AC**, pH 6.9; Clayton and Tretiak, 1972); (2) Tris, borate, citrate, lithium hydroxide (**TBCL**, pH 8.7; Ridgway et al., 1970); (3) Tris, citrate (**TC**, pH 7.0; Shaw and Prasad, 1970); (4) Tris, citrate (**TC**, pH 8.0; Selander et al., 1971); (5) Tris, borate, EDTA (**TBE**, pH 8.5; Boyer et al., 1963); (6) Tris-citrate (0.005 M), MgCl (0.02 M) gel buffer adjusted with NaOH to pH 7.5 and a borate (0.03 M) tray buffer adjusted with NaOH to pH 8.6 (**TCM**).

Allele frequency estimates were calculated for each population, including the unknowns, and used to generate a distance matrix of Cavalli-Sforza and Edwards chord distances (Cavalli-Sforza and Edwards, 1967). These distance values were in turn used to construct a phenogram (UPGMA) using the computer program BIOSYS-1 (Swofford and Selander, 1981).

Two separate statistical analyses were used to test whether the unknown samples originated from Adak Island, as claimed by the owner of the confiscated crabs, or from some other eastern Bering Sea population, as suspected by enforcement personnel. First, heterogeneity chi-square tests were performed to test the null hypothesis of panmixia between the two Adak Island collections and among the Adak and confiscated samples. Degrees of freedom for an M by N contingency table, where M is the number of populations and N the number of alleles, were calculated as $(M\text{-}1)(N\text{-}1)$.

Second, a discriminant analysis was performed using SPSS^X (Nie, 1983) to describe the linear function that maximized separation between eastern Bering Sea (represented by the Norton Sound population because the Bristol Bay sample size was too small to accurately characterize the population) and the pooled Adak Island populations and to identify the loci contributing significantly to their separation. At each polymorphic locus, the number of discriminating variables was equivalent to N-1 where N is the number of alleles, and the most common allele was the one eliminated. Each individual was scored according to number of doses of particular alleles. Seven polymorphic loci were included in the analysis (*Ah*, *Alp*, *Gpi*, *Mdh1*, *Pgdh*, *Ldh3*, *Peplt2*), producing eight discriminating variables

Table 1. Forty-two allozyme loci examined in this study. Included are Enzyme Commission number, locus abbreviation, tissue studied, and electrophoresis buffer. Tissue abbreviations are: (M) muscle, (H) heart, (GL) gill, and (HP) hepatopancreas. Buffers are as described in the text.

Enzyme	E.C. Number	Locus	Tissue	Buffer
Acid phosphatase	3.1.3.2	*Acp1*	HP	TCM
Aconitate hydratase	4.2.1.3	*Ah*	HP	TBCL
Adenosine deaminase	3.5.4.4	*Ada2*	HP	TCM
Alanine amino-transferase	2.6.1.2	*Alat*	M	TBCL
Alkaline phosphatase	3.1.3.1	*Alp*	HP	TCM
Aspartate amino-transferase	2.6.1.1	*Aat*	M	TBE
Creatine kinase	2.7.3.2	*Ck2*	H	TC8.0
Cytochrome-b_5 reductase	1.8.1.4	*Cybr2*	H	TBCL
Esterase	3.1.1.1	*Est1*	GL	TBE
		Est2	GL	TBE
		Est3	GL	TBE
		Est4	GL	TBE
Fructose-biphosphate aldolase	4.1.2.13	*Fb1*	M	AC6.9
		Fb2	M	AC6.9
Fumarate hydratase	4.2.1.2	*Fh1*	M	TBE
b-N-acetylgalactos-aminidase	3.2.1.53	*bGala2*	GL	TBCL
		bGala3	GL	TBCL
N-acetyl-b-glucos-aminidase	3.2.1.30	*bGa1*	GL	TBCL
		bGa2	GL	TBCL
Glucose-6-phosphate isomerase	5.3.1.9	*Gpi*	M	TBCL
b-Glucuronidase	3.2.1.31	*bGus*	HP	TBCL
Glyceraldehyde-3-phosphate dehydro-genase	1.2.1.12	*Gapdh*	M	TC7.0

Table 1. Continued.

Enzyme	E.C. Number
Glycerol-3-phosphate dehydrogenase	1.1.1.8
Isocitrate dehydro-genase	1.1.1.42
Lactate dehydrogenase	1.1.1.27
Malate dehydrogenase	1.1.1.37
Malic enzyme	1.1.1.40
Mannose-6-phosphate isomerase	5.3.1.8
Peptidase-Lt[1]	3.4._._
Phosphoglucomutase	5.4.2.2
Phosphogluconate dehydrogenase	1.1.1.44
Superoxide dismutase	1.15.1.1
Triose-phosphate isomerase	5.3.1.1
Tripeptide amino-peptidase[2]	3.4.11.4

[1] Resolved with DL-leucyl-DL-tyrosine

[2] Resolved with DL-leucylglycylglycine

Table 1. Continued.

Enzyme	E.C. Number	Locus	Tissue	Buffer
Glycerol-3-phosphate dehydrogenase	1.1.1.8	*Gpdh1*	M	AC6.9
		Gpdh2	M	AC6.9
Isocitrate dehydrogenase	1.1.1.42	*Idh1*	M	TC7.0
		Idh2	M	TC7.0
Lactate dehydrogenase	1.1.1.27	*Ldh2*	M	TBCL
		Ldh3	M	TBCL
Malate dehydrogenase	1.1.1.37	*Mdh1*	M	AC6.9
		Mdh2	M	AC6.9
Malic enzyme	1.1.1.40	*Me*	H	TC8.0
Mannose-6-phosphate isomerase	5.3.1.8	*Mpi*	M	TBE
Peptidase-Lt[1]	3.4._._	*Peplt1*	M	TBCL
		Peplt2	M	TBCL
Phosphoglucomutase	5.4.2.2	*Pgm1*	M	TC7.0
		Pgm2	M	TC7.0
Phosphogluconate dehydrogenase	1.1.1.44	*Pgdh*	M	TC7.0
Superoxide dismutase	1.15.1.1	*Sod1*	H	TBCL
		Sod2	GL	TBCL
		Sod3	M	TBCL
Triose-phosphate isomerase	5.3.1.1	*Tpi*	M	TCM
Tripeptide aminopeptidase[2]	3.4.11.4	*Tpep*	M	TBCL

[1] Resolved with DL-leucyl-DL-tyrosine

[2] Resolved with DL-leucylglycylglycine

(two variables described *Pgdh*). Discriminant function coefficients were standardized by dividing each by the largest coefficient. The absolute value of each standardized value was interpreted as the relative contribution of each variable to discrimination.

Next, the resultant function was used to test the integrity of the discrimination procedure. We classified individual specimens from the eastern Bering Sea and Adak Island populations using the discriminant function and compared these to theoretical group membership. Last we used the discriminant function to classify confiscated crab specimens of unknown origin.

RESULTS

Of the 42 loci resolved, 14 were polymorphic in at least one population of crabs. Of these 14 loci, 11 (*Ada2*, *Ah*, *Est3*, *Gapdh*, *Gpi*, *Gpdh2*, *Ldh2*, *Mdh1*, *Peplt2*, *Pgm2*, *Sod3*) had only low frequency variants (< 0.05), while the remainder were variable at a frequency ≥ 0.05 (*Alp*, *Pgdh*, *Ldh3*). Accordingly, average heterozygosity was low, ranging from 0.013 to 0.025. Pertinent to this project, eight loci were polymorphic in the Adak, eastern Bering Sea, and unknown collections (Table 2).

The overall similarity among populations across all loci is depicted in the phenogram (Figure 2). A central cluster composed of all Southeast Alaska (sites. 1-7) is formed at a genetic distance of approximately 0.032. This cluster is connected to two subgroups including sites in the central and western Gulf of

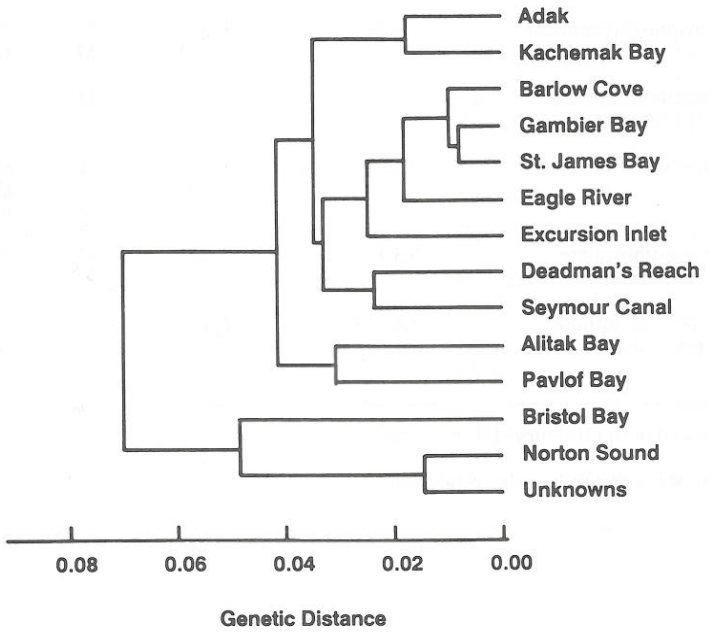

Figure 2. Phenogram based on Cavalli-Sforza and Edwards chord distance (Cavalli-Sforza and Edwards, 1967) depicting overall similarity among red king crab collections in Alaska.

Table 2. Allele frequency estimates and samp
red king crab populations. Alleles are ide
the most common allele in Adak Island whic

Locus and Alleles	Popul: Adak Island	Bristo Bay
Ah		
	(82)	(4)
100	1.00	1.00
90	0.00	0.00
Alp		
	(69)	(6)
100	0.76	0.25
129	0.24	0.75
Est3		
	(89)	(4)
100	1.00	0.75
102	0.00	0.25
Gpi		
	(86)	(6)
100	1.00	1.00
169	0.00	0.00
Ldh3		
	(89)	(6)
100	0.97	1.00
95	0.03	0.00
Mdh1		
	(88)	(6)
100	1.00	1.00
30	0.00	0.00
Peplt2		
	(85)	(6)
100	0.99	1.00
121	0.01	0.00
Pgdh		
	(81)	(6)
100	0.70	0.50
104	0.29	0.50
90	0.01	0.00
94	0.00	0.00

Table 2. Allele frequency estimates and sample sizes (in parentheses) for Alaska red king crab populations. Alleles are identified by their mobility relative to the most common allele in Adak Island which is assigned a mobility of 100.

Locus and Alleles	Population			
	Adak Island	Bristol Bay	Norton Sound	Unknowns
Ah	(82)	(4)	(92)	(95)
100	1.00	1.00	0.97	0.96
90	0.00	0.00	0.03	0.04
Alp	(69)	(6)	(77)	(69)
100	0.76	0.25	0.23	0.20
129	0.24	0.75	0.77	0.80
Est3	(89)	(4)	(90)	(98)
100	1.00	0.75	0.99	0.98
102	0.00	0.25	0.01	0.02
Gpi	(86)	(6)	(90)	(98)
100	1.00	1.00	0.97	0.99
169	0.00	0.00	0.03	0.01
Ldh3	(89)	(6)	(94)	(98)
100	0.97	1.00	1.00	1.00
95	0.03	0.00	0.00	0.00
Mdh1	(88)	(6)	(93)	(98)
100	1.00	1.00	0.99	0.99
30	0.00	0.00	0.01	0.01
Peplt2	(85)	(6)	(92)	(98)
100	0.99	1.00	1.00	1.00
121	0.01	0.00	0.00	0.00
Pgdh	(81)	(6)	(85)	(96)
100	0.70	0.50	0.52	0.48
104	0.29	0.50	0.45	0.51
90	0.01	0.00	0.02	0.01
94	0.00	0.00	0.01	0.00

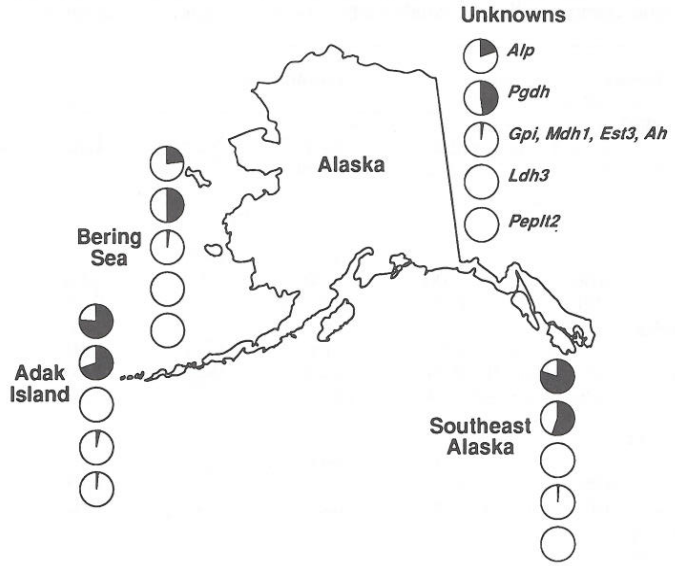

Figure 3. Pie diagrams showing allele frequencies at eight polymorphic loci in representative collections from the eastern Bering Sea and Adak Island. Also shown are pooled frequencies from seven Southeast Alaska collections and the frequencies observed in the unknown samples.

Alaska: (1) Adak Island and Kachemak Bay and (2) Alitak Bay and Pavlof Bay. A separate main branch, including the Bristol Bay (site 12), Norton Sound (site 13), and the unknown population joins the Gulf of Alaska branch at a genetic distance of approximately 0.07. The unknown samples cluster with the Norton Sound and Bristol Bay populations and not with those from Adak Island. The genetic similarity value between Norton Sound and the unknowns was 0.015; genetic similarity between Adak Island and the unknowns was 0.069.

The genetic similarity between the eastern Bering Sea collection and the unknowns can also be seen on a locus-by-locus basis. Figure 3 depicts the frequencies of the Adak Island, eastern Bering Sea, unknowns, and pooled Southeast Alaska populations for six polymorphic loci. For example, Adak Island has a frequency of 0.761 for the common allele at *Alp*. The eastern Bering Sea and unknowns have frequencies of 0.227 and 0.203, respectively. Similarly, the common allele at *Pgdh* occurs at a frequency of 0.698 in Adak Island; but is consistently lower in the eastern Bering Sea and unknown populations with frequencies of 0.500 and 0.479.

Two tests of heterogeneity were performed. In the first we tested for heterogeneity between the two Adak Island collections at the four loci for which they were polymorphic (*Alp*, *Pgdh*, *Peplt2*, or *Ldh3*; Table 2). No evidence of heterogeneity ($P < 0.01$) was found. Significant heterogeneity was detected between pooled Adak and unknown collections, and the null hypothesis of panmixia was rejected ($P < 0.01$) at *Pgdh* and *Alp* (Table 3).

Table 3. Results from chi-square heteroge
confiscated crabs of unknown origin.

		P
	X^2	d
Adak1 - Adak2	1.5	2
Adak1 - Adak2 - Unknowns	21.6	4

One significant function was derived (X^2
discriminant analysis. *Alp* and *Pgdh* provide
based on the values of standardized dis
Discriminant function scores for each indivi
(eastern Bering Sea and Adak Island) were pl
the collection of unknown origin (Figure 4
Bering Sea and unknown individuals overlap
value being 1.6. In contrast, the most freque
be from Adak Island was -1.6. The classific
analysis was able to classify approximately 8
their correct population (Table 4). The pre
group was 87% eastern Bering Sea and 12%
individuals misclassified (13-15%) was ind
unknown individuals classified as Adak Island

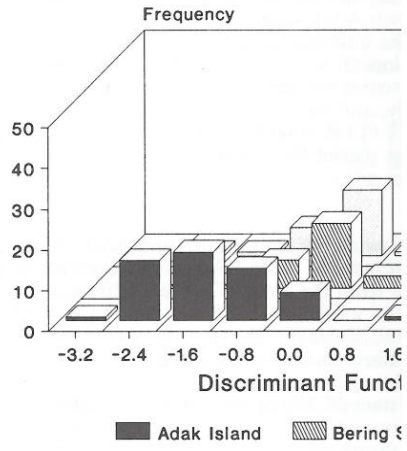

Figure 4. Discriminant function scores for ir
eastern Bering Sea populations and for unkr

Table 3. Results from chi-square heterogeneity analysis of Adak Island and confiscated crabs of unknown origin.

	Pgdh			*Alp*		
	X^2	df	*P*	X^2	df	*P*
Adak1 - Adak2	1.5	2	0.47	1.2	1	0.28
Adak1 - Adak2 - Unknowns	21.6	4	<0.001	88.5	2	<0.001

One significant function was derived (X^2 = 96.67, 3 df, $P < 0.001$) in the discriminant analysis. *Alp* and *Pgdh* provided the greatest discriminating power based on the values of standardized discriminant function coefficients. Discriminant function scores for each individual from the two base populations (eastern Bering Sea and Adak Island) were plotted on a frequency histogram with the collection of unknown origin (Figure 4). The distribution of the eastern Bering Sea and unknown individuals overlap considerably with the most frequent value being 1.6. In contrast, the most frequent value of the individuals known to be from Adak Island was -1.6. The classification procedure of the discriminant analysis was able to classify approximately 85-88% of the known individuals into their correct population (Table 4). The predicted membership of the unknown group was 87% eastern Bering Sea and 12% Adak Island. The percent of known individuals misclassified (13-15%) was indistinguishable from the percent of unknown individuals classified as Adak Island (13%).

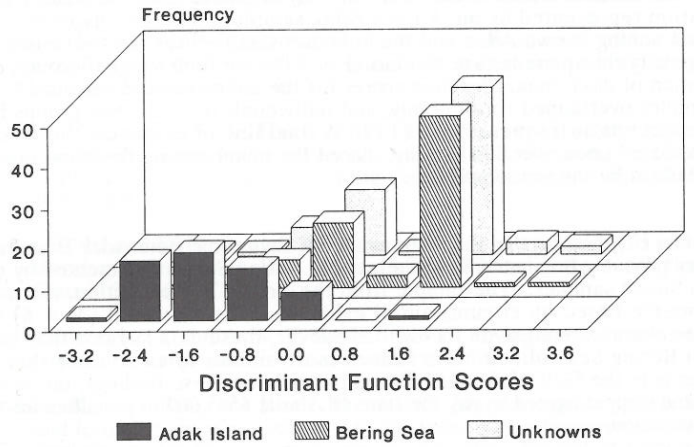

Figure 4. Discriminant function scores for individuals from the Adak Island and eastern Bering Sea populations and for unknown individuals.

Table 4. Classification results from the discriminant analysis of red king crab populations.

Actual Group Membership	*N*	Predicted Group Membership: Adak Island	Predicted Group Membership: Bering Sea
Adak Island	54	46 85.2%	8 14.8%
Bering Sea	72	9 12.5%	63 87.5%
Unknowns	71	9 12.7%	62 87.3%

DISCUSSION

Red king crab from major geographic regions have genetically differentiated despite the fact that the average amount of genetic variability within populations is low. There is also evidence of subdivision within each region. These data should be particularly useful in defining management units of self-recruiting populations.

The data also have considerable potential to aid in enforcement of crab fishing regulations. At least three separate lines of genetic evidence argue that the confiscated crabs analyzed in this study did not originate from the Adak Island population represented by our known Adak samples. The null hypothesis of panmixia among known Adak and the unknown samples was rejected based on heterogeneity chi-square tests at two loci ($P < 0.001$ for both tests). Secondly the distribution of discriminant function scores for the unknowns and eastern Bering Sea samples overlapped considerably, and individuals from the two groups had the identical most frequent score (1.6). A final line of evidence, the cluster analysis, based upon overall similarity, placed the unknowns on the same branch as the eastern Bering Sea samples.

These data clearly show that the crabs could not have come from Adak Island and that they probably originated from the eastern Bering Sea as represented by our Norton Sound samples. The sample from the Bristol Bay collection, the most likely source based on circumstantial evidence, was too small ($N = 6$) for accurate characterization on its own. However, these data suggest that both eastern Bering Sea collections are much more similar to each other than to collections in the Gulf of Alaska. Based partially on these findings, the vessel owner and skipper agreed to pay the state of Alaska $565,000 in penalties for the fishing violation.

Forensic application of genetic data in fisheries is not new, although it has not seen widespread use. In our laboratory we have identified confiscated fillets of rockfish (genus *Sebastes*) to species (Seeb, 1986), and we have assigned the continent of origin to confiscated chum salmon (*Oncorhynchus keta*; Seeb and

Seeb, 1986). With the advances in new g
sequencing and DNA fingerprinting, forensic a
in importance. Additionally, the knowledge t
may be identified to population of origin may
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Seeb, 1986). With the advances in new genetic techniques such as DNA sequencing and DNA fingerprinting, forensic applications are destined to increase in importance. Additionally, the knowledge by fishermen that unknown samples may be identified to population of origin may deter illegal fishing and improved the quality of catch statistics used to manage crab fisheries in the future.

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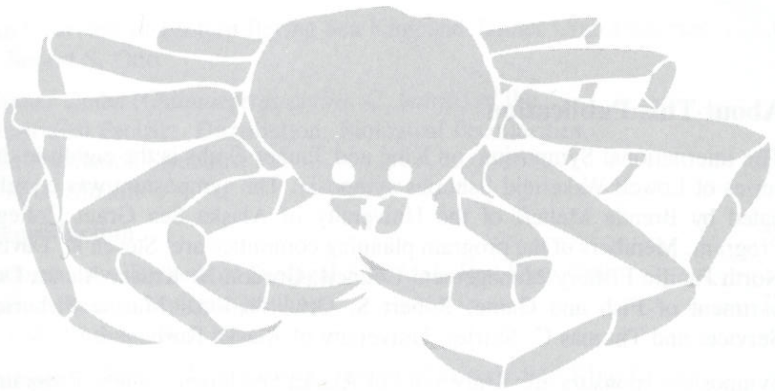

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