Bull. Southern California Acad. Sci.
86(1), 1987, pp. 34–40

Population Genetics of an Introduced Species: *Bairdiella icistius* in the Salton Sea

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Abstract.—The bairdiella, *Bairdiella icistius* (Jordan and Gilbert), in the Salton Sea are the progeny of a successful introduction made in the 1950's. They form a central link in a productive and heavily utilized sportfishery. Genetic variability at 56 enzyme and protein loci was studied by means of starch and polyacrylamide gel electrophoresis. Eight loci were polymorphic, and all polymorphic loci were close to Hardy-Weinberg equilibrium. Average heterozygosity per locus was 0.043, which is within the typical range for marine fish species. There appeared to be fewer rare alleles than expected in a population at equilibrium. The Salton Sea habitat is harsh and changing. The amount of genetic variability present in the bairdiella is an indication of the ability of this population to adapt to environmental change.

Any introduction of a species into a new habitat constitutes an experiment on the significance of the founder effect. The introduction of the bairdiella, *Bairdiella icistius* (Jordan and Gilbert), into the Salton Sea is an example of a successful founder event. From an initial population of 67 individuals, the population rapidly increased into the millions. The case of the bairdiella is particularly amenable to study because the population has been well documented since its inception. The date, number, and point of origin of the founders is well known, and the course of development of the population has been followed regularly up to the present.

The bairdiella is a small fish of the family Sciaenidae. The fish is abundant in the Gulf of California, where it is fished commercially (Berdegue 1956). Two introductions of bairdiella were made into the Salton Sea. In 1950, 57 fish were transplanted from San Felipe, Baja California, Mexico, and in 1951, an additional 10 fish were taken from the same location (Whitney 1961). These 67 fish represent the total known introduction. Whitney estimated that juvenile fish that were spawned from the first planting reached reproductive maturity within two years, and that the population of bairdiella was several million by 1954.

The bairdiella is currently one of the most abundant species in the Salton Sea. It not only supports a major sportfishery itself, but is the main forage fish for the larger introduced game fishes (e.g., orangemouth corvina, *Cynoscion xanthulus*, Walker et al. 1961). The Salton Sea contains a simplified and truncated food web, with a few species dominating. The total biomass in the lake is large, and supports an active sportfishery. The number of angler hours and the catch per unit effort are among the highest of any inland body of water in California (Black 1983).

Since the Salton Sea was formed in 1904–1907, the level of the lake has fluctuated considerably. The salinity has increased to a present level of 38 parts per

Table 1. Enzymes, electrophoretic buffers, tissue source, and number of loci scored for *Bairdiella icistius*. Buffer systems: POUL = discontinuous Borate-Tris-citrate, "Poulik" (Selander et al. 1971); TC 7 = Tris-citrate-EDTA, pH 7.0 (Ayala et al. 1973); TC 8 = Tris-citrate, pH 8.0 (Selander et al. 1971, electrode buffer diluted 1/5); TBE 9.2 = Tris-borate-EDTA, pH 9.2 (Ayala et al. 1973); EBT = Tris-borate-EDTA, pH 8.6 (Whitt et al. 1976); Acryl = acrylamide gel (see Methods). Tissue sources: B = brain, E = eye, H = heart, L = liver, M = muscle.

Enzyme	Locus abbreviation	E.C. number	Buffer	Tissue source
Adenylate kinase	*Ak-A*	2.7.4.3	TC 7	M
Alcohol dehydrogenase	*Adh-A*	1.1.1.1	EBT	L
Aldolase	*Ald-A*	4.1.2.13	TC 7	M
Aspartate aminotransferase	*S-Aat-A*	2.6.1.1	TC 7	L
	M-Aat-A			L
Creatine kinase	*Ck-A*	2.7.3.2	TC 7	M
	Ck-B			B
Esterase	*Est-1*	—	Acryl	L
	Est-2			L
	Est-3			L
	Est-4			L
	Est-5			L
	Est-6			H
	Est-7			H
	Est-8			H
Fumarase	*Fum-A*	4.2.1.2	TBE 9.2	L
General proteins	*Gp-1*	—	Acryl	M
	Gp-2			M
	Gp-3			M
	Gp-4			M
	Gp-5			M
	Gp-6			H
	Gp-7			H
	Gp-8			H
	Gp-9			H
	Gp-10			H
	Gp-11			H
	Gp-12			H
	Gp-13			H
	Gp-14			H
Glucosephosphate isomerase	*Gpi-A*	5.3.1.9	POUL	L
	Gpi-B			M
Glucose-6-phosphate dehydrogenase	*G6pdh-A*	1.1.1.49	TC 8	L
	G6pdh-B			L
Glyceraldehyde-3-phosphate dehydrogenase	*Gapdh-A*	1.2.1.12	EBT	M
	Gapdh-B			H
Glycerol-3-phosphate dehydrogenase	*G3pdh-A*	1.1.1.8	TC 8	M
	G3pdh-B			L
Hexokinase	*Hk-A*	2.7.1.1	TC 8	L
L-Iditol dehydrogenase	*Iddh-A*	1.1.1.14	TC 8	L
Isocitrate dehydrogenase	*S-Icdh-A*	1.1.1.42	TC 7	L
	M-Icdh-A			M
Lactate dehydrogenase	*Ldh-A*	1.1.1.27	POUL	M
	Ldh-B			H
	Ldh-C			E
Malate dehydrogenase	*S-Mdh-A*	1.1.1.37	TC 7	L
	S-Mdh-B			M

Table 1. Continued.

Enzyme	Locus abbreviation	E.C. number	Buffer	Tissue source
Malic enzyme	*S-Me-A*	1.1.1.40	TC 8	M
Mannosephosphate isomerase	*Mpi-A*	5.3.1.8	TC 8	H
Peptidase	*Pep-A*	–	EBT	B
	Pep-B			L
	Pep-C			L
	Pep-D			L
Phosphoglucomutase	*Pgm-A*	2.7.5.1	POUL	M
	Pgm-B			L
Phosphogluconate dehydrogenase	*Pgdh-A*	1.1.1.43	TC 7	L
Superoxide dismutase	*Sod-A*	1.15.1.1	TBE 9.2	L
Xanthine dehydrogenase	*Xdh-A*	1.2.1.37	TC 7	L

thousand (ppt) total dissolved solids, and there are continuing inputs of pesticides and fertilizers from the surrounding agricultural land. The latter inputs, coupled with high temperatures in summer, result in periods of anoxia and fish kills. Several fishes are still reproducing in the Salton Sea at this time, but it is not clear what the time course or significance of continued environmental change will be. There are presently several plans under consideration for the management of the Salton Sea, as a result of which salinity could remain constant or rise as high as 88 ppt (Black 1983). Salinities in excess of 50 ppt are considered to be harmful to the continued reproduction of fishes in the Salton Sea.

The Salton Sea is a harsh and changing environment. Knowledge of the genetic structure of the bairdiella can help predict the likely consequences of continued environmental degradation on a major resource. One possible consequence of a founder event or any population bottleneck is the loss of genetic variation from the population. It is this reservoir of genetic variability that provides the material upon which selection operates, as the population adapts to environmental change. Allozyme electrophoresis can be used to examine genotypes and allele frequencies for a large number of loci that encode for enzymatic or structural proteins. Even if these loci are not themselves significant for adaptation to environmental changes, they are the best estimate of variation in the whole genome, including those loci that can respond to selection.

Methods

Both starch and polyacrylamide gel electrophoresis were used to examine enzyme or protein variation. A total of 24 enzyme or protein stains were used, which resolved the products of 56 loci. The enzymes examined, the electrophoretic conditions, the number of loci resolved and their abbreviations are given in Table 1. Starch gel enzyme electrophoresis followed Selander et al. (1971) with the following exceptions: The stains for ADH, AK, CK, FUM, GAPDH, LDH, and MPI were from Allendorf et al. (1977). Peptidase staining and nomenclature followed Frick (1983). The ALD stain was from Shaw and Prasad (1970), the AAT stain from from May et al. (1979), and the ME stain was from Ayala et al. (1973). All stains that used G6PDH as an intermediate were modified after Buth

Table 2. Allele frequencies, sample sizes and mean heterozygosities per locus (H) for eight polymorphic loci of *Bairdiella icistius* from the Salton Sea. Alleles are named in terms of increasing anodal mobility.

	Locus and sample size							
Allele	*Est-3* 100	*Est-6* 102	*Gp-12* 102	*S-Icdh-A* 102	*Ldh-C* 101	*S-Mdh-B* 100	*Pep-D* 101	*Pgm-B* 99
1	0.140	0.039	0.069	0.020	0.149	0.385	0.574	0.338
2	0.860	0.794	0.931	0.980	0.851	0.615	0.426	0.662
3		0.167						
H	0.242	0.342	0.128	0.039	0.254	0.476	0.491	0.450

and Murphy (1980). The agar overlay method of Brewer (1970) was used for all stains that included an enzyme intermediate. Starch gels were 10% (w/v) Sigma starch.

Polyacrylamide gel electrophoresis was used to resolve esterases and general proteins. Esterases were run on 6% (w/v) acrylamide in the TBE buffer of Maniatis et al. (1982) and stained after Selander et al. (1971) using beta-napthyl acetate as the substrate. General proteins were run on split gels (4–8% w/v) using the discontinuous buffer system of Laemmli (1970) without SDS, and stained with Coomassie Blue.

Data analysis was done with the aid of the BIOSYS-1 package of computer programs (Swofford and Selander 1981).

Fish were collected by gill-net from two locations on the north side of the Salton Sea (North Shore Marina and Bombay Beach), with the cooperation of the California Department of Fish and Game. Fish were packed on dry ice and transported to the laboratory, where they were stored whole at −20°C until used for electrophoresis.

Results

There is substantial genetic variability in the Salton Sea population of bairdiella. Eight loci are polymorphic: *Est-3, Est-6, Gp-12, S-Icdh-A, Ldh-C, S-Mdh-B, Pep-D,* and *Pgm-B.* Allele frequencies for these loci are given in Table 2. The average heterozygosity per locus is $H = 0.043 \pm 0.016$ (S.E.). To put this in perspective, Winans (1980) reviewed the literature on natural populations of 82 species of fishes, for which the mean H was 0.048. Data from two other sciaenids, *Genyonemus lineatus* and *Seriphus politus,* can also be compared at 33 loci studied in common (Beckwitt 1983). The H estimates are 0.030, 0.043 and 0.046 for *Genyonemus, Seriphus,* and *Bairdiella* respectively. All polymorphic loci are close to Hardy-Weinberg equilibrium (Table 3), implying that inbreeding or differential survival of genotypes is not now a significant factor.

Although the average heterozygosity per locus is typical for a fish, the pattern of allele frequencies is not. There are only two loci at which there are rare alleles (frequency less than 0.05). Typically this class is more numerous (Nei 1975). In a sample of 100 diploid individuals, the probability of finding an allele is 0.99 if its true frequency is 0.05; if the true frequency is 0.01, the probability is 0.87. Thus, all but the rarest alleles have been well sampled.

The average number of all alleles per locus is 1.16. Using an analysis similar

Table 3. Exact test of goodness of fit to Hardy-Weinberg equilibrium.

Locus	Common homozygotes	Common/rare heterozygotes	Other genotypes	Probability
Est-3	75	22	3	0.339
Est-6	64	34	4	1.000
Gp-12	89	12	1	0.380
S-Icdh-A	98	4	0	1.000
Ldh-C	73	26	2	1.000
S-Mdh-B	39	45	16	0.673
Pep-D	31	54	16	0.419
Pgm-B	42	47	10	0.656

to Bryant et al. (1981), one can estimate the expected number of alleles per locus in a population at equilibrium. This estimate is highly dependent on the value used for $N_e v$ (N_e = effective population size, v = mutation rate per gene per generation). This value can not be directly estimated from the data, but is likely to be about 0.1 (Nei 1975). Under those conditions, the expected number of alleles in a sample of 100 fish is 1.57. Although this estimate is not likely to be very accurate, it does suggest that alleles could have been lost during the founder event.

One can also compare the pattern of heterozygosity per locus with the expected pattern for a large population at equilibrium. When the data for the bairdiella are compared to the theoretical distribution obtained by Fuerst et al. (1977), there is no significant difference (Kolomogorov-Smirnov test, $P > 0.2$). One cannot exclude the null hypothesis that the Salton Sea population is at equilibrium.

The data are consistent with the known facts of the introduction of the bairdiella into the Salton Sea. The founding population was relatively large (67 individuals) and the bottleneck was of short duration—there were at least 1,000,000 fish in reproductive condition within 3 years. Under these conditions, one would expect the new population to retain nearly all of the heterozygosity of the parent population, but to lose a large number of rare alleles.

Discussion

The founder effect has been discussed at some length in the literature of theoretical population genetics. It is often cited as an important mechanism for speciation (see Carson and Templeton 1984 for review). When a founder population is subject to a severe bottleneck in numbers, there is a chance for the loss or alteration of genetic variability. Nei et al. (1975) discussed the genetic consequences of a population bottleneck. They showed that there will be a decrease in heterozygosity that is dependent not only on the size of the bottleneck, but also on the rate of population growth after the bottleneck. They also showed that the loss of neutral alleles from the population is more dependent on the size of the bottleneck and less so on its duration. These results have since been extended and generalized by Chakraborty and Nei (1977), Sirkomma (1983), and Maruyama and Fuerst (1984).

There have been few explicit tests of the genetic consequences of a population bottleneck. Several studies have observed decreased genetic variability in peripheral or relict populations, and inferred a bottleneck or founder event as the cause

(Avise and Selander 1972; Kat 1982; Larruga et al. 1983). One striking example is the elephant seal, hunted to near extinction and now without any genetic variation demonstrable by enzyme electrophoresis (Bonnell and Selander 1974).

Introduced species have been studied as examples of founder events. Bryant et al. (1981) studied the face fly, an introduced pest. They found a non-significant decrease in heterozygosity at 14 electrophoretic loci between North American and European populations, but a loss of up to 50% of the alleles in the introduced populations. Turner (1984) examined artificial refugium populations of the desert pupfish, and showed little difference from the parent populations, in terms of heterozygosity or number of alleles.

The bairdiella of the Salton Sea harbor considerable genetic variability, equal to most natural populations of marine fishes. Thus, there is considerable potential for adaption to environmental change. However, the possibility that rare alleles are lacking from the Salton Sea population may be important. If the bairdiella are called upon to adapt to radically changing physical factors, some rare allele could be vital. Such speculation can only be verified with data from the parent population.

Acknowledgments

I would like to thank personnel of the VANTUNA Research Group, particularly M. Matsui and S. Smith, as well as G. Black of the California Department of Fish and Game for help in collecting fishes. M. Matsui also contributed her considerable knowledge of the natural history of the Salton Sea. I would also like to thank D. Buth for advice on enzyme nomenclature. This study was performed under contract from Southern California Edison Company, and is a contribution of the VANTUNA Research Group, Occidental College, Los Angeles, California.

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Accepted for publication 5 June 1986.